

Late Triassic plant fossils from the Prince Charles Mountains, East Antarctica

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Abstract: Megafloral remains recovered from the Jetty Member and the upper part of the Flagstone Bench Formation, Amery Group include *Dicroidium* and *Pagiophyllum*. *Dicroidium zuberi* and *D. crassinervis* forma *stelznerianum* occur with *Pteruchus dubius* and support a Mid to Late Triassic age. A new species of conifer, *Pagiophyllum papillatus*, is recognized along with an undetermined conifer pollen cone.

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Key words: East Antarctica, Triassic, *Dicroidium*, *Pteruchus*, *Pagiophyllum*

Introduction

Palaeozoic and Mesozoic sedimentary rocks occur on the western side of the Lambert Graben (northern Prince Charles Mountains) where they crop out on the east side of Loewe and Manning massifs and in the bluffs along the shores of Beaver and Radok lakes (Fig. 1). They are the only known strata of these ages in East Antarctica between 0° and 150° E. Previous workers suggested a Late Permian age (Mond 1972, McKelvey & Stephenson 1990) based on palynology (Balme & Playford 1967, Kemp 1973) and macrofloras (White 1973), but recent collections of *Dicroidium* Gothan and coniferous leaves from Jetty Peninsula indicate that the upper part of the sequence ranges into the Triassic (Webb & Fielding 1993).

Dicroidium, a foliage genus of the Corystospermaceae, was one of the most diverse and varied elements of Gondwana vegetation occurring in fossil floras from South America, South Africa, India, Madagascar, Australia, New Zealand and the Transantarctic Mountains (Plumstead 1962, Anderson & Anderson 1983). Often a dominant component of assemblages (Retallack 1977, Anderson & Anderson 1983), *Dicroidium* is widely recorded as occurring in association with ovulate (*Umkomasia* Thomas) and microsporangiate (*Pteruchus* Thomas) fructifications. The foliage is morphologically variable, ranging from small linear leaved forms (*D. elongatum* (Carruthers) Archangelsky *sensu lato*) to broad and dissected forms such as *D. odontopteroides* (Morris) Gothan *sensu lato* and *D. dubium* (Feistmantel) Gothan *sensu lato*. This diversity in form is not surprising given the broad palaeolatitudinal range the genus occupied, from 30–80° S, and the diverse ecological niches it filled (Anderson & Anderson 1983). Temporally, the genus ranges from latest Permian to latest Triassic (Retallack 1980).

In contrast to the corystosperms, conifers were rarely dominant in Southern Hemisphere Triassic vegetation, but formed a persistent component of Early Mesozoic Gondwana floras

(Retallack 1977, Anderson & Anderson 1989).

We report here on some corystosperm foliage and microsporangiate structures (*Dicroidium* and *Pteruchus*), conifer shoots and a cone from Jetty Peninsula in the northern Prince Charles Mountains, and comment on their implications for the age of the strata and the palaeoenvironment and depositional environment.

Stratigraphy and geology

Amery Group sediments were laid down in the Lambert Graben. The sedimentary rocks crop out in the northern Prince Charles Mountains in the vicinity of Beaver Lake, and are bounded to the west by Precambrian basement and to the east by the Lambert Glacier (Fig. 1). Crohn (1959) first described the Amery Group as Permian, and this was subsequently supported by plant megafossil and palynological investigation of the Radok Lake area (White 1973, Balme & Playford 1967, Kemp 1973, Playford 1990) and Flagstone Bench (Dibner 1978). A Triassic age for the uppermost sediments on Jetty Peninsula was postulated by Ravich *et al.* (1977), and confirmed by the discovery of *Dicroidium* leaf fossils by Webb & Fielding (1993). Lithologically similar sedimentary rocks have been reported from ODP Hole 740 in Prydz Bay (Fig. 1) (Turner 1991, 1993).

The basal part of the sequence on Jetty Peninsula consists of at least 140 m of sedimentary rocks. The lower 60 m are weakly lithified alternating sands, gravels and palaeosols (Jetty Member). These floodplain sediments of the Jetty Member are largely unfossiliferous. They are high in iron oxides, and have the rusty tinge typical of “red bed” sequences. The palaeosols are well developed and the tops are full of sand-filled mudcracks. The Jetty Member is overlain by at least 80 m of arkosic sandstones (upper Flagstone Bench Formation) and consists of channel sandstones which contain sparse amounts of silicified wood together with casts and moulds of trunks and branches. The

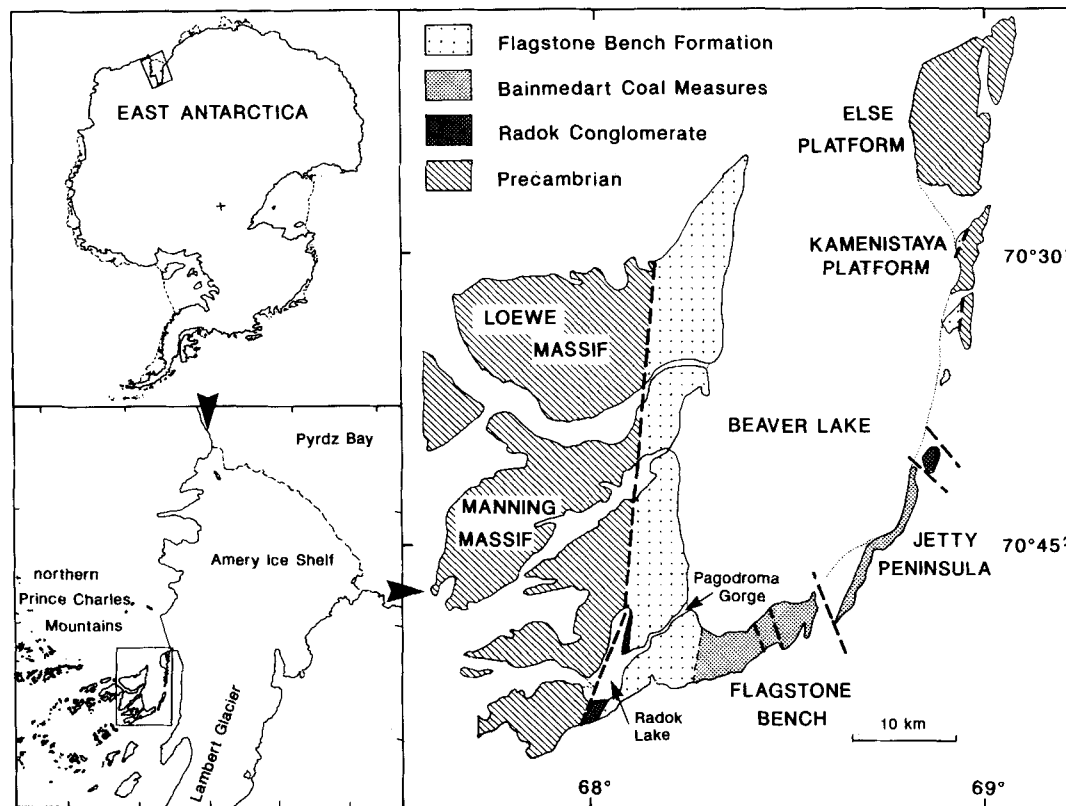


Fig. 1. Location and geological sketch map of the Beaver Lake area, northern Prince Charles Mountains, East Antarctica.

sequence is interpreted as an alluvial floodplain deposit (Jetty Member) accumulating in seasonally arid conditions that were replaced by high energy river channels (upper Flagstone Bench Formation). The plant assemblage discussed in this paper was largely collected from thin, finely laminated siltstone and sandstone layers near the middle of the otherwise coarsely arkosic upper Flagstone Bench Formation, but several other localities were collected at or near the base of the upper part of the Flagstone Bench Formation (Fig. 2).

Materials and methods

Plant material is preserved as compressions and small fusinized fragments in dark grey, micaceous siltstones and fine sandstones, and as cuticular mats between sandstone units. The most easily observed specimens occur in light grey siltstones where individual *Dicroidium* fronds and pinnules stand out in strong relief and flake off the rock as they dry out. However, the majority of plant material is densely matted and difficult to distinguish in hand specimen. The rock dries to a dark grey colour, further obscuring macroscopic detail.

Specimens were prepared either by freeing portions of foliage from the rock using needles and then cleaning them in 40% hydrofluoric acid, or by direct bulk maceration of quantities of matrix in 40% hydrofluoric acid. Organic residues were sieved and examined under a dissecting microscope. Specimens were either mounted whole on scanning electron microscope stubs or macerated in 20% chromic acid and the cuticles cleared using dilute ammonia. Specimens for light microscopy were stained

with safranin-O and mounted in either histomount or glycerine jelly. Specimens for scanning electron microscopy were coated with gold/palladium and examined using a JEOL JSM 840 microscope at the School of Botany, University of Melbourne. All illustrated specimens are lodged in the palaeontology collections of the Museum of Victoria (NMV). Locality information is given in Fig. 2.

Systematic palaeobotany

Family Corystospermaceae
Form-genus *Dicroidium* Gothan

Type species. *Dicroidium odontopteroides* (Morris) Gothan

Dicroidium zuberi (Szajnocha 1888) Archangelsky 1968

Fig. 3

Description: Fragments of bipinnate fronds up to 100 mm long, bearing subopposite pinnules. Pinnules 5–18 mm long and 4–10 mm wide, generally rhombic to square in shape but some are rectangular, ovate or falcate (Figs 3a–c). Pinnule apex obtuse; margin entire, commonly slightly expanded into a broad lobe on the abaxial margin. Venation odontopteroid, veins arising from rachis in three to five groups, dichotomosing up to four times and arching towards the pinnule margins (Fig. 3d).

Pinnules amphistomatic, with equal densities on upper and lower leaf surface. Epidermal cells 45–90 μm long and 23–53 μm wide, all with a well developed papilla (Fig. 3g), anticlinal walls sinuous and strongly buttressed (Fig. 3e).

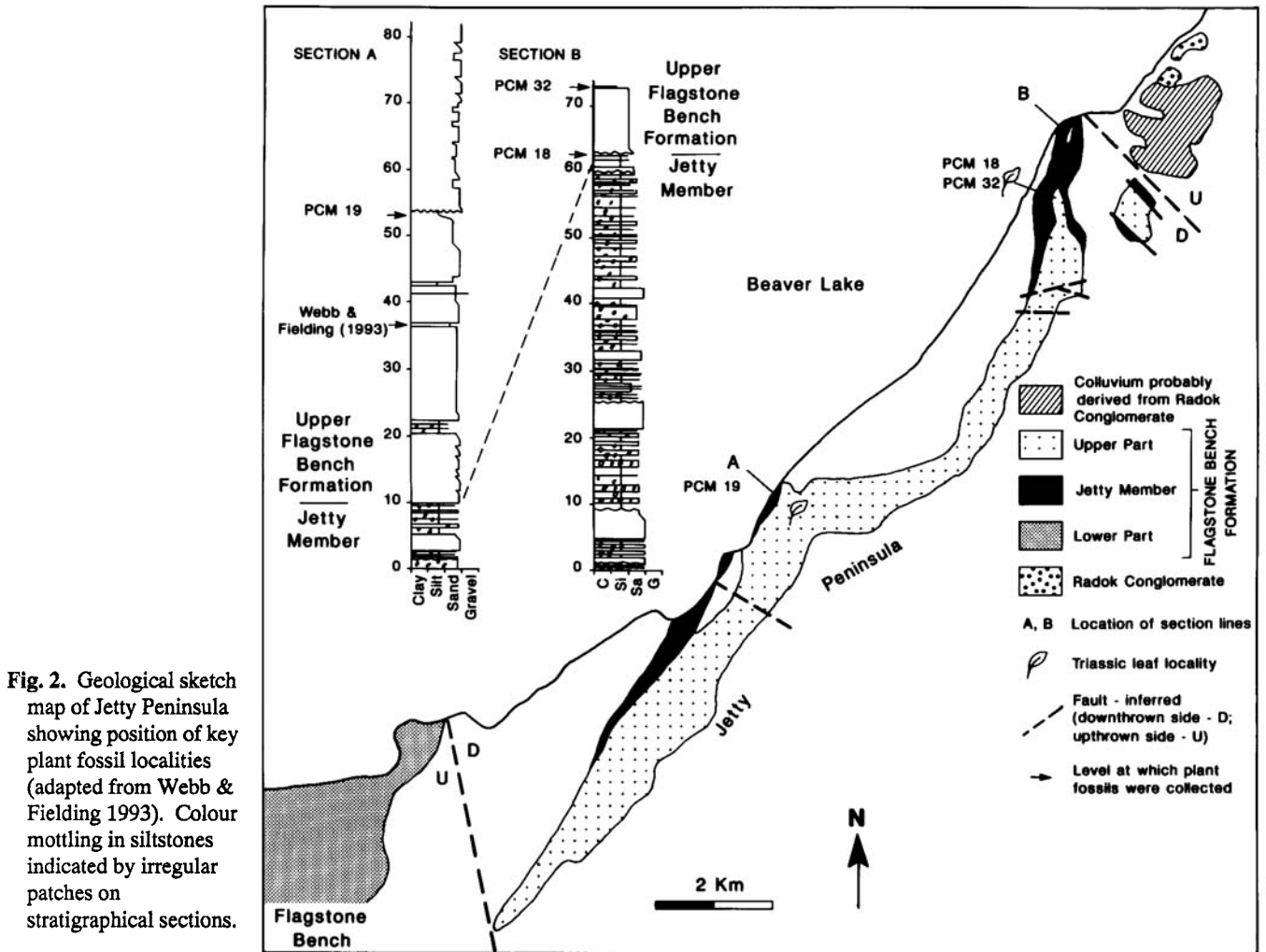


Fig. 2. Geological sketch map of Jetty Peninsula showing position of key plant fossil localities (adapted from Webb & Fielding 1993). Colour mottling in siltstones indicated by irregular patches on stratigraphical sections.

Papillae squat and dome shaped, 8–10 μm in diameter. Epidermal cells over rachis more elongate, 60–120 μm long and 30–60 μm wide, with fewer papillate cells.

Stomatal apparatus comprising four to five subsidiary cells consisting of two polar cells and two or three lateral cells (Fig. 3f). Subsidiary cells 25–50 μm long and 25–40 μm wide, cell walls slightly sinuous and buttressed. Guard cells 15–23 μm long and 8–17 μm wide. Guard cell cuticle with distinct transverse ridges, cuticle adjacent to stomatal aperture forming a smooth lip. Outer surface of stomatal aperture smooth (Fig. 3h).

Remarks: *Dicroidium zuberi*, originally described as *Cardiopteris zuberi* by Szajnocha (1888), has had a chequered taxonomic history. It has been transferred between several genera, and comprises a number of synonymous species. The synonymy has been thoroughly discussed leading to different conclusions by Townrow (1957), Bonetti (1966), Archangelsky (1968), Retallack (1977) and Anderson & Anderson (1983); the latter is followed here and accepts *D. feistmanteli* as a synonym of *D. zuberi*. *Dicroidium zuberi* is easily distinguished from other species of *Dicroidium* on frond gross morphology and cuticular characters. Few species are bipinnate; *D. dubium*, *D. elongatum*, *D. narrabeense* Dun, *D. superbum* (Shirley)

Townrow, and *D. zuberi* (Anderson & Anderson 1983). Amongst these species only *D. zuberi* has pinnules that are square to rhomboidal or rarely falcate, and with an abaxial margin that is commonly expanded to suggest a broad but weakly developed lobe (Anderson & Anderson 1985). Only *D. odontopteroides* has pinnules of a similar size and shape. *Dicroidium odontopteroides* is once pinnate and pinnules have a distinct midvein, except in *D. odontopteroides* forma *orbiculoides* and some small leaves which have odontopteroid venation (Anderson & Anderson 1983). In contrast *D. zuberi* is bipinnate, venation is odontopteroid; several groups of veins enter the pinnule from the rachis. Cuticular features of *D. zuberi* are also distinctive; anticlinal impressions of epidermal cells walls are markedly sinuous and strongly buttressed. Of other *Dicroidium* species for which cuticular detail is known, only *D. dubium* subsp. *switzifolium* has even slightly sinuous and buttressed epidermal cell walls (Anderson & Anderson 1983).

Dicroidium zuberi is extremely abundant at all of the leaf-bearing localities sampled on Jetty Peninsula, and is by far the commonest foliage type present. It occurs as mats of compressed leaves in fine silty to sandy sediment interbedded with thick accumulations of coarse sandstone channel sequences. The variation in pinnule morphology (Fig. 3a–d) encompasses the

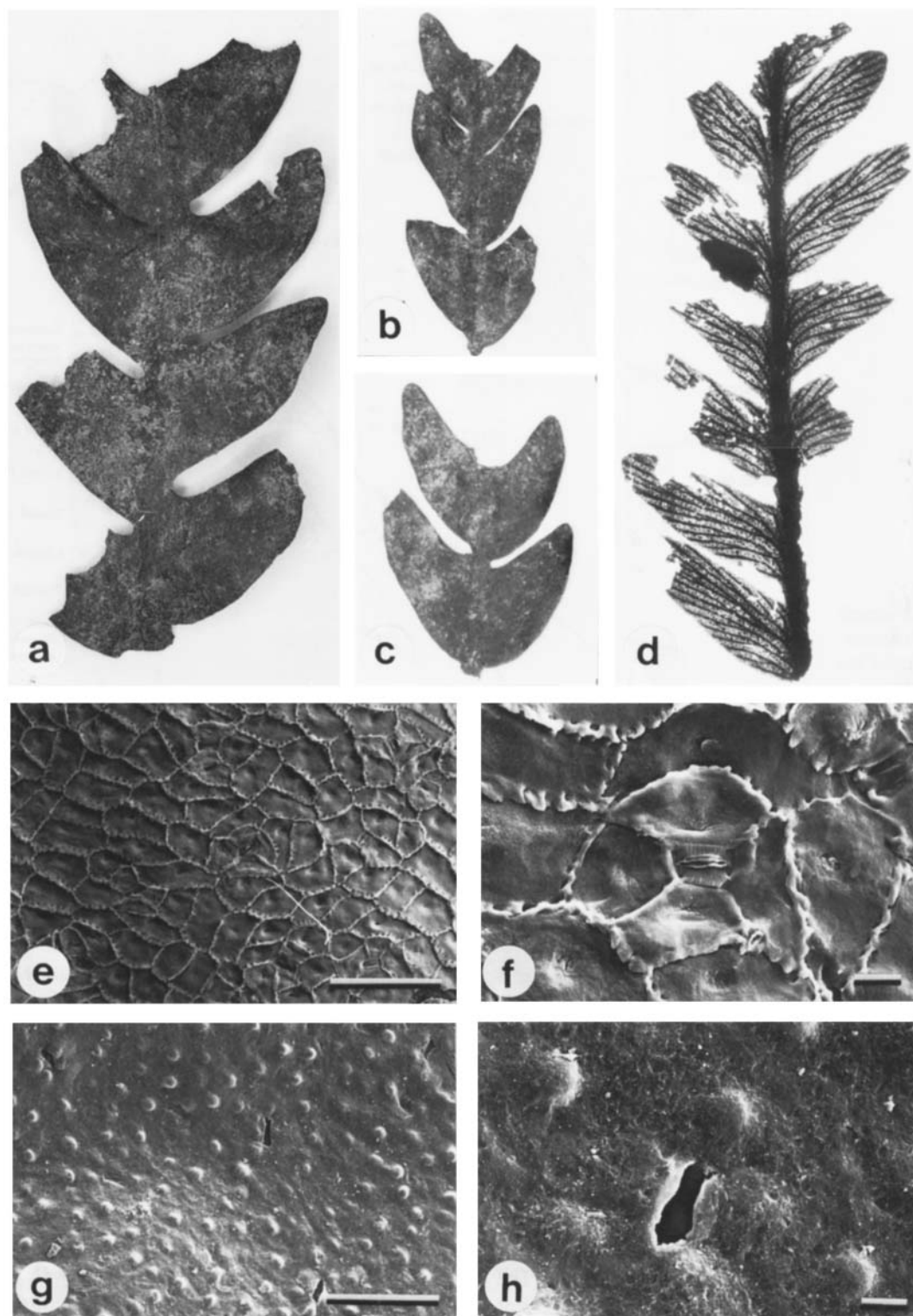


Fig. 3. *Dicroidium zuberi*. **a–c.** Range in frond morphology. **a.** NMVP198396, $\times 3$. **b, c.** Part of a larger specimen NMVP198397, $\times 3$. **d.** Detail of venation illustrating groups of basicopic veins entering the pinnule base, NMVP198398, $\times 3$. **e–h.** NMVP198397. **e.** Internal surface of pinnule, illustrating sinuous epidermal cell walls with strong buttressing and papillae bases. **f.** Internal surface of stomatal apparatus. **g.** Outer pinnule surface illustrating the strongly papillate nature of the leaf. **h.** External details of stomatal aperture. Scale bars: **e, g** = 100 μm ; **f, h** = 10 μm .

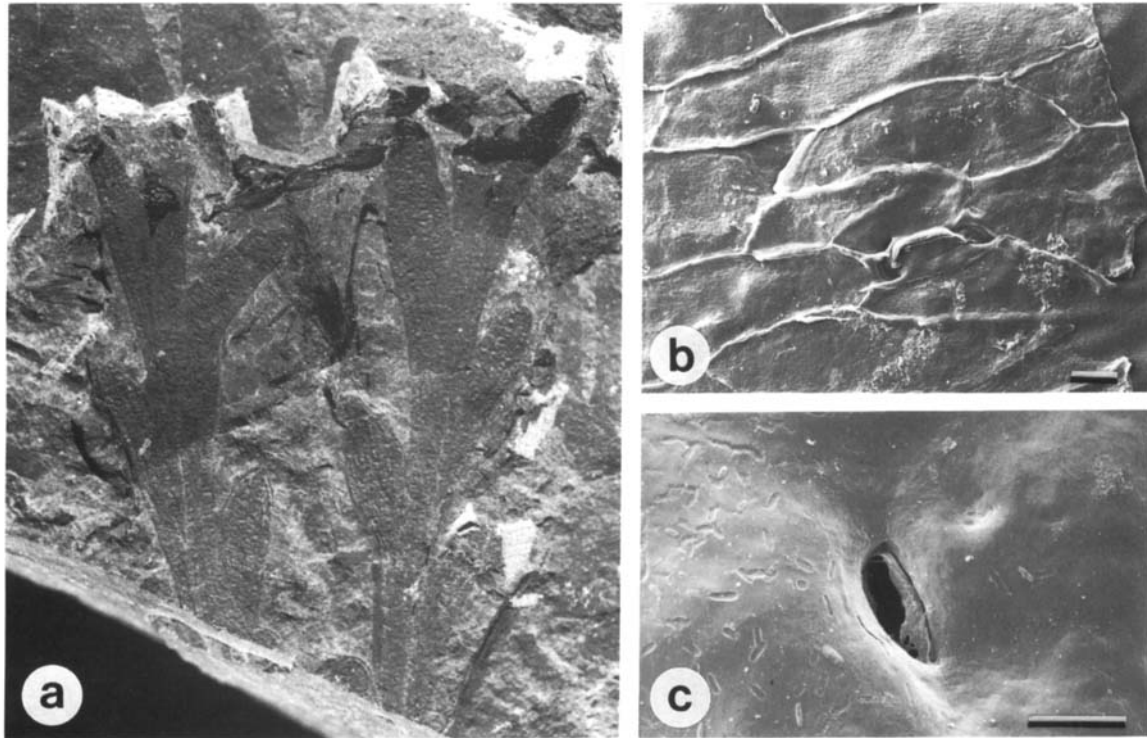


Fig. 4. *Dicroidium crassinervis* forma *stelzerianum*. a–c. NMVP198403. a. Leaf morphology, $\times 3$. b. Internal leaf surface illustrating details of stomata. c. External surface of leaf showing stomatal aperture. Scale bars: b, c = 10 μm .

range illustrated by Anderson & Anderson (1983) from square rhomboidal to falcate.

Material examined: Over 100 slabs were collected in the field and examined in the laboratory. A representative range of morphological variation were assigned numbers NMVP198396–198402, all from locality PCM 19. Isolated leaves and cuticles were also examined from localities PCM 18, 32 (Fig. 2).

Dicroidium crassinervis (Geinitz) Anderson & Anderson
1983

forma *stelzerianum* (Geinitz) Anderson & Anderson
1983

Fig. 4

Description: Fragments of pinnate fronds up to 30 mm long and 12 mm wide. Pinnules up to 8 mm long and up to 3 mm wide, rounded triangular to triangular, veins barely developed, one or two dichotomosing once or rarely twice, midrib absent (Fig. 4a).

Pinnules amphistomatic, equal densities on upper and lower surfaces. Epidermal cells 45–120 μm long and 26–48 μm wide, slightly longer and more elongate over rachis, anticlinal walls straight, epidermal cells without papillae.

Stomatal apparatus predominantly oriented longitudinally with respect to the pinnule axis comprising four rarely five subsidiary cells (Fig. 4b, c). Subsidiary cells 33–75 μm long and 20–34 μm wide, lateral cells longer than polar cells, cell walls

straight, not buttressed.

Remarks: Frond fragments of this species are far less common than *D. zuberi*. Specimens were recovered from all localities, but only as pinnule fragments in bulk macerated residues. Only one specimen preserved in a very fine grained siltstone was recognizable as a hand specimen.

Material examined: One specimen from Webb & Fielding (1993) locality, NMVP198403. Additional cuticular fragments were present in bulk macerations from localities PCM 18, 19, and 32.

Form-genus *Pteruchus* Thomas 1933
Type species. *Pteruchus africanus* Thomas 1933 emend.
Townrow 1962

Pteruchus dubius Thomas 1933 emend. Townrow 1962
Fig. 5

Description. Elongate microsporophylls up to 32 mm long and 8 mm wide, laminar, margins entire, midrib present, bearing microsporangia on one surface (Fig. 5a, c).

Epidermal cells elongated longitudinally, 80–140 μm long and 20–34 μm wide, walls straight. Epidermal cells between pollen sacs with well developed trichomes at least 67 μm long (Fig. 5g). Microsporangia numbering more than 100 per sporophyll, up to 2 mm long, and 500 μm wide, oblongate in outline, dehiscence via a twisted, longitudinal split (Fig. 5b).

Pollen bisaccate, conforming to the dispersed palynomorph genus *Alisporites*. Individual grains 46–93 μm in diameter,

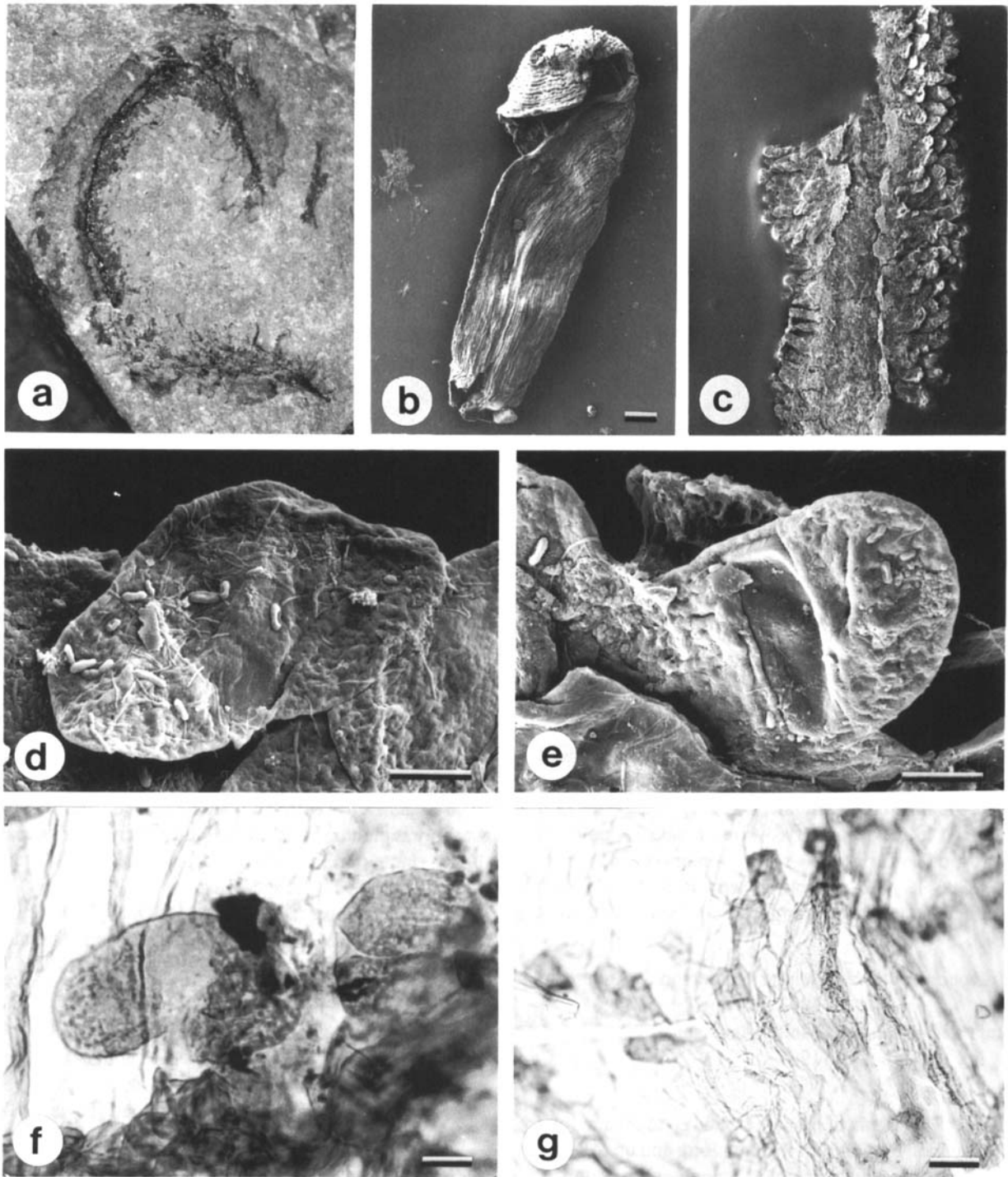


Fig. 5. *Pteruchus dubius sensu lato*. **a.** Dispersed sporophyll, NMVP 198404, $\times 6$. **b.** Microsporangia with single longitudinal split. **c.** Dispersed sporophyll illustrating the attachment of microsporangia to one side of the lamina, NMVP198406, $\times 5.5$. **d.** *Alisporites* sp. distal surface. **e.** *Alisporites* sp. proximal surface. **f.** *Alisporites* sp. transmitted light. **g.** Epidermal surface with trichomes. Scale bars: d–g = 10 μm ; b, = 100 μm .

sacci 26–33 μm wide and 26–35 μm high, ornamentation comprising internal endoreticulations and outer micropits (Fig. 5d–f).

Remarks: A few macrospecimens show several sporophylls attached by short stalks to the same axis, but their orientation is unclear and there is no indication of phyllotactic pattern. Although it is difficult to determine the structure of the sporophylls, they appear to have one surface uniformly covered with microsporangia. This is supported by the numerous fragments recovered by bulk maceration, which are all laminar portions c. 8 mm wide with densely packed microsporangia on one surface only. The position of the microsporangia on one surface of a bilaterally symmetrical structure supports the hypothesis that the microsporophylls are leaf or partial leaf homologues. The length of the individual microsporophylls, some of which are over 30 mm long, suggests they may be equivalent to whole pinnules or, even fronds, rather than individual pinnae.

Sporophylls from Jetty Peninsula are similar to specimens described as *Pterorrachis barrealensis* Frenguelli 1942 from the Middle Triassic Barreal Formation, Argentina, and specimens likened to *P. barrealensis* by Retallack (1977) from the Ipswich and Sydney basins of eastern Australia. Townrow (1962) considered *Pterorrachis barrealensis* to be synonymous with *Pteruchus dubius*, originally described by Thomas (1933) from the Molteno Beds of southern Africa. Petriella (1980) formally transferred them to this species as *P. dubius* var. *barrealensis*. Retallack (1980), however, concluded that Frenguelli's specimens and others from eastern Australia were sufficiently different to *P. dubius* to maintain separate species designation (Table I). The specimens from Jetty Peninsula have characters intermediate between the Australian and African specimens and are assigned to *Pteruchus dubius* in the broad sense.

Townrow (1962) and Retallack (1977) used shared cuticular characters and evidence of association to suggest that *P. dubius* (including *Pterorrachis barrealensis*) represented the microsporangiate organs belonging to *Dicroidium zuberi* in at least Australian and South African localities, and the relative abundance of the similar type amongst dense leaf beds of *D. zuberi* on Jetty Peninsula argues for a similar conclusion.

Material examined: NMVP198404, 198406–198410 all from locality PCM19. Isolated sporophylls and pollen sacs were also recovered in bulk macerations from PCM 18, 19, and 32.

Order CONIFERALES

Form-genus *Pagiophyllum* Heer

Type species. *Pagiophyllum circinatum* (Saporta) Heer

Pagiophyllum papillatus sp. nov.

Fig. 6

Etymology: From the Latin *papill* meaning a nipple referring to the strongly papillate nature of the leaf surface and stomata.

Holotype: NMVP198413 from locality PCM 19.

Diagnosis: Small shoots, preserved fragments up to 100 mm long, bearing small lanceolate leaves; leaves abaxially keeled, adaxially concave, 1–5 mm long and 1–3 mm wide (Fig. 6a–c),

margins finely denticulate. Leaves amphistomatic, stomata arranged in parallel longitudinal rows, stomatal density greater on upper surface (Fig. 6d, e). Leaf surface strongly papillate, each epidermal cell with a small rounded papilla up to 7 μm in diameter and 13 μm high (Fig. 6f). Stomatal pit overarched by four to seven papillae projecting from the subsidiary cells, papillae ranging from 4–18 μm long (Fig. 6g).

Epidermal cells 26–97 μm long and 20–41 μm wide, rectangular, oriented longitudinally, walls straight (Fig. 6h). Cells between stomatal rows longer. Papillae bases rounded, not prominent. Stomatal apparatus deeply sunken, composed of four to seven papillate subsidiary cells; subsidiary cells 27–40 μm long and 13–20 μm wide, cuticular micromorphology the same as the epidermal cells (Fig. 6h). Guard cells sunken below the subsidiary cells at the base of the stomatal pit, 28–40 μm long and 10–17 μm wide, cuticle up to 12 μm thick.

Cells beneath epidermis rectangular with bands of fibres between stomatal bands, mesophyll cells rounded poorly preserved.

Remarks: Anderson & Anderson (1989) listed only four genera of conifer foliage occurring in the Triassic of Gondwana; *Voltziopsis* Potonie and *Heidiphyllum* Retallack (Voltziaceae), *Rissikia* Townrow (Podocarpaceae) and the form-genus *Pagiophyllum* (*incertae sedis*). The specimens described here fit within the circumscription of *Pagiophyllum* as outlined by Harris (1979, p. 23), in having “Shoot, bearing leaves in a helix; leaf about as broad as its basal cushion, length exceeding width of cushion. Blade not or scarcely narrowed at its base, in section broader horizontally than thick vertically”.

No associated ovulate cones or megasporophylls of suspected conifer affinities were isolated from the sediments, and the pollen cone described below, which is presumed to belong to the same plant, does not shed any light on correct systematic placement. Anderson & Anderson (1989) noted that *Pagiophyllum* could be used for *Voltziopsis* foliage if affiliated ovulate cones demonstrating conclusive Voltzialean affinities were unknown.

Cuticular morphology of *Pagiophyllum papillatus* is quite different from species of *Voltziopsis* previously described. *Voltziopsis angusta* (Walkom) Townrow 1967a, *V. africana* Seward 1934, and *V. wolganensis* Townrow 1967a all have more or less randomly distributed stomata, and subsidiary cells and epidermal cells that totally lack papillae. *Pagiophyllum papillatus* has stomata arranged in distinct longitudinal rows,

Table I. Comparison between *Pteruchus* from Jetty Peninsula and *Pteruchus dubius sensu lato*.

	<i>Pteruchus dubius sensu strictus</i>	“ <i>Pterorrachis barrealensis</i> ”	Jetty Peninsula <i>Pteruchus</i>
Sporophyll length	10–15 mm	60 mm	32 mm
Length/width ratio	4:1	6–8:1	4:1
Sporophyll margin	lobed	entire	entire
Number of sporangia	100	350	>100
Sporangia length/width ratio	2:1	4:1	4:1

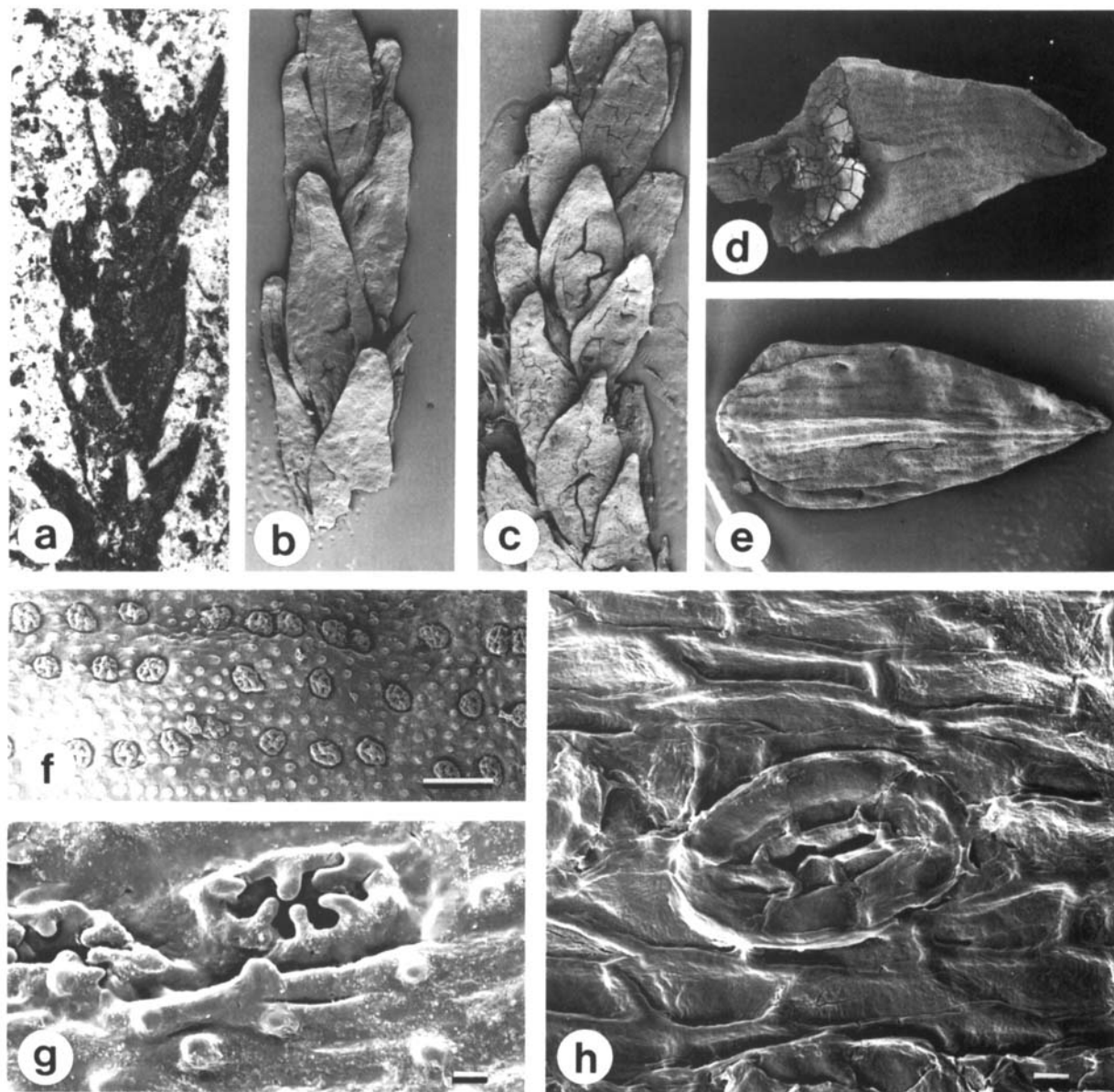


Fig. 6. *Pagiophyllum papillatus* sp. nov. **a–c.** Shoot morphology. **a.** NMVP198411, $\times 4.5$. **b, c.** Fragments from NMVP 198412, $\times 4.5$. **d.** Adaxial leaf surface with numerous stomatal rows, $\times 13$. **e.** Abaxial leaf surface, $\times 13$. **f.** Outer leaf surface illustrating numerous stomata in rows and papillate epidermal cells. **g.** Details of stomatal apparatus with strongly papillate subsidiary cells overarched the stomatal pit. **h.** Internal surface of stomatal apparatus. Scale bars: **f,** = 100 μm ; **g, h,** = 10 μm .

and has subsidiary cell papillae that overarch the stomatal pore and a prominent papilla on each normal epidermal cell. Its densely papillate epidermis is similar to *Pagiophyllum bosei* Pal 1984 from the Upper Triassic (Norian) Tiki Formation of central India. However, *P. bosei* differs from *P. papillatus* in two important features; the stomata are concentrated into a triangular area on each leaf surface in the former, and are not organized into distinct files as in *P. papillatus*. *Pagiophyllum simpsonii* Ash 1970 from the Upper Triassic of America has strongly papillate stomata and epidermal cells, but also has

numerous trichomes on the leaf surface, a feature not observed in *P. papillatus*.

Material examined: Over 100 slabs were collected in the field and examined in the laboratory. A representative range of morphological variation were assigned numbers NMVP198411–198414, all from PCM 19. Additional material was examined in residues bulk macerated from PCM 18, 19, and 32.

Conifer cone indet.
Fig. 7

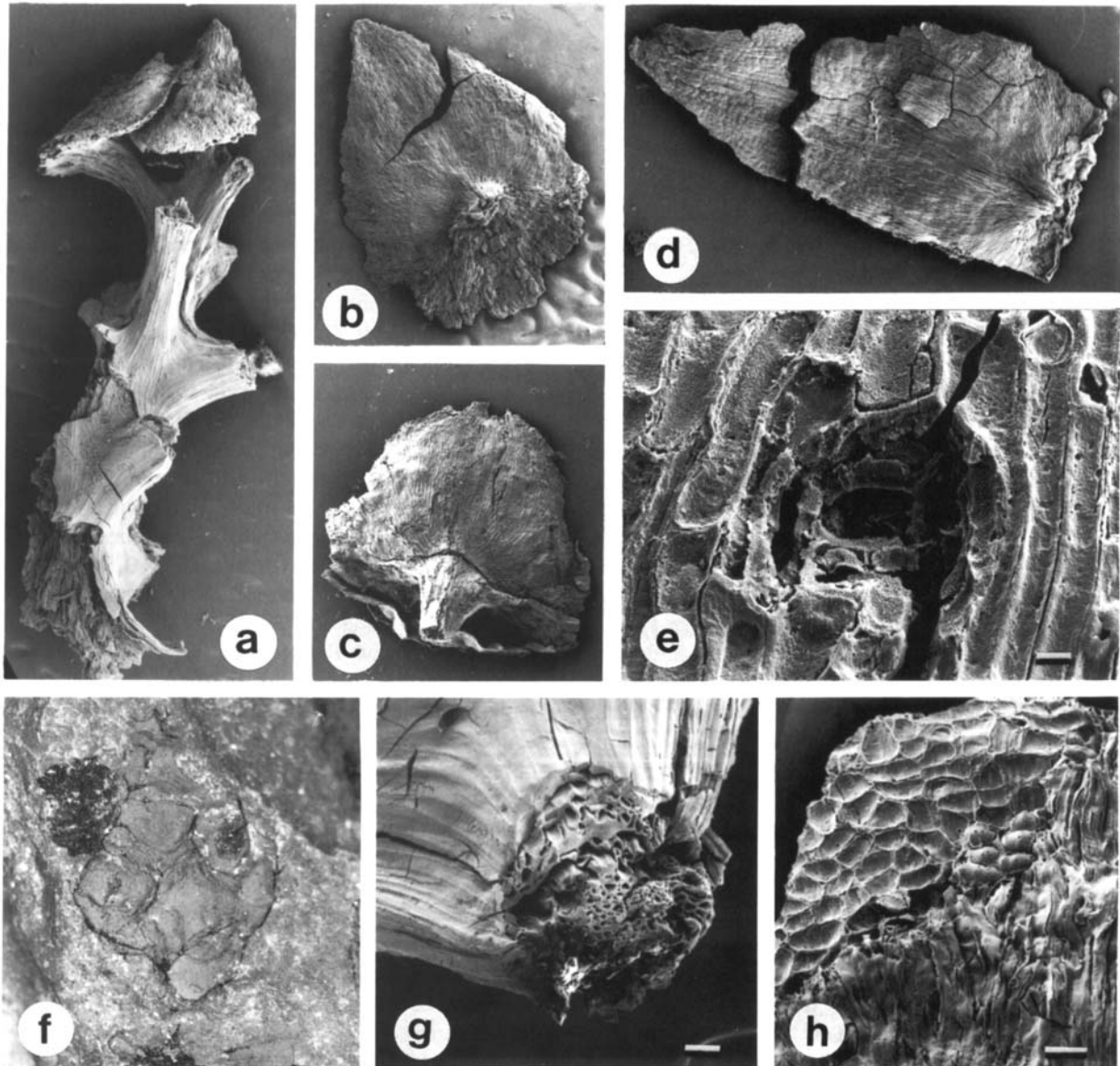


Fig. 7. Conifer pollen cone. **a.** Cone axis with attached sporophylls, NMVP 198415, $\times 30$. **b–d.** Variation in dispersed sporophylls, $\times 22$. **e.** Details of stomatal apparatus. **f.** Compressed cone in rock matrix, NMVP 198405, $\times 7$. **g.** Transverse view of attachment point to cone axis. **h.** Details of the sporophyll lamina illustrating the rounded cortical cells and fibrous cells beneath. Scale bars: **e, g,** = $10\ \mu\text{m}$; **h,** = $20\ \mu\text{m}$.

Description: Small cones at least 10 mm long and 6 mm wide, cylindrical, bearing spirally at least 14 scales (Fig. 7a, f) Scales peltate, attached to cone by a short stalk up to 0.7 mm long, stalk terminating in a ovoid lamina (Fig. 7b–d). Lamina ranging from 0.6 to 3.2 mm high and 0.5 to 2.3 mm wide.

Epidermal cells oblong $20\text{--}50\ \mu\text{m}$ long and $15\text{--}45\ \mu\text{m}$ wide. Stomata sunken, poorly preserved, comprising four? subsidiary cells (Fig. 7e). Fibres beneath epidermis $60\text{--}210\ \mu\text{m}$ long and $15\text{--}23\ \mu\text{m}$ wide. Beneath fibres are smaller rounded cortical cells $25\text{--}40\ \mu\text{m}$ in diameter (Fig. 7h).

Remarks: The few cone fragments and sporophylls are preserved as fusainized fragments and although the imagery is

superb (Fig. 7), there are, unfortunately, few characteristics of definitive nature. The overall morphology is characteristic of conifer pollen cones, and the foliage genus *Pagiophyllum* is a common component of the megaf flora. No pollen is preserved *in situ* (as is often the case in fusainized specimens), but the scars indicating the attachment points of sporangial structures are on the lower part of the sporophyll blade, below the insertion point of the stalk, the typical position of pollen sacs in extant conifer cones. The cuticle and epidermal surface of the sporophyll blades are abraded, making comparisons with *Pagiophyllum papillatus* impossible.

Sporophyll blades are variable in length; those near the apex

(Fig. 7a) are quite short (0.6 mm high), but dispersed sporophylls are up to 3.2 mm. The larger size is due to elongation of the sterile portion of the lamina distal to the stalk insertion, i.e., the sporangia-bearing portion appears unchanged. The longest cone fragment is *c.* 10 mm long, but the complete cones may have been considerably longer.

Material examined: NMVP 198405 in hand specimen. All other material examined (NMVP 198415 sem stub) was hand picked from bulk macerated residues from locality PCM 19.

Discussion

Age

The presence of *Dicroidium* clearly demonstrates that at least the coarse arkosic sandstones of the upper Flagstone Bench Formation exposed on southern Jetty Peninsula are Triassic in age. *Dicroidium zuberi* and *D. crassinervis* are both geographically widespread species in the Triassic of Gondwana. *Dicroidium zuberi* ranges from late Early Triassic to latest Triassic, and has been recorded from Australia, New Zealand, southern Africa, northern Argentina and Chile, central India and the Transantarctic Mountains (Anderson & Anderson 1983). *Dicroidium crassinervis* forma *stelznerianum* is more restricted, being confined to the late Middle and early Late Triassic sediments of southern and eastern Australia, southern Africa, northern Argentina and the Transantarctic Mountains (Anderson & Anderson 1983). A Late Triassic (Carnian–Rhaetic) age is supported by the several dispersed megaspores referable to the genera *Cabochochonicus* Batten & Ferguson and *Minerisporites* Potonie (Cantrill & Drinnan 1994). Foster *et al.* (1994) have assigned the palynoflora from the Webb & Fielding (1993) locality to the Australian *Minutosaccus crenulatus* Zone. The microflora contains microspores indicative of the Onslow microflora of Dolby & Balme (1976) and is considered to be Late Triassic (Norian).

The Jetty Member, which conformably underlies the siltstones containing the Norian microflora, may extend down into the Middle or even Early Triassic. The easterly palaeocurrents within the Jetty Member may reflect the Middle Triassic tectonism which was widespread throughout Gondwana (Veevers 1993, Webb & Fielding 1993).

Comparison with other Antarctic floras

Triassic Antarctic megaflores have been recorded from two distinct regions in the Transantarctic Mountains: southern Victoria Land and the Beardmore–Shackleton glacier area. The Lashly Formation of southern Victoria Land ranges from late Early Triassic to Late Triassic in age (Kyle & Schopf 1982, Barrett 1991). It has been subdivided into units A–D (Barrett & Kohn 1975); unit A contains abundant calamitid stems, and *Dicroidium* is common in unit C (Barrett *et al.* 1971). Collections described by Plumstead (1962), Townrow (1967b), Rigby & Schopf (1969), Rigby (1985), Kyle (1976; quoted in Truswell

1991) and Askin (personal communication in Truswell 1991) represent relatively diverse assemblages dominated by *Dicroidium* (10 species known altogether). Species of *Lepidopteris* Schimper, *Sphenobaeria* Florin, *Taeniopteris* Brongniart, *Ginkgoites* Seward and *Rissikia* Townrow have also been recorded; the cycadophyte identifications of Plumstead (1962) may need some revision (Rigby & Schopf 1969, Bose *et al.* 1990). One flora, presumably from the basal part of the Lashly Formation, contains both *Dicroidium* and *Glossopteris* Brongniart (Rigby & Schopf 1969).

In the Beardmore and Shackleton glacier areas, both the Fremouw and overlying Falla formations contain plant fossils. The upper part of the middle member of the Fremouw Formation contains very common calamitid stems, and *Dicroidium* is abundant within the upper member (Barrett *et al.* 1986, Barrett 1991). A silicified peat horizon lies within the upper member, and has yielded exceptionally well preserved foliage, axes and reproductive organs of a marattialean fern, one species of *Dicroidium*, a cycad, a sphenophyte and one or more conifers (Pigg & Taylor 1990, Delevoryas *et al.* 1992, Smoot *et al.* 1985, Taylor & Taylor 1990, Osborn & Taylor 1989, Millay & Taylor 1990, Meyer-Berthaud & Taylor 1991). Palynofloras indicate that the Fremouw Formation is no younger than Anisian (Middle Triassic) (Farabee *et al.* 1990). The lower part of the Falla Formation contains *Dicroidium* in some beds (Barrett *et al.* 1986). Townrow (1967b) described a flora from an erratic of probable Falla Formation collected near Mount Bumstead, with four, perhaps five species of *Dicroidium* as well as a ginkgoalean and a species of *Taeniopteris*.

In comparison to the floras of the Transantarctic Mountains, the assemblage from the Jetty Peninsula is also dominated by *Dicroidium*, but has a slightly lower diversity, with its two species of *Dicroidium*, a conifer and a cycadophyte (a fragment of a frond was observed in material examined). *Pagiophyllum* is absent in the Transantarctic Mountains; its presence in the Flagstone Bench Formation may reflect the proximity of the Prince Charles Mountains to the Indian landmass in the Triassic, as *Pagiophyllum* is known from the Late Triassic of India (Pal 1984).

The only other reported Antarctic Triassic flora is from Williams Point on Livingston Island (Orlando 1968, Lacey & Lucas 1981, Banerji & Lemoigne 1987). This locality occurs as a squeeze-up structure within a sill. The material is fragmentary and recent collections of new fossils include angiosperms (Rees & Smellie 1989, Chapman & Smellie 1992) and *Phyllopteroides* Medwell (D.J. Cantrill personal observation), indicating a mid-Cretaceous age.

Palaeoenvironmental and palaeoclimatic implications

The Jetty Member is characterized by a distinctive red-bed sequence with well developed mud-cracked red and green palaeosols (Webb & Fielding 1993). This is in stark contrast to the underlying Permian strata of the Bainmedart Coal Measures, which consist of interbedded sandstones and coal seams up to

several metres in thickness. The replacement of swamp by red bed deposits is a common feature in Permo-Triassic continental basins worldwide (Frakes 1979). For example, in Australia coal measures are abundant in the Permian, lacking in the Early Triassic and uncommon in the Middle Triassic (they do occur in the Clarence-Moreton Basin at Nymboida). The transition from Permian coal-bearing to Early Triassic red bed sequences has been interpreted as indicating a change to warmer and drier climatic conditions with greater seasonality, including equatorial monsoons (Parrish *et al.* 1982, Kutzbach & Gallimore 1989). For example, Turner (1993) considered that red bed deposits from Prydz Bay (probable correlatives of the Jetty Member, and likely to be Middle Triassic or older) imply average annual temperatures in excess of 15°C and average precipitation of at least 800–900 mm, with a seasonal dry period.

Subsequently the climate became more humid, as demonstrated by the change from Early Triassic red bed strata to Late Triassic coal-bearing sequences in Australia, where Late Triassic coal measures are widespread and occur at palaeogeographic localities well inland (e.g. Leigh Creek, South Australia). The Late Triassic in this region was a time of increasing rainfall and lower evaporation, leading to higher water tables and swampy environments. This change is also evident in East Antarctica, but is less well marked. The mud cracked red beds of the Jetty Member are succeeded by the upper Flagstone Bench Formation, which lacks mud cracks and consists of sandstones with interbedded unoxidized grey siltstones containing plant fossils described herein. The plant material occurs as *Dicroidium* dominated mats of leaves at most a few centimetres thick; there are no coaly layers or other evidence of swamp communities. In fact the most common foliage types (*Dicroidium* and *Pagiophyllum*) have thick robust cuticles with a papillate epidermis and sunken stomatal apparatus (Figs 3, 6), features generally associated with a water limited environment. This suggests that the plants experienced severe water stress for at least part of the year, indicating that although the Late Triassic climate in East Antarctica may have been more humid than in the Early Triassic, it was still seasonally dry.

This seasonality of climate is also indirectly supported by the abundance of fusain within the plant bearing sediments. *Pagiophyllum* within the Flagstone Bench Formation is commonly preserved as fusain, a product of wildfires, suggesting that for part of the year the vegetation dried out enough to be flammable. Only *Pagiophyllum* and parts of conifer cones are fusainized, whereas compressed plant material comprises both *Pagiophyllum* and *Dicroidium*. This indicates that the plants may have been spatially separated into two communities, one consisting of *Dicroidium* (\pm *Pagiophyllum*) in wetter environments, the other of *Pagiophyllum* in drier fire-prone areas. Alternatively, *Dicroidium* may be difficult to fusainize, as the leaves are less woody than those of *Pagiophyllum*.

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