

Megaflora of the Australian Triassic–Jurassic: a taxonomic revision

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ABSTRACT. Umkomasiaceans are the most commonly recorded components of Gondwanan Triassic floras but they are not represented subsequently in that region. Their diversity appears to have substantially declined prior to the Rhaetian. Lower and Middle Jurassic floras in Australia and elsewhere in Gondwana are strikingly different from those of the Triassic, comprising ferns, lycopods, conifers, cycads, and bennettitaleans. The fern *Cladophlebis* Brongniart 1849 emend. Seward 1894 dominated coal-forming paludal environments during the Middle Jurassic in Queensland and it is one of the most commonly preserved plants in the Eastern Gondwanan Jurassic. Ginkgoaleans were present in Eastern Gondwana until near the end-Triassic but were absent below ca 60°S palaeolatitude during the Early and Middle Jurassic.

The type specimen of *Dicroidium superbum* (Shirley 1898) Townrow 1957 emend. nov. has been inaccurately represented in the published record. Consequently, many specimens belonging to the species have been incorrectly assigned to other umkomasiacean species. Misidentifications and considerably enlarged circumscriptions of some species have resulted in an erroneous and simplistic morpho-continuum concept supposedly linking umkomasiacean fronds. Several commonly occurring umkomasiacean species are re-assessed with particular attention to their type specimens, two of which are accurately figured here for the first time. This re-assessment, together with evidence from allied fructifications and wood, supports the view that umkomasiacean fronds belong to several genera. Most umkomasiacean lineages probably terminated prior to the Rhaetian; however, *Zuberia* Frenguelli 1943 emend. Artabe 1990 persisted to near the close of the Triassic.

KEYWORDS: pteridosperms, Beaniaceae, Ginkgoaceae, Isoetaceae, Osmundaceae, Umkomasiaceae, Triassic, Jurassic, Gondwana

INTRODUCTION

The largest collection of megascopic plant remains from the Upper Triassic of Australasia is from the Carnian–lowermost Norian Ipswich Basin, resulting in a dataset that is heavily biased towards that basin. Pteridosperms, chiefly umkomasiaceans, dominate megafloral assemblages of the Ipswich Basin. Prior to this study little was known about the flora of the upper Carnian Tarong Basin (Pattemore et al. 2015b, Pattemore 2016) and the Rhaetian of the Callide Basin (Jell & McKellar 2013), both located in Queensland.

Several plant organs from the post-Triassic of Eastern Gondwana have been regarded as pteridospermous; however, evidence for such affiliation is limited and speculative (Pattemore

et al. 2015a). Furthermore, the palynofloral record suggests a substantial decline and termination of the umkomasiaceans near the end-Triassic (Pattemore et al. 2015a). There is a remarkable lack of post-Triassic fructifications from Australasia that definitely can be regarded as pteridospermous. This study focuses on the Upper Triassic–Middle Jurassic of Australia and particularly on the umkomasiaceans which dominated the Gondwanan Upper Triassic but then apparently terminated near the end-Triassic in that region. Newly collected specimens from the Upper Triassic through Middle Jurassic of Queensland and megafloral records from the Gondwanan Lower Triassic through Middle Jurassic are included within the scope of the

study to better understand the decline of the Umkomasiaceae and succeeding floral assemblages.

Early in the present study it became evident that the types of some umkomasiacean species had been inaccurately or inadequately represented in publications, leading to many misidentifications. The taxonomy of newly and previously published umkomasiacean fronds is considered here, with particular attention to the type material of several of the most commonly occurring and representative umkomasiacean species. Views on the taxonomic placement of umkomasiacean fronds have diverged widely since reviews by Gothan (1912), Frenguelli (1943), and Townrow (1957) variously attributed them to one or more genera. The group's phylogeny, spatio-temporal distribution, and affiliated fructifications have recently been examined by Pattemore et al. (2015a) and Pattemore (2016). These studies suggest that *Umkomasia* Thomas 1933 cannot be regarded as a monophyletic group (based on presently included species) and that umkomasiaceans are probably more generically diverse than has been accepted by many authors, hence, closer to the placement envisaged by Frenguelli (1943) than by many subsequent authors (e.g. Archangelsky 1968, Anderson & Anderson 1983, 2003, Bomfleur & Kerp 2010). Retallack (1977) partially adopted Frenguelli's nomenclature and recently a more generically diverse taxonomy has been applied by some authors (e.g. Artabe 1990, Stipanovic et al. 1996, Ottone 2006, Artabe et al. 2007, Troncoso & Herbst 2007).

MATERIAL AND METHODS

Queensland specimens described herein are held in the Queensland Museum, Brisbane, and are distributed among three collections therein: Queensland Museum (QMF), Geological Survey of Queensland (GSQF), and The University of Queensland (UQF). Specimens from Victoria and South Australia are held by Museum Victoria (MVP and GSV), Melbourne. New material comprises previously undescribed specimens from the Queensland Museum and specimens collected from four Queensland coal mines:

1. Meandu Mine (26.836346°S; 151.894089°E), near Nanango [Tarong Basin];
2. Callide Mine (24.313320°S; 150.634339°E), near Biloela [Callide Basin];
3. New Acland Mine (27.298553°S, 151.722557°E), near Oakey [Clarence-Moreton Basin];
4. Jeebropilly Mine (27.646382°S, 152.673961°E), near Rosewood [Clarence-Moreton Basin].

Mine specimens were recovered from fresh spoil heaps with the assistance of mine staff (see Acknowledgements). All other specimens are from well-known fossil sites in eastern Australia as indicated in the text and Figures 1 and 2. All listed specimens are megascopic unless otherwise stated.

Cuticle was physically removed and then treated with acid for ca 7 days (5–9% hydrofluoric acid + 30% nitric acid). Specimens examined by scanning electron microscopy (SEM) were mounted on stubs with double-sided adhesive tabs and imaged using a Hitachi TM3030plus SEM (standard observation mode, charge-up reduction enabled, accelerating voltage 15kV). Those used for transmitted-light microscopy (TLM) were cleared with 0.5–1% sodium hypochlorite and stained with safranin (1% solution). Staining times varied for each species (6–15 minutes) as noted in the text. A Motic BA80 microscope with a standard SLR camera attachment was used for TLM and permanent slides were prepared using CytoSeal 60, a toluene-based resin. Stack focusing of images was performed using ImageJ software (Schneider et al. 2012).

Rocks with preserved plant remains from Jurassic coal measures (Jeebropilly and New Acland; Fig. 2) have a high clay content. The cuticle from those specimens proved invariably fragmented. Alternative extraction techniques were attempted such as using polyethylene peels (Kouwenberg et al. 2007), painting the cuticle with fingernail lacquer and immersion of the rock in water. The rock usually disintegrated using the latter method. However, the cuticle was highly fragmented regardless of the applied technique, suggesting the presence of micro-fractures that were probably caused by expansion and contraction of the claystone due to varying moisture content. Thus, no usable cuticle could be prepared from those sites. Likewise, Rigby (1978) was unable to prepare cuticle from specimens collected from a mine located near to the Jeebropilly Mine (discussed below).

Systematic assignment above family herein follows Meyen (1984) and Roux (2009) unless otherwise stated. Terminology applied to megascopic material is based on Stanley & Ross (1983) and Andrews (1990) and that applied to epidermal detail follows Baranova (1987), Barclay et al. (2007) and Yeats & Rose (2013). All references to the International Code of Nomenclature (ICN) are based on McNeill et al. (2012).

SITE NOTES AND GEOLOGY

The chronostratigraphy of the Queensland Upper Triassic through Lower Cretaceous was summarised by McKellar (2013) and that of the Middle Triassic Esk Trough, Queensland, by Purdy (2013); that of other areas of Australasia and beyond are noted in the text. Names of formations are given in the text except for the small intermontane Tarong Basin where strata are only informally identified as the Tarong beds (Jell 2013).

Specimens from the Upper Triassic Callide Basin were collected from the Dunn Creek mine area (Jorgensen & Fielding 1996, fig. 2), near the Callide A Power Station. A disconformity in the basin separates upper Carnian and lower Rhaetian coal-bearing strata (Jell & McKellar 2013); however, most of the

basin's coal reserve is located above the disconformity. The Rhaetian Callide Seam is the most economically important; it is up to 23 m thick at the Dunn Creek locality (Jorgensen & Fielding 1996). The specimens described herein are all preserved in a grey, very fine grained mudstone. The low-diversity collection resembles those of O'Sullivan (1977) and Webb (1980) from the same site and all are regarded herein to be derived from the Callide Seam Member (lower Rhaetian). However, as the specimens were collected from spoil, it is possible that the collection includes material from outside that member.

Strata in the Dinmore Quarry, Ipswich, Queensland, have been variously assigned to the Tivoli Formation (Playford & Rigby 1988, Pattemore & Rigby 2005) and the Blackstone Formation (Raven et al. 2015); both formations are included in the Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: Purdy & Cranfield 2013). Quarry strata are considered herein to belong to the uppermost Tivoli Formation, following Pattemore & Rigby (2005).

Megafloral assemblages at the Jeebropilly and New Acland sites (Middle Jurassic Walloon Coal Measures, Clarence-Moreton Basin: Jell et al. 2013, McKellar 2013) represent a low-diversity flora. The bulk of vegetative material at both mines is attributable to *Cladophlebis* (discussed below). The collection from Jeebropilly also includes fragmentary leaves (QMF58713, QMF58714) resembling specimens that were identified by Rigby (1978) as *Lycopodites gracilis* (Morris in Oldham & Morris 1863) Seward & Sahni 1920 from the Walloon Coal Measures (Rosewood, Queensland: Fig. 2). Material from New Acland includes several fragmentary leaves resembling specimens that were identified by McLoughlin & Drinnan (1995) as *Taeniopteris* sp. cf. *T. spatulata* McClelland 1850 and “parallel-veined foliage/axes” also from the Walloon Coal Measures (Mudlapilly, Queensland: Fig. 2). The fragmentary condition of these specimens in the present collections (Jeebropilly and New Acland) precludes any meaningful addition to those published descriptions.

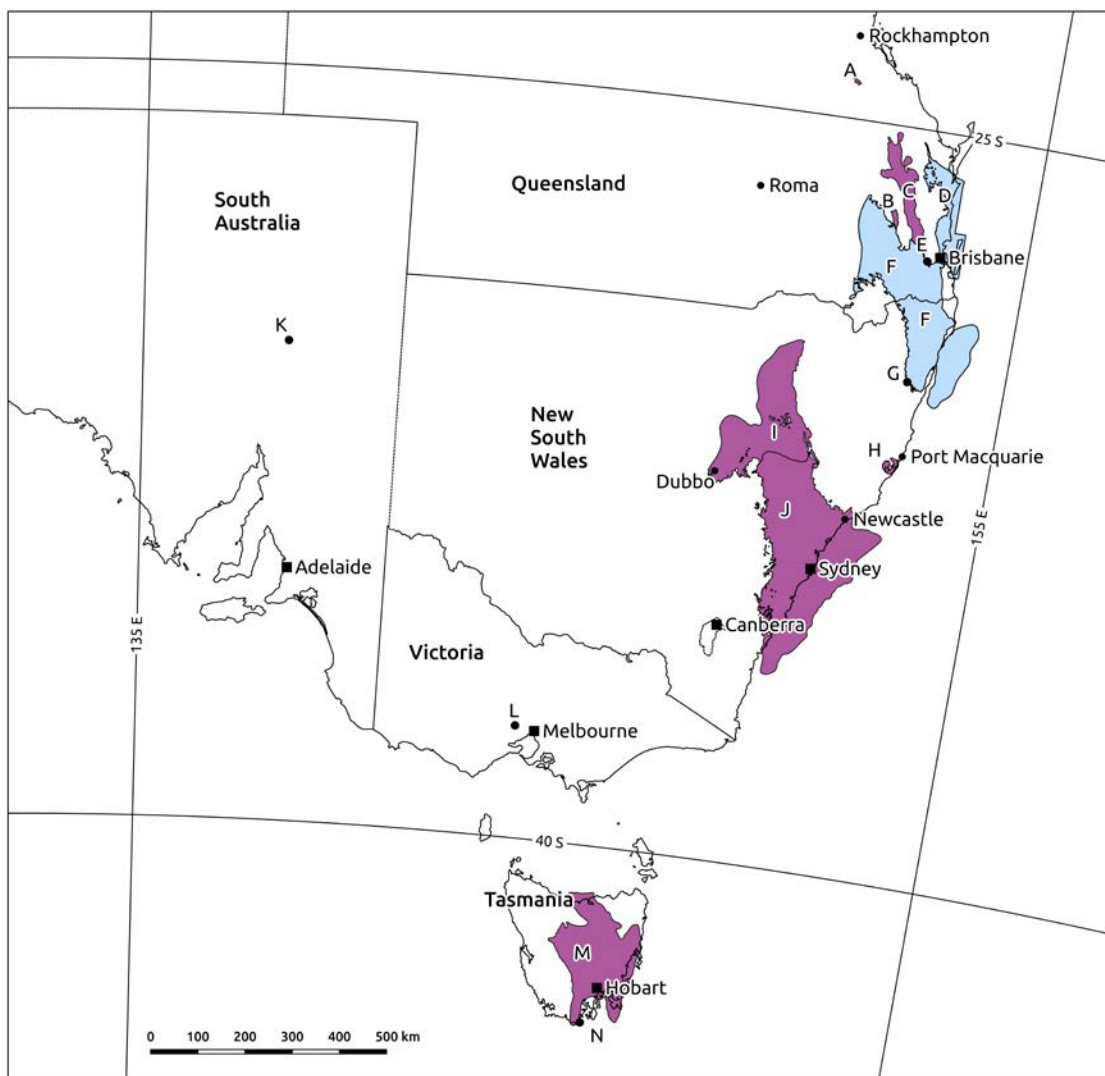


Fig. 1. Triassic–Jurassic basins in southeast Australia that are relevant to the present study. Triassic (purple): **A** – Callide Basin; **B** – Tarong Basin; **C** – Esk Trough; **E** – Ipswich Basin (see Fig. 2); **G** – Nymboida Sub-Basin; **H** – Lorne Basin; **I** – Gunnedah basin; **J** – Sydney Basin; **K** – Leigh Creek Coal Measures comprising five intramontane basins (Kwitko 1995); **M** – Tasmania Basin. Jurassic (blue): **D** – Nambour Basin; **F** – Clarence-Moreton Basin (Fig. 2); **N** – Lune River area, Tasmania. ?Post-Triassic: **L** – Yandoit Hill and Bacchus Marsh, Victoria (see text). Data sources: Geoscience Australia; Queensland Department of Natural Resources and Mines

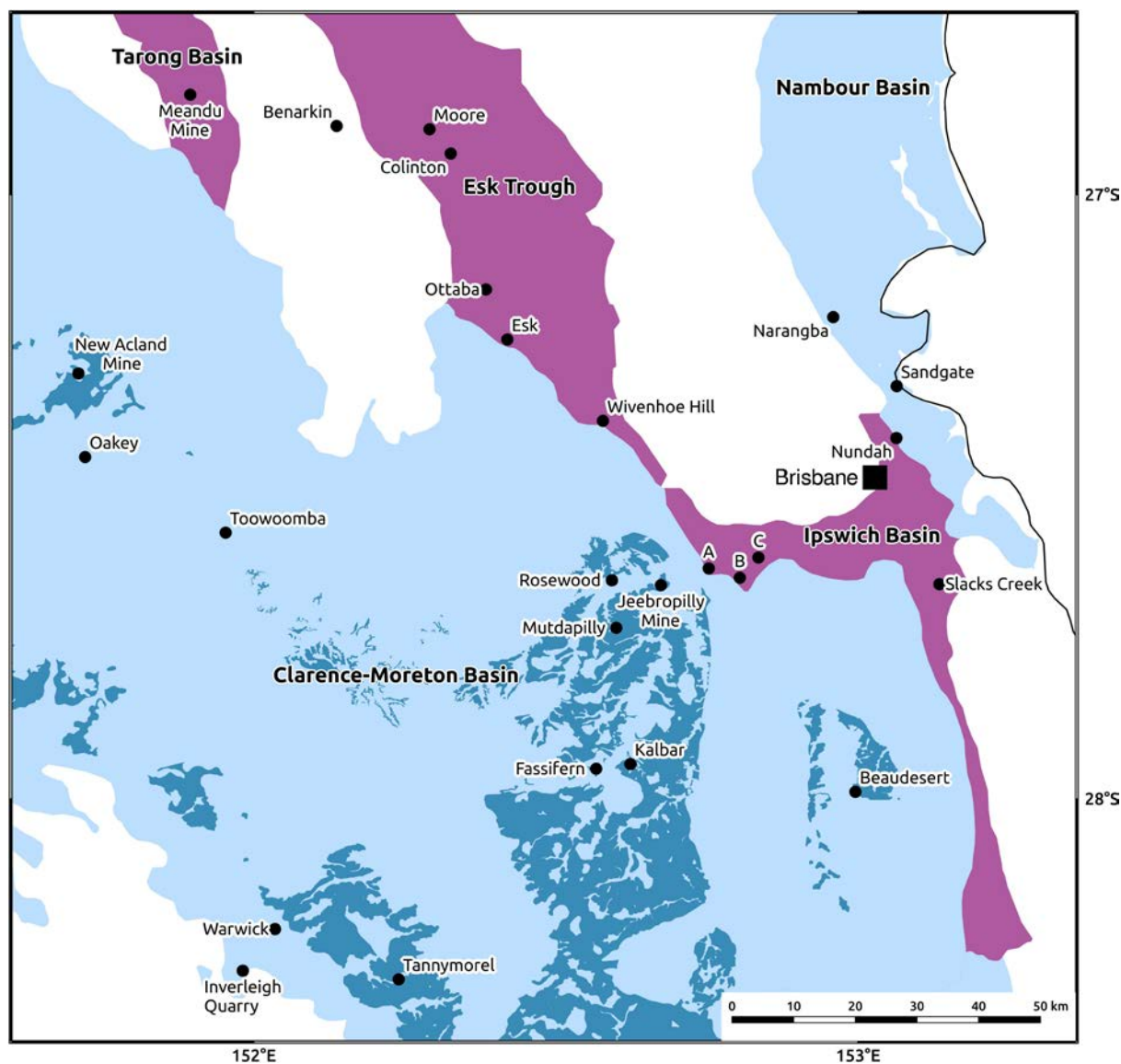


Fig. 2. Triassic–Jurassic basins in southeast Queensland. Colour key: Triassic (purple); Jurassic (light blue); Middle Jurassic, outcrop of the Walloon Coal Measures (dark blue). Location key: **A** – Denmark Hill; **B** – Blackstone Hill; **C** – Dinmore Quarry. Data source: Queensland Department of Natural Resources and Mines

SYSTEMATIC PALAEOBOTANY

Division: **Lycopodiophyta**

Class: **Lycopodiopsida**

Order: **Isoetales**

Family: **Isoetaceae** Reichenbach 1828

Genus: ***Isoetites***

Münster & Unger in Münster 1842

Type species. *Isoetites crociformis* Münster & Unger in Münster 1842, by monotypy.

Collected from Daiting, Bavaria, Germany (Münster 1842, pp. 107–108) from the Mörnsheim Formation, Upper Jurassic (lower Tithonian: Röper 2005, Burnham 2007).

***Isoetites* sp.**

Fig. 3

Material. QMF57844: Meandu Mine, Queensland; Tarong Basin (upper Carnian).

Description. Leaves narrowly lanceolate, 0.25 mm wide distally, ca 1 mm wide basally and ca 90 mm long. All foliage apparently diverging from narrow base (<5 mm wide); attachment arrangement unclear. No indication of stem, corm-like base, or roots or root-like

structures. Original plant material apparently very thick prior to preservation as the central part of the specimen is coalified with 2–3 mm depth and a cleat-like coal block structure is evident.

Discussion. Leaves resemble those of isoetaleans or equisetaleans. The lack of attachment to an equisetalean-like stem or corm-like base perhaps suggests that it is an immature quillwort or possibly the apical portion of a larger subarborescent lycophyte such as *Pleuromeia* Corda ex Giebel 1853, *Lycopia* Kustatscher, Wachtler & van Konijnenburg-van Cittert 2010 or *Tomioistrobus* Neuburg 1936 emend. Retallack 1997. These genera are restricted to the Lower–Middle Triassic and *Lycopia* is known only from the Anisian of the Northern Hemisphere. If individual leaves of this specimen were found dispersed they would be regarded as equisetalean and referable to *Neocalamites* Halle 1908. The leaves are arranged in a tuft whereas *Neocalamites* is more or less evenly distributed around a stem node (Halle 1908). Key studies of Australian Triassic lycophytes include Helby & Martin (1965), Retallack (1975, 1997), White (1981), and Holmes (2000, 2001a).

The quillwort genus *Isoetes* Linnaeus 1753 was erected for extant isoetaleans but the genus is also commonly applied to fossil material (e.g. Drinnan & Chambers 1986, Retallack 1997). Pigg (2001) considered the earliest unequivocal occurrence of this genus to be from the Jurassic of North America. That view is based on a more strict definition of the genus than that used by others (cf. Kustatscher et al. 2010). The relationship between fossil and extant representatives is not well understood, but recent phylogenetic analysis, based on the DNA of extant species, suggests a Triassic–Early Cretaceous origin for the genus (Larsén & Rydin 2016). *Isoetites* was established for plant fossils that resemble *Isoetes* (Seward 1910), and recent changes to the ICN vis-à-vis the definition of fossil-taxon and deletion of the concept of morphotaxon (Zijlstra 2014) suggest *Isoetes* is applied more appropriately to extant material only.

The specimen examined herein resembles *Isoetites* sp. of Jansson et al. (2008) from the Lower Jurassic of the Clarence–Moreton Basin, Queensland but it has longer leaves. More broadly, it resembles *Isoetes beestonii* Retallack 1997 from the Lower Triassic of the Sydney Basin and *Isoetites brandneri* Kustatscher et al. 2010 from the Anisian of Italy; however, both

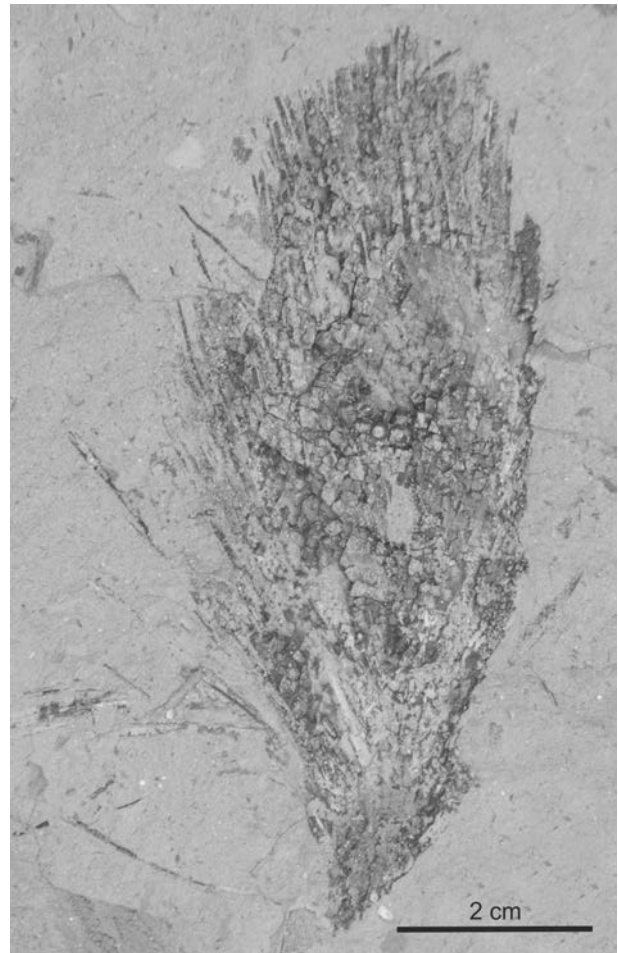


Fig. 3. *Isoetites* sp., QMF57844; Meandu Mine, Queensland; Tarong Basin (upper Carnian), Queensland

of these have fewer and broader leaves. *Isoetites elegans* Walkom 1944 is attached to a much larger circular structure (ca 30 mm in diameter) and also has fewer and broader leaves. Walkom's (1944) collection from near Perth, Western Australia (precise location unknown) was considered to be Jurassic in age. His specimens were probably from the Lower Cretaceous Leederville Formation or Dandaragan Sandstone (Hocking et al. 1976, Mory et al. 2005), and thus would be considerably younger than the specimen described herein. *Isoetites* identified from the Lower Cretaceous of the Gippsland Basin, Victoria, Australia, also have fewer and broader leaves and expanded bases (Drinnan & Chambers 1986, McLoughlin et al. 2002). Individual leaves recorded from the Lower Jurassic Shafer Peak Formation in North Victoria Land (Mount Carson), Antarctica, by Bommfleur et al. (2011a, fig. 4a–c) and assigned to an unnamed species of *Isoetites* resemble those described here in width and length.

Pleuromeia Corda ex Giebel 1853 has been reported from the Lower–Middle Triassic

of Gondwana (Retallack 1975, 1995, 1997, Cantrill & Webb 1998) and the Triassic of the Northern Hemisphere (Pigg 1992). Spores and cones affiliated with the *Pleuromeiaceae* Potonié in Engler and Prantl 1902 are found throughout the Triassic (Retallack 1975, 1997, Balme 1995). Other key studies of *Pleuromeia* include Kon’no (1973) and Grauvogel-Stamm & Lugardon (2001). The spelling of “*Pleuromeia*” has become the widely used orthography but the original and valid spelling of the genus is *Pleuromeia*. Wang Qi (2008) summarised the somewhat contorted nomenclatural history of this genus and the several orthographic variants that have arisen. To achieve nomenclatural stability, Wang Qi (2008) proposed conserving the name *Pleuromeia*. Likewise, spelling of the family name *Pleuromoiaceae* by H. Potonié in Engler & Prantl (1902, p. 754) is largely unused in modern times and the variant *Pleuromeiaceae* is now widely if not exclusively adopted. If Wang Qi’s proposal is accepted, then the spelling *Pleuromeiaceae* is consequently validated (ICN, Article 18.3).

If the specimen described herein is from an isoetalean or pleuromeian parent plant, a more robust corm-like base and roots would be expected to have survived preferentially to the leaves; neither of these plant groups are known to have shed tufts of leaves. The lack of any indication of attachment to a corm-like structure or roots suggests that the tuft represents immature isoetalean leaves with a poorly developed base. Alternatively, it was shed from an equisetalean stem node or perhaps is the extreme apical portion of a lycopod stem such as *Lycopodium*. It is possible that the thick coalified region of the specimen masks a stem; if so, attribution to *Lycopodium* could be favoured.

Division: **Pteridophyta**

Class: **Osmundopsida**

Order: **Osmundales**

Family: **Osmundaceae** Brown 1810

Discussion. Erection of the family has been variously attributed to Augier (1801, pp. 33, 35), Brown (1810, p. 161) and Berchtold & Presl (1820, p. 272). Augier’s (1801) proposal (invalid: ICN, Article 18.4) was validated

by Martynov (1820, pp. 444–445); however, Brown (1810) has priority.

Genus: ***Cladophlebis***

Brongniart 1849 emend. Seward 1894

Type species. *Cladophlebis denticulata* (Brongniart 1834) Schimper 1874 following Doweld’s (2013) conservation proposal. That author’s designated lectotype is from the Middle Jurassic (lower Bajocian) of Yorkshire, England.

Doweld (2013) noted that *Cladophlebis* is typified by a Carboniferous pteridosperm, but specimens attributed to the genus chiefly include Mesozoic ferns. Subsequent alternative typifications are inadmissible (Doweld 2013); e.g. *C. albertsii* (Dunker 1846) Brongniart 1849 has been widely but incorrectly identified as the type species. *Cladophlebis denticulata* is one of the better-understood species of the genus, but Doweld (2013) noted that without conservation the name is illegitimate, being nomenclaturally superfluous.

Diagnosis. See Seward (1894, p. 88).

Discussion. Several species from the Mesozoic of Europe were included in the genus by Brongniart (1849, pp. 103, 105, 107, errata on p. 127). His errata are somewhat unclear; however, later work indicates his intent (Brongniart 1850, p. 195). At and since erection of the genus, material has been included that variously has uncertain or inconsistent higher taxonomic affinity (i.e. attributions to the genus doubtfully represent a monophyletic group). However, following generic clarification by Doweld (2013) the higher taxonomic placement of *Cladophlebis* has been identified based on the type species; that author’s attribution is followed herein. Fertile fronds allied with *Cladophlebis denticulata* were included in the *Osmundaceae* by Harris (1961, pp. 78–86); their sporangia are mounted along the underside of veins. Sporangia in representatives of the family are not grouped into sori (Andrews 1990, p. 263).

Cladophlebis* sp. cf. *C. australis
(Morris in Strzelecki 1845) Schimper 1874

Fig. 4

Synonymy.

1917a *Cladophlebis australis* (Morris); Walkom, pl. 5, fig. 2a (only).

- 1966 *Cladophlebis australis* (Morris) Seward; Hill et al., pl. J3, figs 1, 2.
 1969 *Cladophlebis australis* (Morris) Seward 1904; Gould (unpubl.), frontispiece.
 1978 *Cladophlebis mendozaensis* (Geinitz) Frenguelli 1947; Rigby, p. 527, fig. 3.
 1987 *Cladophlebis indica* (Oldham & Morris) Sahni & Rao 1933; Tidwell et al., pp. 160, 162, fig. 2A(i–v), pl. 1, figs 4, 7, pl. 2, figs 5, 6.
 1995 *Cladophlebis australis* (Morris) Seward 1904; McLoughlin & Drinnan, pp. 258–260, figs 2C, 2F, 3A, 3C (only).

Type material. The type material of *Cladophlebis australis* was collected from Upper Triassic coal measures of the Tasmania Basin (Retallack 1983, p. 135). Schimper (1874, p. 660) recombined *Pecopteris australis* Morris in Strzelecki 1845 [basionym] with *Cladophlebis*. Retallack (1983) did not support Herbst's (1978, p. 9) designated neotype from the Victorian Cretaceous.

Diagnosis. Diagnosis of *Pecopteris australis* by Morris in Strzelecki (1845, p. 248). Retallack (1983) placed greater importance on conformity with characters of the type specimen than did many previous authors (e.g. Frenguelli 1947, Herbst 1978). He did not emend the species diagnosis but noted that an emendation is required.

Material. GSQF197 (Fig. 4C), GSQF445 (Fig. 4D): Beaudesert, Queensland; Walloon Coal Measures (Bathonian), Clarence-Moreton Basin. The specimens were figured by Hill et al. (1966, pl. J3, fig. 1) and Walkom (1917a, pl. 5, fig. 2a), respectively as *Cladophlebis australis*.

QMF58711, QMF58712 (Fig. 4B): Jeebropilly Coal Mine, Queensland; Walloon Coal Measures (Bathonian), Clarence-Moreton Basin.

QMF58731, QMF58732, QMF58735, QMF58736, QMF58740, QMF58741, QMF58746 (Fig. 4A), QMF58747, QMF58753, QMF58754, QMF58756, QMF58757, QMF58768, QMF58776: New Acland Coal Mine, Queensland; Walloon Coal Measures (Bathonian), Clarence-Moreton Basin.

UQF47850: Tannymorel Colliery, near Warwick, Queensland; Walloon Coal Measures (Bathonian), Clarence-Moreton Basin.

Occurrence. Retallack (1983) regarded *Cladophlebis australis* as being restricted to the Gondwanan Middle and Upper Triassic. His strict interpretation of the species was based chiefly on veins that consistently fork

twice (i.e. vein bifurcates, then both divisions bifurcate again). Specimens included in the species by Frenguelli (1947) span much of the Gondwanan Mesozoic. He did not consider consistently twice-forked venation to be important in distinguishing the species. However, as noted above, Retallack (1983) placed greater emphasis on conformity with the type material. Twice-forked venation appears to be considerably less common in Jurassic specimens, despite otherwise resembling the species (discussed below).

Description. Frond bipinnate, >400 mm long, >100 mm wide (all specimens incomplete). Rachis 1–5 mm wide. Pinnae opposite to alternate, ca 65 mm long, extending from rachis at 50–80°. Pinnules opposite to alternate, entire, straight to falcate, extending from pinna-rachis sub-perpendicularly. Larger pinnules slightly sinuate, dentate or serrate. Pinnules 10–17 mm long, 3–5 mm wide, smaller near pinnae apices and in distal portion of frond. Pinnule bases commonly decurrent but tending toward constricted in larger pinnules. Pinnule apex acutely rounded to pointed. Costule branching very acutely from pinna-rachis, curving away and extending to pinnule apex, prominent for most of its length. In larger pinnules, up to 14 veins arising either side of costule, extending from costule very acutely, curving away, forking once near midrib, one divided portion may fork again but rarely both. All pinnules are sterile.

Discussion. Fronds were preserved prolifically at both the New Acland and Jeebropilly mines. They were the most abundant megafloreal component at those sites and were almost always preserved in thick layers comprising many superimposed fronds. Thus, collection of well preserved individual fronds was difficult. The rocks have a high clay content, tending to fracture perpendicularly to the bedding plane (particularly at Jeebropilly); thus, the rocks generally broke into small blocks. The longest specimen recorded herein (QMF58753; 230 mm, incomplete) was preserved in a sandy lens. However, during collection, incomplete fronds were seen to exceed 400 mm in length. There is no appreciable difference between specimens from the Jeebropilly and New Acland sites. The cuticle is thin and, as noted above, fragments during preparation; thus, no epidermal detail is available. The specimens from Beaudesert

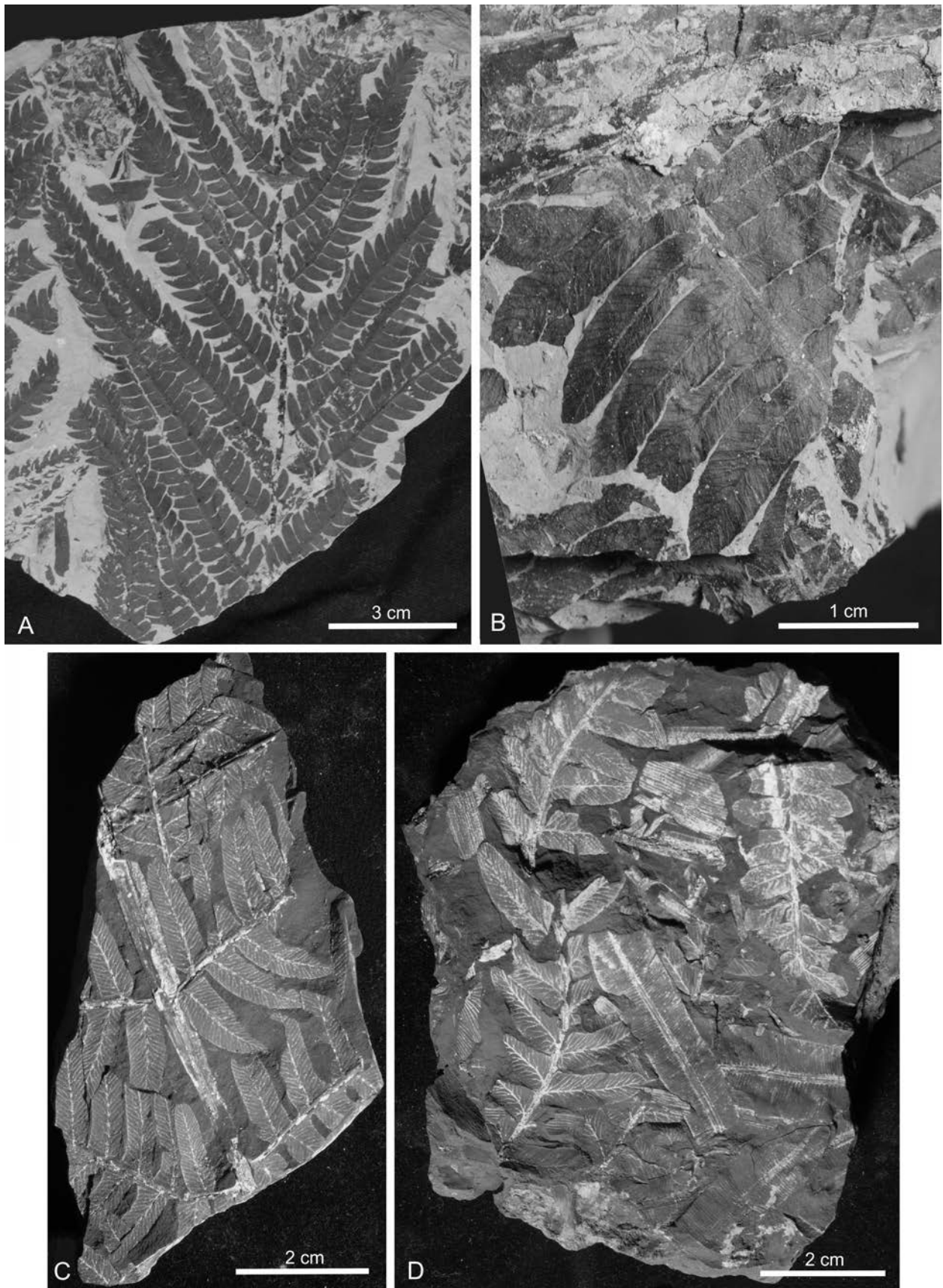


Fig. 4. A–D: *Cladophlebis* sp. cf. *C. australis* (Morris in Strzelecki 1845) Schimper 1874; Walloon Coal Measures, Clarence-Moreton Basin (Bathonian, Middle Jurassic), Queensland. **A:** QMF58746; New Acland Mine, Queensland. **B:** QMF58712; Jeebropilly Mine, Queensland (low-angle illumination and enhanced contrast). **C:** GSQF197; Beaudesert, Queensland. **D:** GSQF445; Beaudesert, Queensland; this specimen and other leaves on the slab were described and figured by Walkom (1917a, pp. 3–5, 30–32, pl. 5, fig. 2)

(GSQF197, GSQF445: Fig. 4C, D) are not carbonaceous. Pinnule size in these specimens is equivalent to that of larger pinnules from the Jeebropilly and New Acland sites.

Rigby (1978) assigned specimens to *Cladophlebis mendozaensis* (Geinitz 1876) Frenguelli 1947 from the nearby Rosewood Colliery (now closed: formerly the Normanton Mine, near Rosewood, Queensland; Gould 1969, fig. 3). They were preserved abundantly at the site (some up to 400 mm long; Rigby 1978) and resemble the specimens described in the present study. He was unable to prepare cuticle for optical assessment, and SEM imaging was unsuccessful because of poor preservation. Palynofloras from the Rosewood Colliery (McKellar 1978) are chiefly allied with lycopods, ferns, and conifers (based on Balme 1995). Several large fronds (220 mm long, incomplete) were figured as *C. australis* by Gould (1969, frontispiece). They were collected from the Caledonian No. 6 Mine (Walloon Coal Measures), which was located 8 km north-west of the Jeebropilly Mine. Gould (1968) recorded equisetalean remains from three mines (Acland, Sugarloaf, and Mt. Elliot, all now closed: Walloon Coal Measures) that were variously located near the New Acland and Jeebropilly mines.

Cladophlebis mendozaensis, based on a unipinnate specimen with strongly crenate (or perhaps lobed) pinnules, was figured by Geinitz (1876, pl. 2, figs 4a, b) and collected from near Mendoza, Argentina (Middle or Upper Triassic, Cuyo Basin: Kokogian et al. 2001, Morel et al. 2003). Frenguelli (1947, pp. 60–63) recombined Geinitz's *Hymenophyllites mendozaensis* with *Cladophlebis* but he also included several bipinnate specimens with entire, sinuate, and crenate pinnules in the species. No specimens described herein have strongly crenate margins; nor do any other figured specimens assigned to *Cladophlebis* from the Walloon Coal Measures (Walkom 1917a, Gould 1969, Rigby 1978, McLoughlin & Drinnan 1995). Walkom (1924b) erected *C. johnstonii* with Upper Triassic Tasmanian specimens; it is almost certainly a junior synonym of *C. mendozaensis*.

Shirley (1898, p. 17, pl. 12) erected *Scoleopteris australis* with specimens from Denmark Hill, Ipswich Basin (Carnian–lower Norian). He figured separate fertile and sterile fronds although he described specimens that include

both types of pinnules on the same frond. Walkom (1917a) included Shirley's species in *Cladophlebis australis*. Other specimens from the same location were identified by Shirley (1898) as *Todea australis* Renault 1883 but were neither described nor figured. However, Walkom (1917a, p. 2) noted that he had not encountered any fertile specimens resembling those from New South Wales that were figured by Renault (1883, pp. 81–82, pl. 11) as *T. australis*; the precise collection location of Renault's specimens is unknown. McLoughlin & Drinnan (1995) assigned fertile and sterile specimens to *Cladophlebis australis* from Mutdapilly (Walloon Coal Measures: Fig. 2), Queensland. No organic connection between sterile and fertile pinnules was identified. If any of the above noted fertile specimens were confirmed as representatives of *C. australis*, then the presence of sori suggests that the species differs significantly from the type species of *Cladophlebis* (probably to a familial level: Andrews 1990, p. 263).

Jones & de Jersey (1947b, pl. 2, fig. 4) figured specimen UQF7639 (re-examined herein) as *Cladophlebis roylei* Arber 1901 from the Lower Jurassic (?Marburg Subgroup) of the Nambour Basin at Brighton, near Sandgate, Queensland; it is unipinnate but is possibly a portion of a pinna from a bipinnate frond. Similarly, specimen QMF50954 (re-examined herein: previously undescribed, but from a collection by Jansson et al. 2008) from the Lower Jurassic Marburg Subgroup of the Clarence-Moreton Basin at Inverleigh Quarry, near Warwick, Queensland, may be a portion of a pinna from a bipinnate frond. Both of the above noted specimens are very poorly preserved but resemble the specimens described herein in their limited available characters. They have once-forked venation and possibly included a few occurrences of a second vein dichotomy (unclear). Geological and megafloreal correlation of the southern Nambour Basin with the Marburg Subgroup of the Clarence-Moreton Basin was discussed by Pattemore (2000), Pattemore & Rigby (2005), and Pattemore et al. (2014, p. 58) and references therein.

A specimen from the Lower–Middle Jurassic (Toarcian–Aalenian) Cockleshell Gully Formation of the Perth Basin, Western Australia, was identified as ?*Cladophlebis* sp. by McLoughlin & Pott (2009, p. 118, fig. 4C); however, it is too poor for useful comparison. Their description

indicates that the specimen is an improbable representative of *C. australis*. Tenison-Woods (1884) reported various ferns and conifers from the Ballimore Coal Mine, east of Dubbo, New South Wales (probably from the Middle Jurassic, Purlawaugh Formation, Surat Basin: Tottredell et al. 2009, fig. 2). The only specimen possibly resembling *C. australis* was assigned to *Alethopteris concinna* (erected by that author) but its collection location is doubtful. He noted that it may be from the Carnian–lower Norian Ipswich Basin (Tenison-Woods 1884, pp. 112–113, pl. 9, fig. 1). White (1963, 1964) attributed several fragments to *C. australis* from the Blantyre Sandstone, Eromanga Basin, Queensland (Middle–Late Jurassic: Cook et al. 2013) but they were neither figured nor sufficiently described for confident identification.

Cladophlebis concinna (Presl in Sternberg 1838) du Toit 1927 was recorded by Jones & de Jersey (1947a, text-figs 4, 5, pl. 1, fig. 4) from Sandgate, Queensland (Lower Jurassic Brighton beds, ?Marburg Subgroup, Nambour Basin). Their specimens (UQF7640, UQF7641) were re-examined herein. The pinnules have a sinuous midrib and in that and other characters they do not resemble *C. australis*. *Pecopteris concinna* [basonym] was erected with ?Lower Jurassic specimens from Bamberg, Germany (Sternberg 1838, p. 149, Barbacka et al. 2014). Harris (1931, pp. 58–60) recombined the species as *Rhinopteris concinna* [type species] and included fertile and sterile fronds in the genus.

Ferns, conifers and bennettitales were reported from Lower Jurassic (Toarcian) strata near Lune River, southern Tasmania (Tidwell et al. 1987, Calver 2009, and references therein). *Cladophlebis indica* (Oldham & Morris 1863) Schimper 1874 was identified from that site by Tidwell et al. (1987), having pinnules with once-forked venation, although, near the base of some pinnules, one divided segment may fork again. In this and other characters they resemble the specimens described herein from the Walloon Coal Measures. *Cladophlebis indica* was based on specimens (Oldham & Morris 1863, pp. 47–50, pl. 27, figs 1–3) from the Lower Cretaceous of the Rajmahal Hills, approximately 8 km west of Sahibganj, Jharkhand, India (Feistmantel 1880b, p. x). Oldham & Morris (1863, p. 48) noted its resemblance to *C. australis*, only differing in having exclusively once-forked secondary venation. Frenguelli (1947) and Retallack

(1980b) included specimens in the species from the Triassic of Argentina and New Zealand, respectively, those specimens having consistently once-forked venation.

Arber's (1917) specimens that were figured as *Cladophlebis denticulata* and *C. australis* from various locations in the New Zealand Jurassic resemble the specimens described in the present study. They all apparently lack the twice-forked venation that was identified by Retallack (1983) as characteristic of Triassic representatives of *C. australis*. Arber (1917) and Bell et al. (1956) identified *C. australis* from the Ladinian (Middle Triassic) of New Zealand (Mt. Potts and Benmore Dam, South Island) and they also lack consistently twice-forked venation. Arber (1917) noted that the species is the most common plant preserved in New Zealand's Mesozoic. Thorn (2001, fig. 6d) assigned a small pinnate fragment from the Middle Jurassic of New Zealand to an unnamed species of *Cladophlebis* that shows a single occurrence of twice-forked venation. Specimen GSQF445 (Fig. 4D) from the Middle Jurassic of Queensland also includes a few occurrences of twice-forked venation.

Holmes (2001b) described fertile fern fronds belonging to several genera from the Anisian Nymboida Coal Measures, New South Wales. Sterile pinnules on fronds that were assigned to *Osmundopsis scalaris* Holmes 2001b resemble *Cladophlebis australis* but their venation appears to be consistently once-forked. *Osmundopsis* was erected by Harris (1931, p. 48) and its diagnosis was emended by Harris (1961, p. 99). The genus comprises strongly dimorphic sterile and fertile fronds, the latter lacking laminae, having only sporangia mounted on filiform structures. Holmes (2001b) also erected *Nymbofelicia aggregata* based on sterile and fertile fragments. Its sterile pinnules resemble those of *Cladophlebis* and fertile specimens have several paired sori. No fertile pinnules were identified in material described herein. Holmes (2003) reported numerous non-fertile fern fronds, also from the Nymboida Coal Measures; many were referred to new species of *Cladophlebis* and to new genera. Specimens assigned to his monotypic genus *Nymbophlebis* resemble *C. australis* in having consistently twice-forked venation but they show much greater variation in pinnule shape than previously recorded in the latter species. Likewise, Anderson & Anderson (2008) erected several

Cladophlebis species with specimens from the Carnian Molteno Formation, South Africa that were primarily distinguished by pinnule size and venation.

The type specimen of *Cladophlebis denticulata* [type species] from the Middle Jurassic (Bajocian) of Yorkshire has pinnules that are strongly and consistently serrate, are not basally constricted, and venation appears to fork once only. However, specimens subsequently assigned to the species by Harris (1961), also from Yorkshire (“lower-middle Deltaic Series”, Bajocian: van Konijnenburg-van Cittert 1978, Slater & Wellman 2015), show a wider range of characters, having pinnule venation that uncommonly includes a second dichotomy (basally). Harris’s (1961) emended diagnosis of the species indicates that pinnules are always serrate and up to twice the length of those described herein. Contrary to Seward (1904), *C. denticulata* and *C. australis* were differentiated by Harris (1961, p. 80) and Retallack (1983); that view is supported herein.

Halle (1913) erected *Cladophlebis oblonga* and *C. antarctica* with specimens from the ?uppermost Triassic–Lower Jurassic of Hope Bay, Antarctic Peninsula, and he assigned specimens to several other species of *Cladophlebis* from the same location. The age of those specimens had been regarded as Late Jurassic or Early Cretaceous; however, radiometric dating has placed an upper limit of Middle Jurassic age on the host strata, now known as the Mount Flora Formation, Botany Bay Group (Rees 1993, Cantrill 2000) of the “Botany Bay Group basins” (following Hathway 2000). Fossil plants have also been described from the ?Upper Triassic–Lower Jurassic of nearby Botany Bay (Camp Hill Formation, Botany Bay Group: Rees 1993, Rees & Cleal 2004, and references therein) and from other approximately coeval formations on the Antarctic Peninsula or neighbouring islands (Barale et al. 1994, Cantrill 2000, fig. 4, Cantrill & Poole 2012, pp. 161–188). Cantrill & Hunter (2005) identified *C. antarctica* from the younger (?Late Jurassic: Hathway 2000) Latady Basin on the Antarctic Peninsula. Palynofloral assemblages from both Hope and Botany bays have proven too poorly preserved for reliable dating (Rees & Cleal 2004), the currently accepted Early Jurassic date being based on megascopic plant remains. However, some recorded species suggest a latest Triassic age (Rees 1993, Rees & Cleal 2004). Much material

has been assigned to the aforementioned *Cladophlebis* species from the Botany Bay Group and from coeval strata in the region (Gee 1989, Cantrill 2000, Rees & Cleal 2004, Birkenmajer & Ociepa 2008, and references therein). Speciation has largely followed the approach of Halle (1913), distinguishing species on minor megascopic characters (e.g. key used by Rees & Cleal 2004, p. 25). Furthermore, assignment of specimens to the type species of the genus is questionable, as none appears to be strongly and consistently serrate and the pinnules are considerably smaller than those of the Yorkshire material (discussed above). Notably, other than the lack of consistently twice-forked venation, all the specimens assigned to *Cladophlebis* by Rees & Cleal (2004) and Birkenmajer & Ociepa (2008) are possibly within the natural variation of *C. australis*.

The specimens from the Middle Jurassic Walloon Coal Measures described herein resemble *Cladophlebis australis* but they do not exhibit the consistently twice-forked venation that is characteristic of the species if Retallack’s (1983) strict circumscription is adopted. Specimens commonly have once-forked venation, and one divided segment may fork again but rarely both. It is unclear whether this difference is representative of speciation or a result of environmental conditions. Hence, the specimens described herein are compared with, rather than positively assigned to, *C. australis*.

Division: **Pinophyta**

Class: **Ginkgoopsida**

Order: **Peltaspermales**

Family: **Umkomasiaceae** Petriella 1981

Discussion. Representatives of the Umkomasiaceae and their phylogeny, speciation and spatio-temporal distribution were discussed by Pattemore et al. (2015a). It is improbable that the family survived into the post-Triassic globally (Pattemore 2016). A purported representative of *Umkomasia* from the Lower Cretaceous of Mongolia (Shi Gongle et al. 2016) does not belong in the genus, nor in the Umkomasiaceae (Rothwell & Stockey 2016).

Thomas (1933) erected the *Corystospermaceae*; however, that name (or its use as

a basis for a higher-ranking name) is not adopted herein, being nomenclaturally superfluous (Petriella 1981, Pattemore et al. 2015a, ICN Articles 16.1, 18.1). Meyen's (1984) placement of the Umkomasiaceae in Ginkgoopsida was supported by Anderson & Anderson (2003) and Gordenko & Broushkin (2015), and is followed in the present study.

Genus: *Dicroidium*

Gothan 1912 emend. Townrow 1957

Synonymy.

1912 *Dicroidium* Gothan, pp. 75–80.

1943 *Dicroidiopsis* Frenguelli, pp. 285–289.

1943 *Diplasiophyllum* Frenguelli, pp. 289–300.

Type species. *Dicroidium odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 by subsequent designation (Townrow 1957). The type material (discussed below) was collected from Jerusalem, Tasmania from strata associated with Triassic coal measures (Carnian–Norian: Reid et al. 2014) of the Tasmania Basin.

Diagnosis. See Townrow (1957, p. 26).

Discussion. Morris in Strzelecki (1845, p. 249, pl. 6, figs 2–4) erected *Pecopteris odontopteroides*, figuring three unipinnatifid to unipinnate fragments that he regarded as probable pinnae from a bipinnate frond. Thus, the species was diagnosed as bipinnate – a point of confusion that was not resolved until much later (Gothan 1912). None of Morris's figured specimens includes a rachis bifurcation. Caruthers (1872, pp. 355–356, pl. 27, figs 2, 3) attributed unipinnatifid–unipinnate specimens with bifurcating rachides to the species from the Carnian–lowermost Norian Ipswich Basin, Queensland (collected from the Tivoli Mine: Tivoli Seam of the Tivoli Formation; The Brisbane Courier 1871, p. 3, Whitmore 1981, 1985). Geinitz (1876) assigned remarkably similar material to his species *Thinnfeldia crassinervis* from the Argentine Triassic, the resemblance being noted by Feistmantel (1880a), and the species was later included in *T. odontopteroides* by Feistmantel (1889).

Pecopteris odontopteroides was recombined as *Thinnfeldia odontopteroides* by Feistmantel (1878, pp. 89, 105–106, pl. 14, fig. 5, pl. 15, figs 3–7, pl. 16, fig. 1), who also attributed several unipinnate and bipinnate specimens to the species from Clarke's Hill (Middle Triassic, Wianamatta Group, Sydney Basin: Retallack 1977,

1980a), Sydney. Feistmantel (1879, pp. 165–169, pl. 9, figs 1, 2) emended the specific diagnosis based on a large bipinnate specimen with a bifurcating rachis that was collected from Mt. Victoria (Olenekian, uppermost Narabeen Group, Sydney Basin: Retallack 1977, 1980a, Metcalfe et al. 2015, fig. 13). Feistmantel's (1879) site was probably the locality known today as Mt. Piddington, several hundred metres south of the town of Mt. Victoria (Tenison-Woods 1882, p. 52). Feistmantel noted considerable pinnae/pinnule morphological variation in the specimen and more generally in other specimens attributed to the species. However, he regarded the larger bipinnate specimen as representing a more mature growth stage than that of previously described material (a view that was favoured for some time: Feistmantel 1880a, 1887, 1888, 1889, Seward 1908, 1910, pp. 538–541). Another bipinnate specimen was figured by Curran (1885, pl. 9, fig. 4) from the Napperby Formation (Early–Middle Triassic: Cameron et al. 1999, Totterdell et al. 2009, fig. 2) in the Gunnedah Basin, near Dubbo, New South Wales (NSW). Substantial morphological variation in broadly similar material from various localities in the Triassic of eastern Australia became evident to Tenison-Woods (1884) and Johnston (1885, 1886, 1888); both authors erected additional species and varieties and Johnston (1893) proposed *T. feistmantelii* for Feistmantel's (1879) bipinnate specimen from Mt. Victoria (above). Gothan (1912) erected *Dicroidium*, determining that this group of plants with bifurcating rachides is in fact distinct from *Thinnfeldia*. He identified four species as belonging to the genus:

- *D. odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 [unipinnate];
- *D. lancifolium* (Szajnoch 1888) Gothan 1912 [unipinnate];
- *D. dubium* (Feistmantel 1878) Gothan 1912 [bipinnatifid];
- *D. feistmantelii* (Johnston 1893) Gothan 1912 [bipinnate].

The latter two recombinations were only tentatively proposed but were soon supported (Antevs 1914). Gothan (1912) evidently overlooked Johnston's (1893) species, *Thinnfeldia feistmantelii* (Walkom 1917a, pp. 13–14, Frenguelli 1943, p. 305). However, Gothan's (1912, pl. 16, fig. 1) figured specimen (reproduced from Feistmantel 1879, pl. 9, fig. 1) was given the same name by Johnston (1893). Frenguelli

(1943) recombined the species as *Zuberia feistmantelii* (Tab. 1; discussed below).

Following Gothan's (1912) erection of *Dicroidium*, many genera, species, subspecies, varieties and formae have been proposed for umkomasiacean leaves (e.g. Frenguelli 1943, Townrow 1957, Retallack 1977, Anderson & Anderson 1983). It has been suggested that umkomasiaceans diversified markedly during the Triassic as a result of sympatric speciation (Anderson & Anderson 1983) but that mode of speciation in the family is doubtful (Pattemore et al. 2015a, p. 698). Moreover, reliably established species representing genuine

umkomasiacean fructifications are few (Pattemore 2016), suggesting that speciation based on morphological variation in leaves is an unreliable indicator of actual biological species diversity. Furthermore, as detailed below, Anderson & Anderson (1983) assigned numerous specimens to various species that bear no resemblance to the type material of the relevant species, thus exaggerating a perceived “continuum” of characters among species. If those improperly assigned specimens are correctly attributed (below), then the remaining evidence for that continuum is limited to several aberrant fronds or extremely small fronds.

Table 1. *Dicroidium*, *Johnstonia*, *Xylopteris* and *Zuberia*: frond structure and Gondwanan temporal distribution. Modified from Pattemore et al. (2015a, tabs 2–4) and based on Retallack (1977), Baldoni (1980), Anderson & Anderson (1983), Artabe (1990), Zamuner et al. (2001), Holmes & Anderson (2005a) and the present study. Listed species have Gondwana-wide distribution except for those belonging to *Johnstonia* and *Xylopteris* which have not been reliably recorded from India and New Zealand (Baldoni 1980, Anderson & Anderson 1983, tab. 9.3 and herein)

Species	Frond structure, Gondwanan temporal distribution
<i>Dicroidium odontopteroides</i> (Morris in Strzelecki 1845) Gothan 1912 emend. nov.	unipinnate or unipinnatifid Olenekian–Norian. Retallack (1977) regarded a few unipinnate specimens as Rhaetian in age. However, they are almost certainly from the Carnian–Norian: “Bundamba Series”, probably from the Ipswich Basin, Australia; Paso Flores Fm, Argentina (Morel et al. 2003). Female fructification: <i>Umkomasia uniramia</i> Axsmith et al. 2000. Male fructification: unnamed <i>Pteruchus</i> -like organ (Axsmith et al. 2000). Wood: <i>Kykloxylon</i> Meyer-Berthaud, Taylor & Taylor 1993; see Decombeix et al. (2014, pp. 31–33, tab. 1)
<i>Dicroidium dubium</i> (Feistmantel 1878) Gothan 1912	bipinnatifid Olenekian–Norian. Fructifications unknown. Wood: <i>Kykloxylon</i> ; some specimens allied with <i>Dicroidium fremouwense</i> Pigg 1990 (junior synonym of <i>D. dubium</i>); see Decombeix et al. (2014, pp. 31–33, tab. 1)
<i>Dicroidium superbum</i> (Shirley 1898) Townrow 1957 emend. nov.	bipinnate or bipinnatifid – large morphological variation of pinnules: linear, oblanceolate, obovate, oblong, lobed or unlobed. Anisian–Norian. Fructifications and wood unknown
<i>Zuberia feistmantelii</i> (Johnston 1893) Frenguelli 1943 emend. Artabe 1990	bipinnate – very large fronds (ca 1 m long: Townrow 1957). Olenekian–lower Rhaetian. Youngest specimens are from the Callide Basin (herein). Other species of the genus not included here: see Artabe (1990). Female fructification: <i>Umkomasia geminata</i> (Shirley 1898) Rigby in Playford et al. 1982 emend. Pattemore (2016). Male fructification: <i>Pteruchus dubius</i> Thomas 1933 emend. Townrow 1962. Wood: <i>Rhexoxylon</i> Bancroft 1913 emend. Archangelsky & Brett 1961; see Decombeix et al. (2014, pp. 31–33, tab. 1)
<i>Xylopteris argentina</i> Frenguelli 1943	unipinnate, univeined – 1 to 4 well-spaced pinnules each side of rachis. Carnian–lowermost Norian. Female fructification unknown. ?Male fructification: <i>Paraxylopteris queenslandensis</i> Pattemore & Rigby 2005 (see text). Wood: unknown
<i>Xylopteris elongata</i> (Carruthers 1872) Frenguelli 1943 emend nov.	unipinnate, univeined – >4 pinnules (commonly many more) each side of rachis (Retallack 1977). Anisian–Norian: earliest record possibly Olenekian (Gunnedah Basin: see text). Fructifications and wood unknown
<i>Xylopteris spinifolia</i> (Tenison-Woods 1884) Frenguelli 1943	bipinnate, univeined Anisian–Norian. Fructifications and wood unknown
<i>Johnstonia coriacea</i> (Johnston 1888) Walkom 1924b	Simple Anisian–Norian. Fructifications unknown. Wood uncertain, but see discussion of <i>J. dutoitii</i> (junior synonym of <i>J. coriacea</i>) and “ <i>Jeffersonioxylon</i> ” by Decombeix et al. (2014, p. 31)

Rosewood specimens. Recombination of *Gleichenia lineatum* Tenison-Woods 1884 as *Dicroidium lineatum* by Anderson & Anderson (1970) was followed by Anderson & Anderson (2003, p. 22) and Holmes & Anderson (2005a). The material that Tenison-Woods (1884, pl. 3, fig. 6, pl. 8, fig. 2) used to erect the species was reportedly collected from the Rosewood Scrubs, near Rosewood, Queensland (Kerr 1990, Snars 1997). However, it is probable that he did not personally collect the specimens (Tenison-Woods 1883, p. 97). Furthermore, he did not geologically distinguish the coal measures at Ipswich from those in the Rosewood–Walloon area (Tenison-Woods 1884, p. 66, footnote), the first report of coal from the Rosewood Scrubs being only several years earlier (The Brisbane Courier 1872, p. 5). It was not until much later (Reid 1922) that the coal measures in the Rosewood–Walloon area were identified as stratigraphically distinct from those at Ipswich and of probable Jurassic age; however, Walkom (1915, 1917a, 1917b, 1919b) pre-empted that conclusion based on fossil plants from those areas.

Tenison-Woods's (1884) line-drawn interpretation of *Gleichenia lineatum* showing pinnate fragments with venation suggests affinity with *Dicroidium*. The figure includes a rachis bifurcation although such is not obvious in his photographic figure. He doubted the generic attribution because of the specimen's indistinct venation. The reported collection location indicates that the specimen came from the Walloon Coal Measures (Middle Jurassic) or possibly the Bundamba Group (Lower Jurassic) of the Clarence-Moreton Basin. Subsequent collections from Rosewood and elsewhere in the Walloon Coal Measures (Walkom 1917a, Gould 1969, 1974, Rigby 1978, McLoughlin & Drinnan 1995 and herein) and the Bundamba Group of the Clarence-Moreton and Nambour basins (Jones & de Jersey 1947b, Pattemore 2000, Pattemore & Rigby 2005, Jansson et al. 2008, Pattemore et al. 2014) did not include *Dicroidium*-like material. It seems probable that Tenison-Woods's (1884) specimens from the Rosewood area were compromised, including a mixture of specimens from the Triassic and Jurassic (and possibly younger). That author did not assign specimen numbers; however, the specimen he attributed to *Gleichenia lineatum* is reportedly in the Macleay Museum, University of Sydney (specimen SUM34: Retallack 1977). The specimen

has been neither figured nor described since Tenison-Woods's time.

Descriptions and line drawings based on Tenison-Woods's (1884) specimens from the Rosewood area almost certainly represent a mixed flora and hence should be regarded cautiously. See also *Xylopteris spinifolia* (below) and discussion by Pattemore et al. (2015b, pp. 128–129) concerning other specimens from Rosewood that were described by Tenison-Woods (1884). Some specimens reported by that author from the Ipswich Basin are now known to be of Cenozoic age (Townrow 1967a).

Dicroidium odontopteroides (Morris in Strzelecki 1845) Gothan 1912 emend. nov.

Figs 5–8

Synonymy. The following synonymy list is limited to figured specimens that pertain to the discussion herein. See synonymy lists for *Dicroidium odontopteroides* by Retallack (1977, microfiche frames H23–I8) and Anderson & Anderson (1983, pp. 98–103).

- 1845 *Pecopteris odontopteroides* Morris in Strzelecki, p. 249, pl. 6, figs 2–4. [basonym]
- 1876 *Pecopteris Stelzneriana* Geinitz, p. 6, pl. 2, figs 7, 8.
- 1876 *Thinnfeldia crassinervis* Geinitz, pp. 4–5, pl. 1, figs 10–16.
- 1884 *?Thinnfeldia media* Tenison-Woods, pp. 102–103, pl. 6, fig. 1.
- 1888 *Thinnfeldia odontopteroides* Morris; Szajnocha, pp. 228–230, pl. 1, figs 1–4a.
- 1888 *Thinnfeldia lancifolia* Morris; Szajnocha, pp. 231–232, pl. 1, figs 4b, 5–7.
- 1888 *Thinnfeldia trilobita* Johnston pl. 24, fig. 6, pl. 26, fig. 12.
- 1888 *Thinnfeldia obtusifolia* Johnston, pl. 25, figs 7, 14, pl. 26, fig. 21.
- 1888 *Thinnfeldia superba* Johnston, pl. 26, figs 4, 5.
- 1889 *Thinnfeldia odontopteroides* Feistm. (Morr. sp.); Feistmantel, pp. 62–64, pl. 1, figs 1–6, pl. 2, figs 1, 3, pl. 3, figs 5a, 8.
- 1892 *Thinnfeldia media* Ten. Woods, or *T. indica* Feistmantel; Jack & Etheridge, pl. 18, fig. 10.
- 1898 *Thinnfeldia indica* var. *aquilina* Shirley, p. 21, pl. 6, fig. 2.
- 1898 *Thinnfeldia indica* var. *media* Shirley, p. 21, pl. 5, fig. 1.
- 1912 *Dicroidium odontopteroides* (Morris) Gothan, pl. 16, fig. 5.
- 1912 *Dicroidium lancifolium* Morr. (pro. var); Gothan, pl. 16, figs 2–4.
- 1917a *Thinnfeldia odontopteroides* (Morris); Walkom, pl. 3, fig. 1.
- 1917a *Thinnfeldia acuta* Walkom, pp. 23–24, pl. 3, fig. 4.

- 1917a *Thinnfeldia lancifolia* (Morris); Walkom, pl. 4, fig. 1, pl. 7, fig. 2 (only).
- 1925 *Thinnfeldia lancifolia* (Morris); Walkom, p. 217, pl. 25, fig. 3, pl. 26, figs 1–3, pl. 27, figs 1, 2, 4, 5.
- 1950 *Tetraptilon heteromerum* Frenguelli, pp. 15–19, figs 1A, 1B, 2.
- 1957 *Dicroidium odontopteroides* (Morris) Gothan; Townrow, pl. 2, figs B, C, pl. 3, fig. A.
- 1965 *Dicroidium odontopteroides*; Hill et al., pl. 4, fig. 3.
- 1966 *Dicroidium obtusifolium* [sic] (Johnston) Townrow pp. 128–131, text-figs 1, 2, pl. 1, figs 1–3.
- 1975 *Dicroidium dentatum* (Walkom) Anderson & Anderson; Flint & Gould, pl. 3, fig. 1.
- 1975 ?*Dicroidium*; Flint & Gould, pl. 3, fig. 10.
- 1975 *Dicroidium odontopteroides* (Morris) Gothan; Flint & Gould, pl. 3, fig. 11.
- 1977 *Dicroidium odontopteroides* (Morris) Gothan 1912; Retallack, microfiche frames H23–I8.
- 1977 *Dicroidium lancifolium* (Morris) Gothan 1912; Retallack, microfiche frames H14–H18.
- 1977 *Dicroidium pinnus-distantibus* (Kurtz) Frenguelli 1943; Retallack, microfiche frame I9.
- 1977 *Dicroidium prolongatum* (Mendendez)[sic] Retallack, microfiche frame I10.
- 1982 *Dicroidium odontopteroides* (Morris) Gothan var. *moltenense* Retallack; Holmes, fig. 4A–Da, 4E, 4F.
- 1982 *Dicroidium prolungatum* (Menendez) Retallack 1977; Holmes, fig. 3F, 3G.
- 1983 Aberrants *Dicroidium odontopteroides* subsp. *orbiculoides* Anderson & Anderson, pl. 71, figs 1–16.
- 1983 *Dicroidium* sp. (hybrid); Anderson & Anderson, pl. 87, fig. 3.
- 1983 *Dicroidium coriaceum* forma *crassinervis* [sic] Anderson & Anderson, pl. 52, figs 1–36.
- 1983 *Dicroidium crassinervis* forma *crassinervis* Anderson & Anderson, pl. 31, figs 31–45, 48, pl. 42, figs 36–45, 50, pl. 55, figs 20, 21, pl. 85, figs 8–32, pl. 86, figs 1–3, 5–10.
- 1983 *Dicroidium crassinervis* forma *obtusifolium* Anderson & Anderson, pl. 31, figs 15–23, pl. 42, figs 1–14, 47.
- 1983 *Dicroidium crassinervis* forma *sanifolium* Anderson & Anderson, pl. 53, figs 1, 2.
- 1983 *Dicroidium crassinervis* forma *steltznerianum* Anderson & Anderson, pl. 31, figs 7–14, pl. 56, figs 1–2, pl. 68, figs 2, 4–8, pl. 85, figs 6–7.
- 1983 *Dicroidium crassinervis* forma *trilobitum* Anderson & Anderson, pl. 68, figs 26–30, pl. 85, figs 35, 38–40.
- 1983 *Dicroidium dubium* subsp. *dubium* Anderson & Anderson, pl. 33, figs 1–18, 33, 34, pl. 58, figs 1–19.
- 1983 *Dicroidium dubium* subsp. *tasmaniense* Anderson & Anderson, pl. 44, figs 1–6.
- 1983 *Dicroidium elongatum* forma *rotundipinnulum* Anderson & Anderson, pl. 48, figs 1–8, pl. 73, fig. 17.
- 1983 *Dicroidium elongatum* forma *spinifolium* Anderson & Anderson, pl. 47, figs 24, 27, 28.
- 1983 *Dicroidium odontopteroides* forma *koningifolium* Anderson & Anderson, pl. 66, figs 16–26, 29, 30.
- 1983 *Dicroidium odontopteroides* forma *odontopteroides* Anderson & Anderson, pl. 32, 1–31, pl. 43, figs 1–23, pl. 54, figs 1–16, pl. 57, figs 1–21, pl. 66, figs 1–15, 27, 28, pl. 78, fig. 8, pl. 87, figs 1, 2, pl. 88, fig. 1.
- 1983 *Dicroidium odontopteroides* subsp. *hlatimbifolium* Anderson & Anderson, pl. 39, figs 1–9.
- 1983 *Dicroidium odontopteroides* subsp. *lineatum* Anderson & Anderson, pl. 64, figs 7–29, pl. 65, figs 1–8, 10–19, pl. 78, figs 9–12, pl. 79, figs 1–9, pl. 87, fig. 6.
- 1983 *Dicroidium odontopteroides* subsp. *orbiculoides* Anderson & Anderson, pl. 31, figs 24–30, 46, pl. 42, figs 15–35, 46, 49, pl. 55, figs 5–19, pl. 56, figs 3–31, pl. 64, figs 1–6, pl. 68, figs 9–25, pl. 69, figs 1–13, pl. 78, figs 1–7, pl. 87, fig. 4, pl. 88, fig. 2.
- 1983 Hybrids *D. odontopteroides* subsp. *orbiculoides* X *D. elongatum* forma *elongatum*; Anderson & Anderson, pl. 70, figs 1–13.
- 1992 *Dicroidium odontopteroides*; Taylor et al., fig. 1.
- 1992 *Dicroidium lancifolium*; Taylor et al., fig. 2.
- 1998 *Dicroidium odontopteroides* (Morris) Gothan; Gnaedinger & Herbst, pl. 2, figs a–h.
- 2001 *Dicroidium odontopteroides* (Morris) Gothan; Gnaedinger & Herbst, fig. 3A–J.
- 2001 *Dicroidium lancifolium* (Morris) Gothan; Gnaedinger & Herbst, fig. 3K–N.
- 2005a “*Dicroidium odontopteroides* complex”; Holmes & Anderson, figs 3A–E, 4A–G, 5A–D, 6A, 7A–C, 8A, 9A–C, 10A, 10D, 10E.
- 2005a “*Dicroidium lineatum* complex”; Holmes & Anderson, figs 10B, 10C, 11A, 11B, 11D.
- 2006 *Dicroidium odontopteroides* var. *obtusifolium* Johnston 1885; Ottone, fig. 1E1.
- 2007 *Dicroidium odontopteroides*; Bomfleur et al., fig. 2(1, 2).
- 2010 *Dicroidium odontopteroides* (Morris) Gothan; Bomfleur & Kerp, pls 3–5.
- 2010 *Dicroidium crassinervis* (Geinitz) Anderson et Anderson; Bomfleur & Kerp, pls 6–8.
- 2010 *Dicroidium dubium* (Feistmantel) Gothan; Bomfleur & Kerp, pl. 10, figs 1, 2, pls 11, 12.
- 2010 *Dicroidium* sp. A; Bomfleur & Kerp, pl. 10, figs 6–8, pls 14, 15.
- 2011 *Dicroidium odontopteroides* var. *moltenense* Retallack 1977; Ottone et al., fig. 3.2.
- 2011 *Dicroidium odontopteroides*; Escapa et al., fig. 7a, 7d.
- 2011b *Dicroidium odontopteroides*; Bomfleur et al., figs 3h, 4d.
- 2013 *Dicroidium odontopteroides* (Morris) Gothan; Chatterjee et al., fig. 3J, 3K.

Type material. Morris in Strzelecki (1845, p. 249, pl. 6, figs 2–4) assigned an unidentified number of specimens to his species *Pecopteris*

odontopteroides from Upper Triassic coal measures of the Tasmania Basin. These came from coal mining operations at Jerusalem, Tasmania, located near the Coal River and approximately halfway between Jericho and Richmond (Strzelecki 1845, p. 127; Johnston 1888, map 1; Townrow 1966; Retallack 1981, p. 185). Morris's specimens are held by the Natural History Museum, London, but those attributed to *P. odontopteroides* were unable to be located by Townrow (1957, p. 35).

The specimen figured by Strzelecki (1845, pl. 6, fig. 3) was designated as the lectotype by Townrow (1957), who in 1966 proposed a neotype (University of Tasmania specimen 81932) from the same general area as Strzelecki's site (Jerusalem). His figured specimen (Townrow 1966, pl. 1, fig. 1) is a poor representative of the species, and Retallack (1977) did not regard the nominated neotype as useful. An epitype (Fig. 6) is designated below.

Emended diagnosis. Frond unipinnatifid to unipinnate. Rachis commonly bifurcating once. Pinnules opposite to alternate, branching at 50°–80° but less in apical portion of frond. Pinnule bases slightly decurrent to moderately constricted. Pinnules lanceolate to rhomboidal or almost semi-circular commonly toward base of rachis. Pinnule apices commonly obtuse but may be acute, slightly retuse or irregular. Margins commonly entire but may be slightly sinuate or slightly crenate. Veins branching acutely from rachis, commonly forking at least once. Venation chiefly arises from a single vascular branch off the rachis but, particularly in smaller pinnules, many veins commonly extending independently from the rachis. Midrib absent in shorter pinnules but prominent in longer pinnules.

Material. GSQF304: Colinton, north of Esk, Queensland; Esk Formation, Esk Trough (Anisian). Figured by Jack & Etheridge (1892, pl. 18, fig. 10) as *Thinnfeldia media* Tenison-Woods 1884.

GSQF329 (Fig. 5E) and counterpart GSQF337, UQF20617: Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen GSQF337 was figured by Shirley (1898, p. 21, pl. 6, fig. 2) and attributed to his variety *Thinnfeldia indica* var. *aquilina*. The long basal pinnae in Shirley's line-drawn figure are not attached to the frond.

GSQF332, GSQF333, GSQF336: Petrie's Quarry (west side of Bartley's Hill), Albion, Brisbane, Queensland; Aspley Formation, Kholo Subgroup, Ipswich Basin (Carnian–lowermost Norian). GSQF332 is the type specimen of Walkom's (1917a, pp. 23–24, pl. 3, fig. 4) species, *Thinnfeldia acuta*. GSQF333 was identified as *T. lancifolia* by Walkom (1917a, pp. 21–23). GSQF336 was figured by Shirley (1898, pl. 5, fig. 1) as *T. indica* var. *media* (variety erected by that author) and figured by Hill et al. (1965, pl. 4, fig. 3) as *Dicroidium odontopteroides*.

GSQF611 (part & counterpart), GSQF14502: Nundah Colliery, Brisbane, Queensland; Aspley Formation, Kholo Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen GSQF611 was identified by Walkom (1917a) as *Thinnfeldia odontopteroides*.

QMF42490, UQF64435, UQF64442a/b (part & counterpart, epitype: Fig. 6A, B), UQF64445, UQF64480, UQF64486, UQF64494, UQF64496a/b (part & counterpart; Fig. 5D), UQF64498 (Fig. 5F), UQF64500, UQF64539: Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen UQF64442a/b is designated herein as the epitype supporting the lectotype (Strzelecki 1845, pl. 6, fig. 3) and the neotype (Townrow 1966, pl. 1, fig. 1).

QMF57839–QMF57841, QMF57842 (Fig. 5A–C), QMF57846–QMF57848, QMF57854, QMF57857–QMF57863, QMF57866, QMF57867, QMF57875a, QMF57875b (SEM stub: Fig. 7A–C), QMF57875c (SEM stub), QMF57875d (SEM stub), QMF57875e (SEM stub: Fig. 7D), QMF57875f (TLM slide: Fig. 8C), QMF57875g (TLM slide: Fig. 8A, B), QMF57875h (TLM slide: Fig. 8D), QMF57875i (TLM slide: Fig. 8E, F), QMF57875j (TLM slide): Meandu Mine, Queensland; Tarong Basin (upper Carnian).

UQF23631: Ottaba, north of Esk, Queensland; Esk Formation, Esk Trough (Anisian).

UQF59910, UQF59911: former State Quarry, Slacks Creek, Brisbane, Queensland; Tingalpa Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: Purdy & Cranfield 2013, Pattemore et al. 2015b, tab. 2).

Occurrence. See Tab. 1.

Discussion. *Dicroidium odontopteroides* has been recorded with organic connection to the

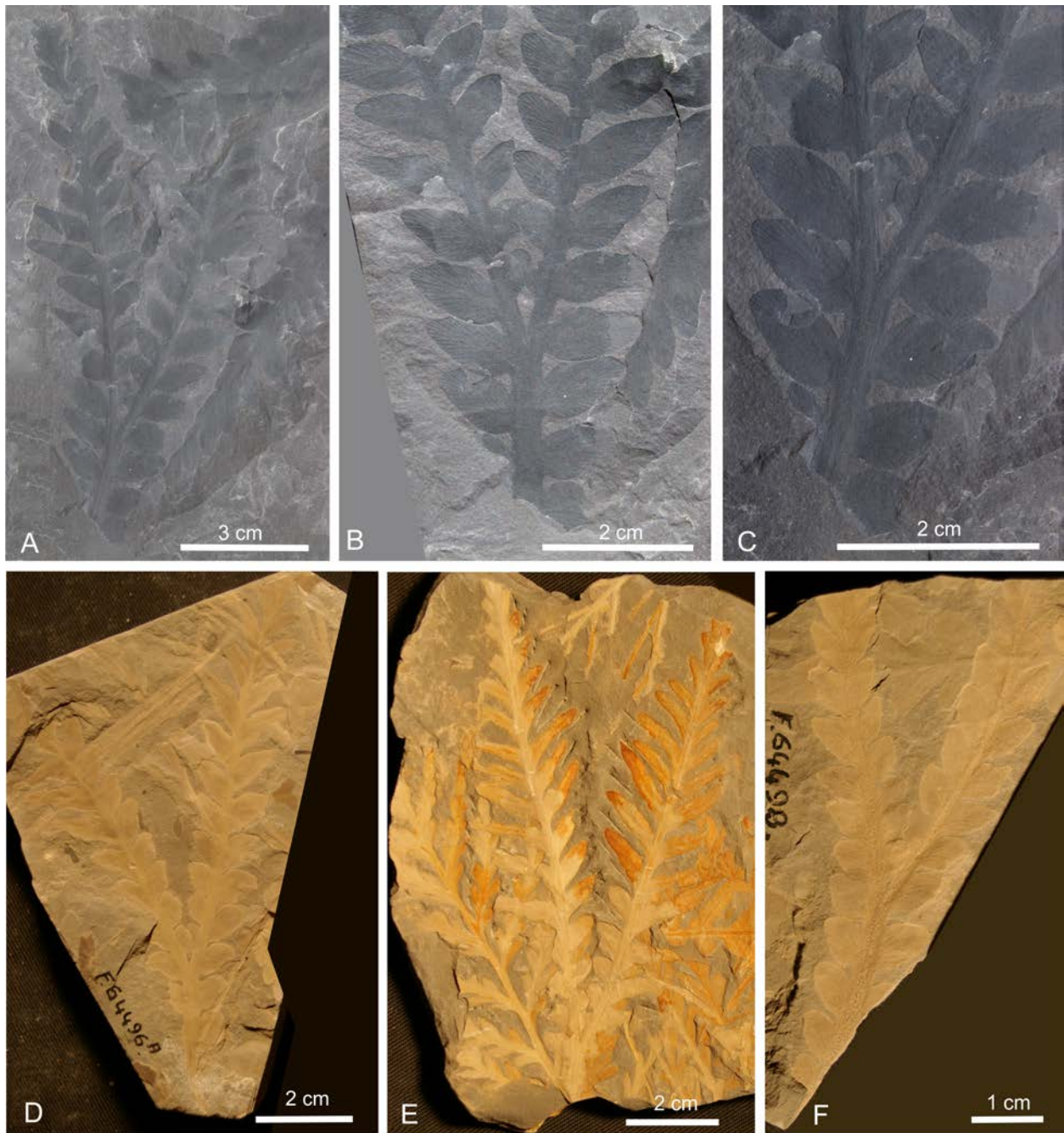


Fig. 5. A–F: *Dicroidium odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 emend. nov. **A–C:** QMF57842; Meandu Mine, Queensland; Tarong Basin (upper Carnian). **B, C:** optical enlargements of A. **D:** UQF64496a; Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). **E:** GSQF329; Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); the counterpart was figured by Shirley (1898, p. 21, pl. 6, fig. 2) as *Thinnfeldia indica* var. *aquilina*. **F:** UQF64498; Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian)

female fructification *Umkomasia uniramia* Axsmith et al. 2000. The fructification has a whorled structure (Axsmith et al. 2000) that differs from the type and other species of the genus (Pattemore et al. 2015a, Pattemore 2016). The frond *Zuberia feistmantelii* probably belonged to the same plant as the female and male fructifications, *U. geminata* and *Pteruchus dubius*, respectively (Tab. 1), based on their abundance at the same locality (Pattemore & Rigby 2005,

Pattemore 2016). The structural differences between *U. uniramia* and *U. geminata* suggest that their host plants were at least generically distinct (see *Zuberia* below).

A large number of species, subspecies, forma, and varieties have been proposed for representatives of *Dicroidium* with unipinnate fronds because of morphological variation (e.g. Retallack 1977, Anderson & Anderson 1983, Gnaedinger & Herbst 1998, 2001). The



Fig. 6. A, B: *Dicroidium odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 emend. nov., UQF64442a/b (part & counterpart; epitype designated herein); Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). A: UQF64442b. B: UQF64442a, optical enlargement of lower portion

specimens examined herein show considerable variation in pinnule shape and size, both within individual fronds and among specimens. Thus, the utility in systematically categorising leaf variation below the level of species is questionable and is not adopted in the present study.

Anderson & Anderson (1983) included numerous specimens that resemble *Dicroidium odontopteroides* in many other species. For example, several figured specimens that were assigned to *D. elongata* (see above synonymy) bear no resemblance to the type specimen of that species, which is unipinnate, univeined and has long and very narrow pinnules (see *Xylopteris elongata* below). As noted for other species herein, Anderson & Anderson (1983) adopted a greatly expanded set of diagnostic characters for some species (chiefly, *D. dubium* and *X. elongata*) that has exaggerated the perception of a continuum of characters among species. If those incorrectly assigned specimens are discounted, then limited evidence remains

(aberrant and very small specimens) to support the concept of a morphological continuum and of hybridisation among species.

Anderson & Anderson (2003, p. 22) proposed that the subspecies identified by Anderson & Anderson (1983) should instead be recognised as species. That proposal is somewhat closer to the approach of Retallack (1977), but quantitative species separation in unipinnate representatives of *Dicroidium* by that author and Anderson & Anderson (2003) is not well defined. Jacob & Jacob (1950) suggested that epidermal characters implied that there were more *Dicroidium* species than is suggested by megascopic frond morphology. However, that suggestion is doubtful, being chiefly reliant upon characters affected by environmental conditions (Barclay et al. 2007, tab. 1).

Tenison-Woods (1884) erected *Thinnfeldia media* based on a specimen from the Lower–Middle Triassic Napperby Formation (Totterdell et al. 2009, fig. 2), Gunnedah Basin, Dubbo,

New South Wales. The species is regarded herein as synonymous with Szajnocha's (1888) *T. lancifolium*; note that Strzelecki (1845, p. xvi) proposed a variety with that name but Szajnocha has priority at species level (ICN, Article 11.2). Despite this, the figured type material of both *T. lancifolium* and *T. media* are probably within the range of natural pinule variation of *Dicroidium odontopteroides*.

Walkom (1928) erected the unipinnate species *Thinnfeldia eskense* based on plant impressions from three sites in the Anisian Esk Trough to the north of Esk, Queensland (Fig. 2). One of his specimens, re-examined herein (UQF1733, lectotype: Retallack 1977), bears pinnules that are ca 70 mm long. Jacob & Jacob's (1950) recombination of the species with *Dicroidium* was supported by Retallack (1977) but neither by Anderson & Anderson (1983) nor by Holmes and Anderson (2005b). The latter authors included Walkom's figured specimens in *Kurtzia* Frenguelli 1942. Pinnule bases are decurrent to moderately constricted as was diagnosed by Walkom (1928). His specimen resembles those figured by Anderson & Anderson (1983) as *D. odontopteroides* f. *koningifolium* from the Carnian of South Africa. Retallack et al. (1977) noted the resemblance of *D. eskense* to other unipinnate species with long pinnules. Those authors identified constricted pinnule bases as a character distinguishing the species (from other unipinnate species), but that character is not consistently represented in the type specimen; the few pinnule bases that apparently show strong constriction are damaged. Thus, the character is of dubious specific (and generic) import. Hill et al. (1965) figured a specimen (UQF1990: re-examined herein) from the Anisian Esk Trough (from near Wivenhoe Hill, Queensland) as "*Thinnfeldia*" *eskense* which has moderately constricted pinnule bases on the acroscopic margin.

Similarly, Dun in Walkom (1925) erected *Thinnfeldia narrabeenense* with unipinnate specimens bearing long pinnules from the Newport Formation (Olenekian: Metcalfe et al. 2015), Narrabeen Group, at Turimetta Head, Sydney Basin (Retallack 1977). The species was recombined with *Dicroidium* by Jacob & Jacob (1950). Anderson & Anderson (1983, p. 107) regarded the species as unipinnate to bipinnate, but that was apparently based on the erroneous inclusion of a bipinnate specimen identified as *T. feistmantelii* by Walkom

(1925, pl. 25, fig. 1). The basis for distinguishing *D. eskense*, *D. odontopteroides*, *D. narrabeenense*, and *D. lancifolium* is limited to pinnule length. The cuticle in those species and that of *D. dubium* (Walkom 1917a, Jacob & Jacob 1950, Townrow 1957, Retallack 1977, Anderson & Anderson 1983, Boucher et al. 1993, Bomfleur & Kerp 2010 and herein) is indistinguishable if allowance is made for possible environmental influence (based on Barclay et al. 2007, tab. 1). Anderson & Anderson (1983) adopted *D. odontopteroides* for unipinnate fronds, including some with very long pinnules (up to 140 mm: *D. odontopteroides* f. *koningifolium*). Their approach (at species level) is useful because the observed size and shape variation in pinnules in much reported material results in a somewhat arbitrary demarcation (i.e. overlap) among unipinnate species.

When Geinitz (1876, pp. 4–5, pl. 1, figs 10–16) erected the unipinnatisect to unipinnate species *Thinnfeldia crassinervis*, he was apparently unaware of Morris's *Pecopteris odontopteroides* (in Strzelecki 1845) and the contribution by Carruthers (1872). Supported herein is Feistmantel's (1889) and Retallack's (1977) inclusion of Geinitz's specimens in *Dicroidium odontopteroides* (or its earlier synonym).

Pecopteris stelzneriana Geinitz 1876 has been variously included in *Dicroidium* (by Frenguelli 1941), *Johnstonia* Walkom 1924b (by Frenguelli 1943 and Retallack 1977) and was considered a junior synonym of *D. crassinervis* (by Anderson & Anderson 1983). The figures and description by Geinitz (1876, p. 6, pl. 2, figs 7, 8) indicate it is a unipinnate frond with discrete pinnules; thus the species is a junior synonym of *D. odontopteroides*. Similarly, Johnston's (1888) *Thinnfeldia trilobita* is based on a unipinnatisect specimen. The species was recombined with *Dicroidium* (by Antevs 1914), *Johnstonia* (by Walkom 1924b), and was considered to be a junior synonym of *D. crassinervis* (by Anderson & Anderson 1983). However, being unipinnatisect it is regarded herein as a junior synonym of *D. odontopteroides*. Unipinnate fragments assigned to *T. trilobita* by Feistmantel (1889, pl. 2, fig. 2) may be the apical portions of adjacent pinnae belonging to *D. superbum* (discussed below).

Jones & de Jersey (1947a, pl. 2, figs 1, 4) assigned two specimens to *Johnstonia* that reportedly include a second rachis bifurcation

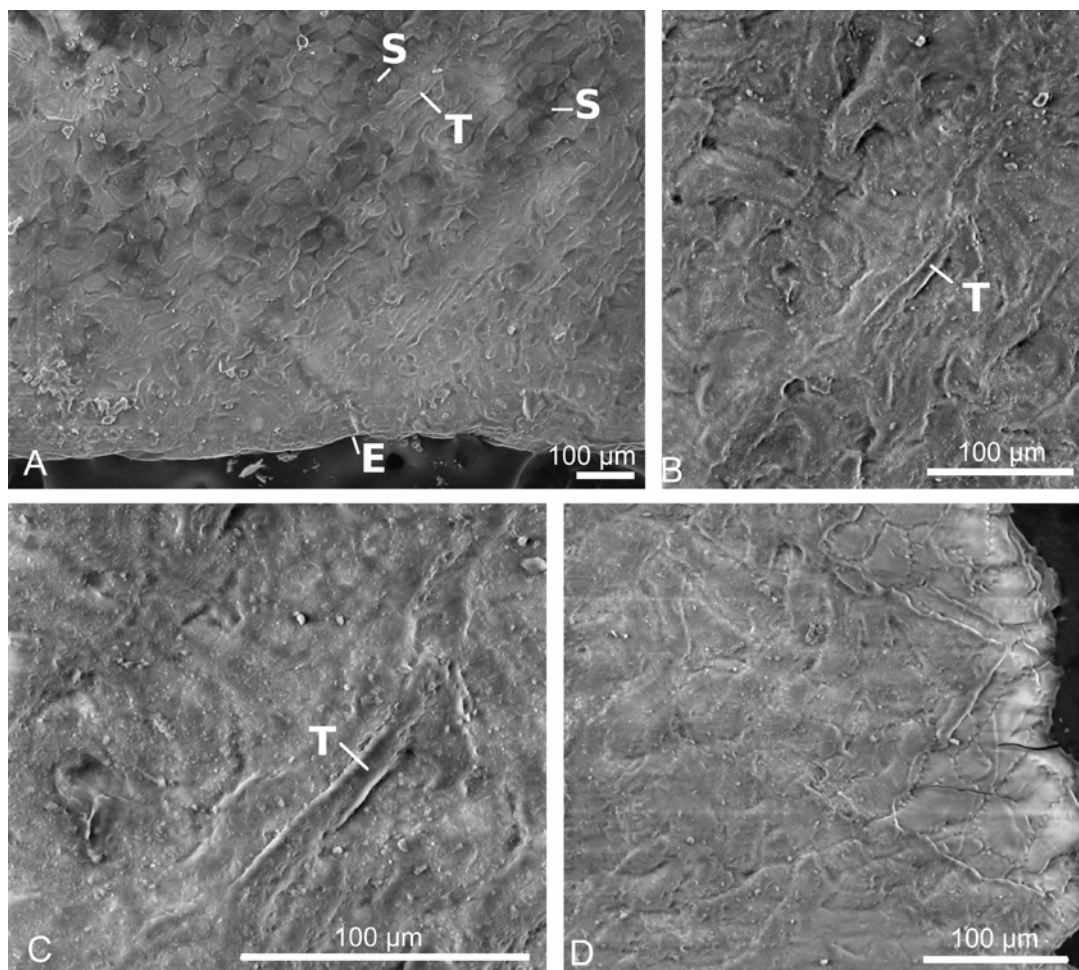


Fig. 7. A–D: *Dicroidium odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 emend. nov.; Meandu Mine, Queensland; Tarong Basin (upper Carnian). A–C: QMF58785b (SEM stub). D: QMF58785e (SEM stub), showing partially removed epicellular layer. Key: T=trichome (or wax crystal, see text); S=stomatal apparatus; E=natural pinnule edge. Only stomata located near “T” are marked

(UQF2248, UQF8110: both re-examined herein). Specimen UQF8110 is a small vegetative fragment, insufficient for generic identification. Specimen UQF2248 resembles *Dicroidium odontopteroides* but the rachis is missing at both points of the presumed bifurcation. The lamina in the vicinity of the uppermost leaf dichotomy does suggest the rachis, if present, would bifurcate at that point. The specimen’s collection location is doubtful, being somewhere along the Kyogle railway line but within Queensland. A possible location several kilometres north of Rathdowney was suggested by Jones & de Jersey (1947a) but without explanation; the records of the Queensland Museum do not identify that location. Lower Jurassic Gatton Sandstone (Clarence-Moreton Basin) outcrops in the Rathdowney area; thus, the specified location is probably incorrect. The railway line extends northward into southern Brisbane, where Upper Triassic strata of the Ipswich Basin are known. Flint & Gould (1975,

pl. 3, fig. 10), Anderson & Anderson (1983, pl. 71, figs 6–16) and Holmes & Anderson (2005a, figs 5A–D, 6A) illustrated fronds resembling *Dicroidium odontopteroides* that have more than one rachis bifurcation. Frenguelli (1950, figs 1A, 1B, 2) erected the monotypic genus *Tetraptilon* with *T. heteromerum* for such fronds. Fronds with more than one rachis bifurcation are apparently restricted to specimens that resemble *D. odontopteroides*. A frond resembling *D. dubium* (Holmes & Anderson 2005a, fig. 6B) is a possible exception.

Bomfleur & Kerp (2010) assigned unipinnate specimens to *Dicroidium dubium* from the Upper Triassic Section Peak Formation at Timber Peak, North Victoria Land, Antarctica. Their distinction of *Dicroidium* species was largely based on venation and cuticle. They suggested that *D. odontopteroides* has “odontopteroid” venation whereas *D. dubium* has “alethopteroid” venation (terms defined by Boureau & Doubringer 1975, pp. 11–16). As shown herein

and in many other unipinnate specimens (Lele 1962, Retallack 1977, Anderson & Anderson 1983) pinnule venation varies greatly with pinnule length: the midrib becomes more strongly developed and prominent with increasing pinnule length. Pinnules without distinct midribs and those with strongly developed midribs occur, in many cases, on the same frond (e.g. Fig. 5 herein). Although their megascopic material was poor, Bomfleur & Kerp (2010) figured some of the best-preserved cuticle that has been extracted from representatives of the genus. Their detailed analysis of the cuticle may be useful for palaeoclimatic interpretation and possibly in understanding the host plants'

position in the environment; however, many of their recorded epidermal characters have limited or no taxonomic value (Barclay et al. 2007, tab. 1). Permineralised specimens from Fremouw Peak in the Central Transantarctic Mountains were attributed to *Dicroidium* by Pigg & Taylor (1987, fig. 1) but are insufficient for specific identification; they may belong to *D. odontopteroides* or perhaps represent adjacent pinnae of *D. dubium*.

Cuticular specimens were prepared herein using material from the Tarong Basin. Cells and stomata on pinnules are generally not aligned, whereas those covering veins and the rachis are commonly aligned. Stomata are stephanocytic

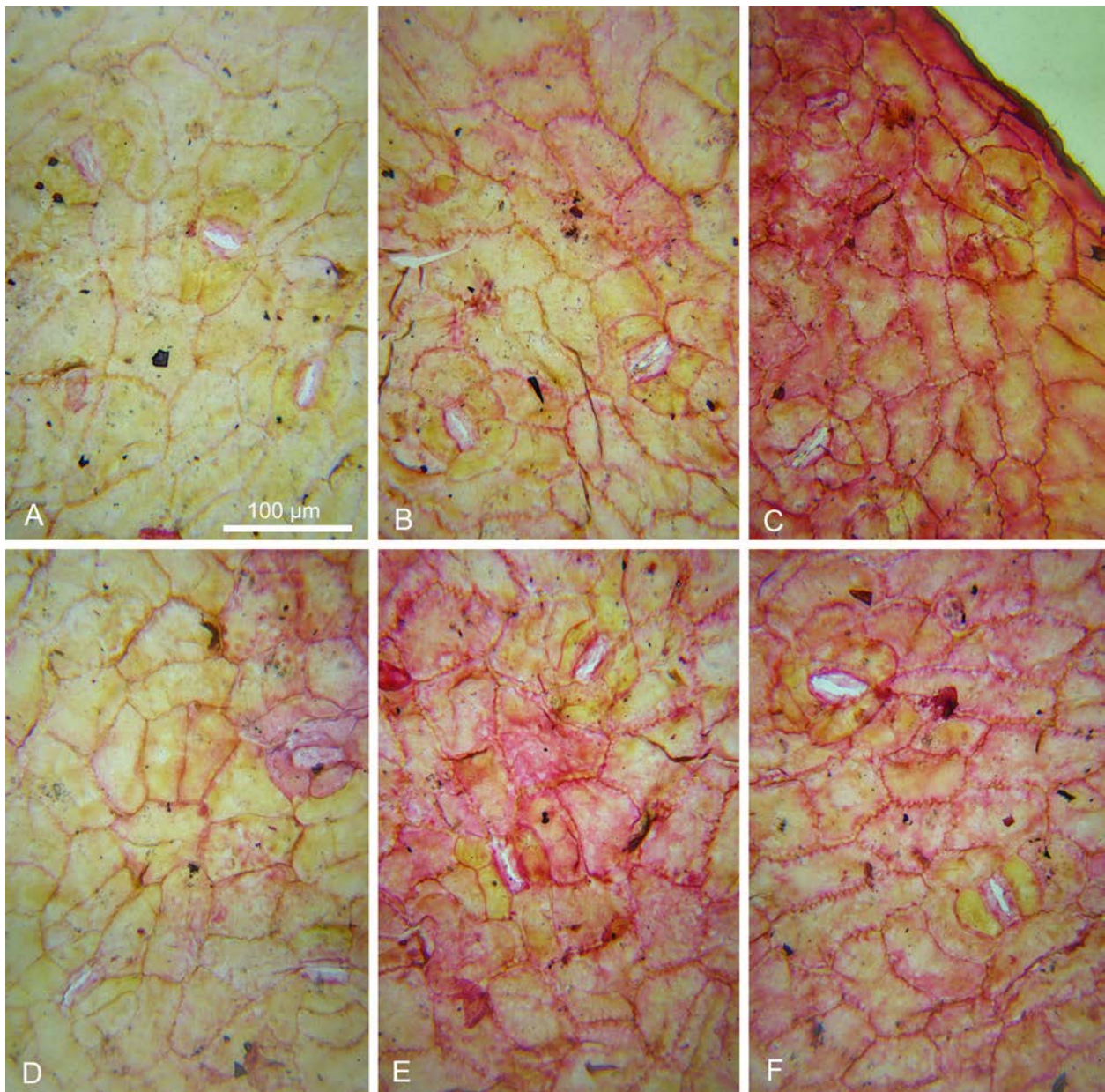


Fig. 8. A–F: *Dicroidium odontopteroides* (Morris in Strzelecki 1845) Gothan 1912 emend. nov.; Meandu Mine, Queensland; Tarong Basin (upper Carnian). A, B: QMF58785g (TLM slide). C: QMF58785f (TLM slide), showing natural pinnule edge. D: QMF58785h (TLM slide). E, F: QMF58785i (TLM slide). Scale: A–F all same scale as shown for A

(Barclay et al. 2007, fig. 3) and epidermal characters are consistent with those recorded by Townrow (1957) and Bomfleur & Kerp (2010), albeit with minor exceptions as noted below. Safranin stain generally coloured one surface of an individual pinnule more strongly than the other, suggesting a difference in cuticular thickness (staining duration: ca 15 minutes). The more strongly coloured surface had a tendency to curl during drying, resulting in greater fragmentation. Stomatal density was similar on both surfaces, varying from 15–35 stomata/mm² and being at the lower end of that range over veins and the rachis. Townrow (1957) and Anderson & Anderson (1983) reported stomatal density to be greater on the lower leaf surface. By contrast, Bomfleur & Kerp (2010) recorded greatest density on the leaf's upper surface. Environmental factors exert a strong influence on stomatal density, and it is chiefly used for estimating carbon dioxide levels in the palaeo-atmosphere (Royer 2001, Barclay et al. 2007, p. 46). Stomata were generally more difficult to identify in SEM images because of the tendency for epicellular cutin to obscure much of the apparatus (Fig. 7).

Papillae have been reported as a common epidermal character in representatives of *Dicroidium odontopteroides* (Townrow 1957, Bomfleur & Kerp 2010). In TLM images papillae are inferred from dark circular shading within cell walls (e.g. Bomfleur & Kerp 2010, pl. 5, figs 1, 2) caused by differential light absorption; however, little structural detail is available via that technique. The leaf surface (Fig. 7) has distinctly convex epidermal cells formed from an epicellular layer of cutin (or other epidermal polymer: see Boom et al. 2005, Gupta et al. 2006 and Yeats & Rose 2013). The cutin is irregularly domed, with one or more peaks in the outline of each cell. A tear in one specimen (Fig. 7D), partially removing the epicellular layer, reveals the underlying periclinal cell wall to be smooth and flat. Crenulation in the anticlinal walls, also visible, is commonly observed in TLM images (e.g. Townrow 1957, text-fig. 5, Bomfleur & Kerp 2010, pl. 5, Fig. 8 herein). The degree of convexity in the epicellular layer appears to diminish toward pinnule margins but the surface otherwise remains rough (Fig. 7A). Convex and rough epidermal cells may indicate that the host plant had adapted to a humid wetland environment (Neinhuis & Barthlott 1997).

Trichome bases were considered rare in the species by Townrow (1957) and Boucher et al. (1993). They were also identified by Anderson & Anderson (1983) and Bomfleur & Kerp (2010) but their position (relative to other features) and frequency was not recorded. Trichome bases were not observed using TLM in the present study. However, a trichome (or epidermal wax crystal: Yeats & Rose 2013, fig. 1A) was identified in a SEM image (Fig. 7A–C: 140 µm long; 17 µm wide basally; 12 µm wide apically). It has a (?sub)circular base and is bent just above the base (probably a preservational effect), the remainder being adpressed to the leaf surface. Its basal shape and size are consistent with the trichome base figured by Bomfleur & Kerp (2010, pl. 5, fig. 10). It is located ca 0.6 mm from a pinnule margin and adjacent to a stoma (Fig. 7A) but its placement vis-à-vis the upper or lower side of the frond, is unknown. The narrowly conical structure appears to have been solid (or possibly now a flattened tube: Fig. 7C). Its size and shape resembles other figured trichomes (e.g. Carpenter 2006, fig. 9) or possibly an epidermal wax crystal structure (e.g. Albersheim et al. 2010, fig. 1.29C) but the latter are apparently unknown in the fossil record (Bargel et al. 2004, p. 174). The morphology and placement of trichomes (or other epicuticular structure) may be useful taxonomically (Barclay et al. 2007).

Dicroidium dubium

(Feistmantel 1878) Gothan 1912

Figs 9, 10

Synonymy. The following synonymy list is limited to figured specimens that pertain to the discussion herein. See also Retallack's (1977) synonymy.

- 1878 *Gleichenia dubia* Feistmantel, p. 106, pl. 15, fig. 8. [basionym]
- 1895 *Thinnfeldia polymorpha* Johnston, p. 62, fig. 16.
- 1912 *Dicroidium dubium* (Feistm.) Gothan, pl. 15, fig. 3.
- 1927 *Pachypteris incisa* (Saporta); du Toit, p. 344, text-fig. 8A.
- 1928 *Thinnfeldia talbragarensis* Walkom; Walkom, p. 460, pl. 27, fig. 1.
- 1943 *Dicroidiopsis incisa* Du Toit; Frenguelli, fig. 22.
- 1950 *Dicroidium australis* Jacob & Jacob, pp. 119–122, figs 20–24.
- 1950 *Dicroidium walkomi* Jacob & Jacob, pp. 122–125, figs 25–27.
- 1977 *Dicroidium dubium* var. *australe* (Jacob & Jacob) Retallack, microfiche frame H8.

- 1977 *Dicroidium dubium* var. *dubium* (Feistmantel) Gothan 1912; Retallack, microfiche frames H7–H10.
- 1977 *Dicroidium dubium* var. *tasmaniense* (Anderson & Anderson) Retallack (in Retallack, Gould & Runnegar 1977); Retallack, microfiche frames H7–H10.
- 1977 *Dicroidium incisum* (Frenguelli) Anderson & Anderson 1970; Retallack, microfiche frame H13.
- 1983 *Dicroidium dubium* subsp. *dubium*; Anderson & Anderson, pl. 33, figs 19–32, 35–37, pl. 53, figs 16–20, 27, pl. 58, figs 20–24, pl. 59, figs 1–11, pl. 65, fig. 9.
- 1983 *Dicroidium dubium* subsp. *tasmaniense*; Anderson & Anderson, pl. 44, figs 7–16, 21, 22.
- 1990 *Dicroidium fremouwensis* Pigg, pp. 130–137, fig. 1, pls 1–5.
- 1993 *Dicroidium dubium* (Feistmantel 1878) Gothan 1912; Boucher et al., p. 45, figs. 9–11.
- 1998 *Dicroidium dubium* (Feistmantel) Gothan; Gnaedinger & Herbst, pl. 1, figs a, b, d.
- 2005a “*Dicroidium dubium* complex”; Holmes & Anderson, figs 13A–C, 14A–C, 16A.
- 2011 *Dicroidium dubium*; Escapa et al., fig. 7e.

Type material. Holotype (MMF3047: Fig. 10 herein and line-drawn by Feistmantel 1878, pl. 15, fig. 8) by effective original designation [ICN, Article 9.1, Note 1]; held in the Palaeontology Collection of the Geological Survey of New South Wales (GSNSW), Londonderry, western Sydney. The specimen's collection site is uncertain but Feistmantel (1890, pp. 111–112, pl. 26, fig. 3) suggested that it is probably from Clarke's Hill, Sydney (Middle Triassic, Wianamatta Group, Sydney Basin: Retallack 1977, 1980a).

Diagnosis. See Feistmantel (1878, p. 106, 1890, pp. 111–112).

Material. GSQF1938: D'Aguilar Highway between Moore and Benarkin, Queensland; Esk Formation, Esk Trough (Anisian). Figured by Walkom (1928, pl. 27, fig. 1) as *Thinnfeldia talbragarensis* Walkom 1921.

QMF57856 (Fig. 9): Meandu Mine, near Nanango, Queensland; Tarong Basin (upper Carnian).

UQF20594: Sheep Station Creek, near Wivenhoe Hill, Queensland; Esk Formation, Esk Trough (Anisian).

UQF64476, UQF64482a/b, UQF64487, UQF64490, UQF64501, UQF64533B, UQF64720, UQF64728, UQF64733a/b: Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

UQF82585, UQF82599: Wivenhoe Hill,

Queensland; Esk Formation, Esk Trough (Anisian).

UQF82597: Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

Occurrence. See Tab. 1.

Description. Fronds bipinnatifid, >240 mm long (incomplete). Rachis 2–4 mm wide, bifurcating once. Pinnae opposite to alternate, <45 mm long, branching from rachis at >50° but less in distal portion of rachis. Pinnae commonly linear to lanceolate, crenate to deeply pinnatifid; but may have entire and rounded pinnules instead of pinnae locally (commonly near rachis bifurcation, between divided rachis segments and in distal portion of frond). Pinnae apices acute to rounded, bases constricted to decurrent. Veins extending from the pinna midrib at a very acute angle but curving away into pinna lobes, commonly bifurcating once or twice.

Discussion. As for *Dicroidium odontopteroides* (above), specimens attributed to *D. dubium*



Fig. 9. *Dicroidium dubium* (Feistmantel 1878) Gothan 1912, QMF57856; Meandu Mine, near Nanango, Queensland; Tarong Basin (upper Carnian)



Fig. 10. *Dicroidium dubium* (Feistmantel 1878) Gothan 1912, MMF3047 (Geological Survey of NSW), holotype; Clarke's Hill, Sydney (see text); Middle Triassic, Wianamatta Group, Sydney Basin. Line-drawn by Feistmantel (1878, pl. 15, fig. 8). Photograph provided by Drs Ian Percival and Yong Yi Zhen, Geological Survey of NSW

herein show considerable variation in pinnae/pinnule shape and size (Fig. 9). Given this variation, systematic categorisation below the rank of species is not adopted. Anderson & Anderson (1983) included many specimens in *D. dubium* that resemble various species of *Zuberia* (below). Most of those specimens were attributed to their subspecies *D. dubium* subsp. *switzifolium* and *D. dubium* subsp. *helvetifolium*. Bomfleur & Kerp (2010, p. 86) noted that Anderson & Anderson (1983) had thereby “considerably widened the species concept of *D. dubium*”. Furthermore, the broader specific circumscription extended not only to bipinnate specimens but also to unipinnate forms (see synonymy for *D. odontopteroides* above). A convincing argument may be made that the characters encompassing *D. dubium* are an extension of those pertaining to *D. odontopteroides* (i.e. long and strongly crenate pinnules: bipinnatifid); however, it is improbable that

those species are closely allied with species of *Zuberia* (bipinnate: Tab.1 and discussed below).

Holmes & Anderson (2005a) applied the epithet “complex” to the nomenclature of various *Dicroidium* species, suggesting a “continuum of variation of form” and further, “intergrading forms that link each complex”. Moreover, they argued that the necessity for typification under the ICN has “exacerbated the problem of dealing with variable fossil populations”. Although not clearly defined in a botanical sense, their use of the terms “complex” and “link” implies a genetic diversity and intermixing both within and among species (apropos of Anderson & Anderson 1983) that has a doubtful basis (Pattemore et al. 2015a, p. 698). There is no evidence to suggest that the “continuum” represents anything other than natural variability within individual species. Their “intergrading forms” are likewise doubtful. For example, a specimen figured by Holmes & Anderson (2005a, fig. 15A) was identified as “*D. dubium* complex” approaching “*D. zuberi* complex”. However, the frond is bipinnate and has at least one intercalary pinnule and thus is almost certainly a representative of *Zuberia* (possibly attributable to the type species of the genus: see Artabe 1990).

Jacob & Jacob (1950) did not explicitly identify *Dicroidium dubium* but they erected two bipinnatifid species, *D. australis* and *D. walkomi*; both were based on specimens from the Olenekian Newport Formation, Narabeen Group, Sydney Basin (Retallack 1977, Metcalfe et al. 2015). These species were putatively distinguished from *D. dubium* based on minor megascopic differences and cuticular characters that are known to be induced by environmental factors (Barclay et al. 2007, tab. 1). Boucher et al. (1993) figured cuticle belonging to *D. dubium* from the Carnian–Norian Falla Formation in the Queen Alexandria Range, Antarctica. No epidermal characters clearly distinguish *D. dubium* and *D. odontopteroides* if possible variations due to environmental conditions are considered (Barclay et al. 2007, tab. 1). Cuticular resemblance of unipinnate and bipinnatifid species of the genus was also noted by Retallack (1977). Specimen QMF57856 (Fig. 9), preserved as a carbonaceous compression, is the only specimen assigned to *D. dubium* from the Tarong Basin (upper Carnian); thus, no potentially destructive analysis was attempted.

Bomfleur & Kerp's (2010) epidermal description varies from that of Anderson & Anderson (1983) mainly in the presence or absence of trichomes. However, the megascopic specimens that were figured by Bomfleur & Kerp (2010, pl. 10, figs 1, 2) and attributed to *Dicroidium dubium* may belong to *D. odontopteroides*; they show no indication of being bipinnatifid. Anderson & Anderson's (1983) cuticular specimens (assigned to *D. dubium* subsp. *switzifolium*) were, as noted above, extracted from specimens that megascopically resemble *Zuberia*. Despite the differences between these reports and the doubtful attributions, the density of trichomes and papillae has little taxonomic value, whereas the type and position of trichomes and papillae in relation to other features (e.g. stomata) may be taxonomically significant (Barclay et al. 2007, tab. 1).

Jones & de Jersey (1947a, pp. 31–33, text-fig. 20, pl. 4, fig. 2, pl. 5, fig. 5) erected *Sphenopteris bergina* with specimens from Goodna, Queensland in the Ipswich Basin (UQF7485, UQF8456: re-examined herein). The specimens are insufficient for confident identification but possibly belong to *Dicroidium dubium*. Similarly, their specimen UQF8210 (re-examined herein) from Denmark Hill, Queensland (Blackstone Formation, Ipswich Basin), was assigned to *Thinnfeldia talbragarensis* Walkom 1921 but it is probably an indifferently preserved representative of *D. dubium* (Jones & de Jersey 1947a, text-fig. 10). Their other figured specimen that was attributed to *T. talbragarensis* (Jones & de Jersey 1947a, text-fig. 9) probably belongs to *D. odontopteroides* (UQF7062: re-examined herein).

Specimen UQF82593 from the former State Quarry, Slacks Creek (Tingalpa Formation, Ipswich Basin: Carnian–lowermost Norian), Brisbane, Queensland, has only a small portion of frond preserved around the rachis bifurcation. As noted above, variation in pinnae morphology is appreciable in that part of the frond; thus, the specimen is tentatively identified herein as *Dicroidium dubium*. The geology of the Slacks Creek area was discussed by Pattemore et al. (2015b, tab. 2) and references therein.

Extremely poorly preserved specimens from the Rhaetian of the South Island, New Zealand, were tentatively regarded as umkomasiacean by Pole & Raine (1994). The specimen

that they compared with *Dicroidium dubium* is known only in broad detail and was suggested to be a portion (40 mm long) of a bipinnate frond with a rachis bifurcation. However, their figured specimen is unconvincing (Pole & Raine 1994, fig. 2E), as is their tentative attribution of another specimen to *Umkomasia*.

Dicroidium superbum (Shirley 1898)

Townrow 1957 emend. nov.

Figs 11, 12

Synonymy.

- 1889 *Thinnfeldia* cf. *trilobita* Johnst.; Feistmantel, pl. 2, figs 2, 2a.
- 1898 *Sphenopteris superba* Shirley, pp. 18–19, pls 4, 8. [basionym]
- 1917a *Sphenopteris superba* Shirley; Walkom, pp. 27–28, pl. 8, fig. 3.
- 1917a *Stenopteris elongata* (Carruthers); Walkom, pl. 6, fig. 4a (only).
- 1926 *Stenopteris elongata* Carruthers; Chapman & Cookson, p. 170, pl. 23, figs 17, 18.
- 1927 *Stenopteris elongata* (Carr.); du Toit, text-fig. 12E, pl. 19, fig. 1.
- 1927 *Stenopteris densifolia* du Toit, p. 364, text-fig. 14A, 14B.
- 1947a *Stenopteris tripinnata* Jones & de Jersey, p. 30, text-fig. 19, pl. 4, fig. 1a, pl. 5, fig. 1.
- 1965 "*Stenopteris*" *tripinnata* Jones & de Jersey; Hill et al., pl. 5, fig. 8.
- 1973 *Xylopteris tripinnata*; Schopf, pl. 4, fig. 2f.
- 1977 *Dicroidium gouldii* Retallack, microfiche frame H12.
- 1977 *Dicroidium natalense* (Frenguelli) Retallack, microfiche frame H22.
- 1977 *Dicroidium superbum* (Shirley) Townrow 1957; Retallack, microfiche frame I12.
- 1977 *Xylopteris tripinnata* (Jones & de Jersey) Schopf 1973; Retallack, microfiche frames J15–J16.
- 1980 *Xylopteris spinifolia* (Tenison-Woods) Frenguelli 1943; Baldoni, fig. 2A–D, pl. 1, figs 5, 6.
- 1980a *Xylopteris tripinnata* (Jones & de Jersey) Frenguelli 1943; Retallack, fig. 12.12A–C.
- 1982 *Dicroidium natalense* (Frenguelli) Retallack 1977; Holmes, fig. 6A.
- 1982 *Dicroidium shirleyi* Holmes, pp. 11–13, figs 5e, 6B.
- 1982 *Dicroidium superbum* (Shirley) Townrow 1957; Holmes, fig. 6C.
- 1982 *Dicroidium spinifolium* (Tenison-Woods) Anderson & Anderson; Holmes, fig. 5D (only).
- 1983 *Dicroidium crassinervis* forma *sanifolium* Anderson & Anderson, pl. 53, figs 3–14.
- 1983 *Dicroidium elongatum* forma *rotundipinnulium* Anderson & Anderson, pl. 38, figs 19–28, pl. 67, figs 10–21, 23, 25, 26, pl. 73, figs 9–16, 18.
- 1983 *Dicroidium elongatum* forma *spinifolium* Anderson & Anderson, pl. 38, figs 29–31, pl. 40,

- figs 30, 31, pl. 46, figs 22–25, pl. 47, figs 8–23, 25, 26, pl. 51, figs 6–12, pl. 63, figs 26–28.
- 1983 *Dicroidium superbum* forma *bipinnatum* Anderson & Anderson, pl. 51, fig. 18.
- 1983 *Dicroidium superbum* forma *superbum* Anderson & Anderson, pl. 49, figs 15–19, pl. 86, fig. 11.
- 1983 *Dicroidium superbum* forma *townrovii* Anderson & Anderson, pl. 49, figs 1–14, pl. 50, figs 1–16, pl. 51, figs 14–17, 19–22, pl. 67, fig. 22.
- 1983 *Dicroidium superbum* subsp. *mazenodifolium* Anderson & Anderson, pl. 86, figs 12–21.
- 1983 Hybrids *Dicroidium elongatum* forma *remotipinnulium* Anderson & Anderson, pl. 63, figs 29–31.
- 2005 *Xylopteris spinifolia* (Tenison-Woods 1883) Frenguelli 1943; Pattemore & Rigby, fig. 5A.
- 2008 *Dicroidium elongatum*; Anderson et al., figs 1–7, 9, 10, 13.
- 2010 *Dicroidium spinifolium* (Tenison-Woods) Anderson et Anderson emend. Bomfleur & Kerp, pl. 10, figs 3–5.
- 2011 *Dicroidium spinifolium*; Escapa et al., fig. 7g.
- 2015a *Xylopteris tripinnata*; Pattemore et al., fig. 6D.

Type material. Lectotype (GSQF274: Fig. 11) by subsequent designation (Jones & de

Jersey 1947a, p. 31); collected from Denmark Hill, Ipswich (Blackstone Formation, Brassall Subgroup, Ipswich Basin: Carnian–lowermost Norian). The specimen was figured by Shirley (1898, pl. 8) and Walkom (1917a, pl. 8, fig. 3) as *Sphenopteris superba*. The following emended diagnosis is based on the type and other specimens as listed below.

Emended diagnosis. Frond bipinnate or bipinnatifid, >180 mm long. Rachis ca 3 mm wide (below bifurcation), bifurcating once. Pinnae opposite to alternate, up to 60 mm long, extending from rachis at <70° near rachis base but <45° in distal portion of frond. Pinnules opposite to alternate, inclined at <45°, commonly having variable morphology along individual pinnae. Pinnules near pinna base: commonly oblong to obovate but may be linear; broadest pinnules commonly having two or three rounded to pointed apical or lateral lobes; basioscopic margin commonly decurrent on pinna-rachis; acrosopic margin varying from basally unconstricted to strongly constricted. Pinnules near pinna apex: commonly linear or oblanceolate, lobed or unlobed. Venation extending from pinna midrib at very acute angle but curving away, commonly bifurcating at least once. Veins commonly arising as single vascular branch from pinna-rachis, but, in pinnules lacking strong basal constriction, some veins arising from pinna-rachis independently.

Material. GSQF274 (lectotype: Fig. 11), GSQF279, UQF6037, UQF8199: Denmark Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimens GSQF274 and GSQF279 were line-drawn by Shirley (1898, pl. 8 and pl. 4, respectively) as *Sphenopteris superba*. Walkom's (1917a, pl. 8, fig. 3) photographic figure of the lectotype is a poor and inaccurate representation of the specimen. Although he indicated that the figure was natural size, three original copies of Walkom's publication examined in the present study indicate that his figure is in fact two-thirds of actual size. Specimen UQF8199 (formerly S64 of Simmonds's collection) was figured by Walkom (1917a, pl. 6, fig. 4a) as *Stenopteris elongata* Carruthers 1872; this specimen is the holotype designated by Jones & de Jersey (1947a, p. 30, text-fig. 19, pl. 4, fig. 1a) for their species *S. tripinnata* and was figured as such by Hill et al. (1965, pl. 5, fig. 8). Specimen UQF6037 was attributed to



Fig. 11. *Dicroidium superbum* (Shirley 1898) Townrow 1957 emend. nov., GSQF274, lectotype; Denmark Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian)

that species by Jones & de Jersey (1947a, pl. 5, fig. 1).

MVP16100: Leigh Creek, South Australia; coal-bearing strata of the Leigh Creek Coal Measures (Anisian–Norian: Kwitko 1995). Figured by Chapman & Cookson (1926, pl. 23, fig. 17) as *Stenopteris elongata*.

QMF42591 (Fig. 12): Blackstone Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Figured by Pattemore & Rigby (2005, fig. 5A) as *Xylopteris spinifolia* (Tenison-Woods 1884) Frenguelli 1943.

QMF52275a/b (part and counterpart): Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Figured by Anderson et al. (2008) as *Dicroidium elongata* (Carruthers 1872) Archangelsky 1968.

UQF64422a/b (part and counterpart), UQF64427: Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

Occurrence. See Tab. 1.

Discussion. *Dicroidium superbum* is the most morphologically variable species of the genus, having pinnules that can be linear, oblanceolate, obovate, oblong, lobed or unlobed, and many forms are commonly represented on an individual pinna as can be seen in the type specimen (GSQF274: Fig. 11), specimen QMF42591 (Fig. 12), and others (e.g. UQF8199). Shirley's (1898, pl. 8) line-drawn figure of the lectotype is inaccurate and inadequately represents pinnule variability. As noted above, Walkom's (1917a, pl. 8, fig. 3) photographic figure of the specimen is also inaccurate and not useful for species identification. Thus, it is not surprising that the species has been widely misunderstood, as is indicated by the nomenclatural diversity identified in the above synonymy list.

Despite designating the lectotype of *Spheopteris superbum*, Jones & de Jersey's (1947a, pl. 5, fig. 2c) only figured specimen (UQF7709: re-examined herein) to be assigned to the species is probably the apical portion of a frond attributable to *Dicroidium dubium*. It seems probable that Jones & de Jersey (1947a) did not examine the lectotype of *D. superbum*, basing their view of the species on Shirley's (1898, pl. 8) inaccurate line drawing. Moreover, they

erected *Stenopteris tripinnata* with specimens (UQF6037, UQF8199: re-examined herein) that closely resemble the type specimen of *D. superbum*; those two species are undoubtedly synonymous. Anderson & Anderson (1983, p. 113) assigned the holotype of *S. tripinnata* (UQF8199) to their forma *D. superbum* f. *tripinnatum*. Specimen QMF42591 (Fig. 12) was attributed to *Xylopteris spinifolia* by Pattemore & Rigby (2005, fig. 5A) but it likewise resembles the type specimen of *D. superbum*.

Some figured specimens cited in the above synonymy have been regarded as representing hybridisation among species. Anderson & Anderson (1983) adopted a greatly expanded set of diagnostic characters encompassing *Xylopteris elongata* (identified by them as *Dicroidium elongata*). The type of that species

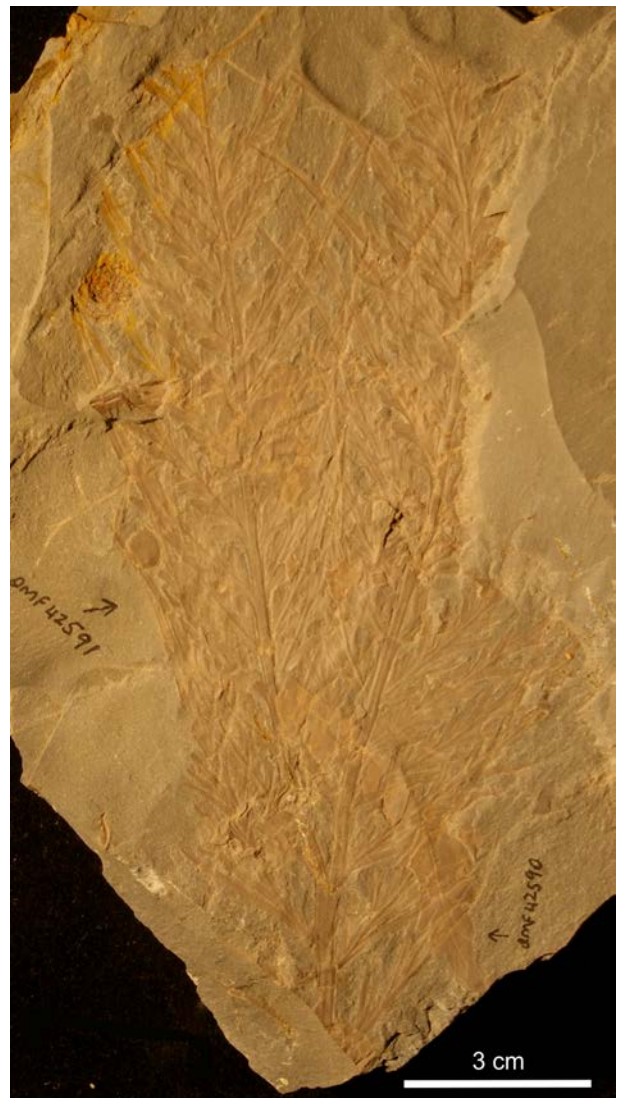


Fig. 12. *Dicroidium superbum* (Shirley 1898) Townrow 1957 emend. nov., QMF42591; Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); collected by R. Knezour

(discussed below) is unipinnate and univeined, but those authors included bipinnatifid and bipinnate fronds with lobed and multiveined pinnules. Many of the specimens they included in that species belong to *D. superbum*; most of these were assigned to their *D. elongata* f. *rotundipinnulium* and *D. elongata* f. *spinifolium* (see above synonymy). Their sensu lato concept of *X. elongata* exaggerates a putative continuum between *Dicroidium* and *Xylopteris*. Pinnules in fronds attributable to *D. superbum* may be linear but a morpho-continuum between that species and *X. elongata* has not been demonstrated: for example development of a rudimentary secondary vascular system in genuine representatives of *Xylopteris*. Also, it was suggested that such a continuum emerged via sympatric speciation (Anderson & Anderson 1983, p. 69), but that is an improbable scenario for the umkomasiaceans (Pattemore et al. 2015a, p. 698).

Townrow's (1957) diagnostic emendation of *Dicroidium superbum* added cuticular detail based on fronds that megascopically resemble *D. dubium*. Those specimens were assigned by Retallack (1977) to his species *D. townrovii*. Although Townrow (1957) described them as bipinnate, he also indicated that the pinna-rachis is "webbed", suggesting they are in fact bipinnatifid (e.g. Townrow 1957, fig. 7E); hence, they are provisionally attributed here to *D. dubium*. Similarly, Gnaedinger & Herbst (1998, fig. 7, pl. 2, fig. i) figured a specimen that they attributed to *D. townrovii* from the Carnian–Norian Laguna Colorada Formation in Patagonia, Argentina. The specimen is likewise probably assignable to *D. dubium* based on their line-drawing. The type specimen of *D. townrovii* (see Retallack 1977, micro-fiche frame I13) is poorly understood and has not been photographically figured.

The cuticle recorded by Bomfleur & Kerp (2010) from fronds they identified as *Dicroidium spinifolia* (Tenison-Woods 1884) Anderson & Anderson 1970 was based on indifferently preserved megascopic material from the Upper Triassic Section Peak Formation in North Victoria Land, Antarctica. Those specimens almost certainly belong to *D. superbum*, having triangular and lobed pinnules (Bomfleur & Kerp 2010, pl. 10, fig. 5). The cuticle from those specimens (Bomfleur & Kerp 2010, pl. 13) is probably the best cuticular record available for the species. Bomfleur & Kerp (2010,

p. 70) confidently distinguished the cuticle from that attributable to *Xylopteris* (discussed below). The stomata are stephanocytic, aligned over veins but tending toward non-alignment elsewhere; however, that is based on limited data (Bomfleur & Kerp 2010, pl. 13).

The cuticle identified as that of *Xylopteris tripinnata* (Jones & de Jersey 1947a) Schopf 1973 by Retallack (1980a, fig. 12.12C) probably belongs to *Dicroidium superbum* but his line-drawn figure is insufficient to confidently determine epidermal characters. At least some of the cuticle described by Baldoni (1980) as that of *X. spinifolia* (Tenison-Woods 1884) Frenguelli 1943 belongs to *D. superbum* (see above synonymy) based in part on her descriptive captions; most of her figured megascopic material is insufficient for confident assignment. A unipinnate specimen assigned to *D. superbum* by Troncoso & Herbst (2007) from Cerro Ranguilí, near the boundary of the 6th and 7th regions, Chile, may be an aberrant representative of *D. odontopteroides*.

Specimen UQF18852 (re-examined herein) from Gaulls Gully, Harlin, north of Ottaba in the Anisian Esk Formation, Esk Trough, Queensland, was figured by Hill et al. (1965, pl. 4, fig. 6) as *Dicroidium superbum*. Those authors assumed that the two frond portions were from a single bifurcated frond. However, no rachis bifurcation is preserved, and the pinnules suggest affiliation with the fern *Nymboidiantum* or possibly *Nymbiella*, both genera being erected by Holmes (2003) based on specimens from the approximately coeval Nymboida Coal Measures, New South Wales.

Genus: *Zuberia*

Frenguelli 1943 emend. Artabe 1990

Synonymy.

1943 *Zuberia* Frenguelli, pp. 300–310.

1957 *Hoegia* Townrow, pp. 47–49.

Type species. *Zuberia zuberi* (Szajnocha 1888) Frenguelli 1943 by subsequent designation (Artabe 1990, p. 146). The type specimen was assigned by Szajnocha (1888) to his species *Cardiopteris zuberi* and was collected from near Cacheuta (precise location unknown), Mendoza Province, Argentina: Cerro de Las Cabras, Potrerillos or Cacheuta formations (Anisian–Carnian: Morel et al. 2003, Cariglino et al. 2016, fig. 3), Cuyo Basin.

Diagnosis. See Artabe (1990, p. 146).

Discussion. *Zuberia* has not been widely accepted, being regarded as a junior synonym of *Dicroidium* by many authors (e.g. Archangelsky 1968, Retallack 1977 and Anderson & Anderson 1983). However, new discoveries provide strong evidence that the two genera are in fact distinct (Artabe 1990, Decombeix et al. 2014, Pattemore 2016). Artabe (1990) reviewed the genus and regarded pinnules arising directly from the rachis, at the bases of pinnae, as intercalary pinnules and an important character distinguishing *Zuberia* and *Dicroidium*. Decombeix et al. (2014, p. 33) noted that wood of stems belonging to *Dicroidium* and *Zuberia* differed generically. Fructifications that have been variously allied with *D. odontopteroides* and *Z. feistmantelii* differ structurally (Tab. 1), that of the latter having a pinnate structure and of the former having a whorled configuration (Pattemore 2016).

Contrary to Retallack (1977) and Anderson & Anderson (1983), *Zuberia feistmantelii* is distinguished from *Z. zuberi* (included in *Dicroidium* by those authors) in the present study, following Frenguelli (1943, 1944) and Artabe (1990). The genus is included in the Umkomasiaceae herein based on allied fructifications (Tab. 1).

***Zuberia feistmantelii* (Johnston 1893)
Frenguelli 1943 emend. Artabe 1990**

Figs 13–15

Synonymy. The following synonymy list is limited to figured specimens that are important to the discussion herein. See Artabe's (1990) synonymy list for the species and lists by Retallack (1977) for his varieties *Dicroidium zuberi* var. *feistmantelii* and *D. zuberi* var. *papillatum*.

- 1879 *Thinnfeldia odontopteroides* (Morr. sp.) Fstm.; Feistmantel, pl. 9, figs 1, 1a, 1b, 2, 2a, pl. 10, fig. 1, 1a–c, pl. 11, fig. 1, 1a, 1b [plates also numbered 27–29, respectively].
- 1893 *Thinnfeldia Feistmantelii* Johnston, pp. 175–176 (not figured). [basonym]
- 1895 *Thinnfeldia Feistenantelli* [sic] (R. M. Johnston); Johnston, fig. 2.
- 1898 *Thinnfeldia odontopteroides* v. *triangulata* Shirley, p. 22, pl. 10, fig. 2.
- 1898 *Thinnfeldia odontopteroides* v. *normalis* Shirley, p. 21, pl. 11.
- 1912 *Dicroidium Feistmanteli* Gothan, pl. 16, fig. 1.
- 1917a *Thinnfeldia Feistmanteli* Johnston; Walkom, pl. 2 only.

- 1926 *Thinnfeldia Feistmanteli* Johnston; Chapman & Cookson, pl. 20, fig. 9, pl. 21, fig. 10.
- 1943 *Zuberia Feistmanteli* (Johnst.) Frenguelli, p. 308, fig. 25.
- 1944 *Zuberia Feistmanteli* Johns.; Frenguelli, pp. 3–9, pls 1–3.
- 1950 *Dicroidium feistmanteli*; Jacob & Jacob, pp. 116–119, fig. 16.
- 1957 *Dicroidium feistmanteli* (Johnston) Gothan; Townrow, fig. 7A, 7B.
- 1957 *Hoegia papillata* Townrow, fig. 8B, 8C.
- 1957 *Hoegia antevsiana* Townrow, fig. 8E.
- 1965 *Dicroidium feistmanteli* (Johnston) Gothan; Hill et al., pl. 4, fig. 4.
- 1977 *Dicroidium zuberi* var. *feistmantelii* (Johnston) Retallack, microfiche frames I15–I16.
- 1977 *Dicroidium zuberi* var. *papillatum* (Townrow) Retallack, microfiche frames I17–I18.
- 1983 *Dicroidium zuberi*; Anderson & Anderson, pl. 36, figs 2–9, pl. 37, figs 1–6, pl. 61, figs 1–13, pl. 62, figs 1–8, pl. 80, figs 3–11, pl. 81, figs 1–7, pl. 82, figs 6–12, pl. 83, fig. 1.
- 1990 *Zuberia papillata* (Townrow) Artabe, pp. 152–153, pl. 2, figs 1, 3.
- 1990 *Zuberia feistmanteli* (Johnston) Frenguelli 1943; Artabe, p. 153, pl. 2, fig. 2.
- 2005 *Dicroidium feistmantelii* (Johnston 1894) Gothan 1912; Pattemore & Rigby, p. 335, fig. 4.
- 2005a “*Dicroidium dubium* complex”; Holmes & Anderson, figs 14D, 14E, 15A, 15D.
- 2005a “*Dicroidium zuberi* complex”; Holmes & Anderson, figs 16B, 16C, 17A–D, 18A.
- 2007 *Zuberia feistmanteli* (Johnston) Frenguelli emend. Artabe 1990; Artabe et al., pp. 288–290, fig. 4E, 4I.

Type material. Lectotype (Feistmantel 1879, pl. 9 [also numbered as 27], fig. 1) by subsequent designation (Townrow 1957: note in his synonymy list); collected from Mt. Victoria (probably several hundred metres to the south at Mt. Piddington) in the Olenekian of the Sydney Basin (uppermost Narrabeen Group: Retallack 1977, 1980a, Metcalfe et al. 2015, fig. 13). Feistmantel's figure was reproduced in several publications (Feistmantel 1890, pl. 25, figs 1, 2, Gothan 1912, pl. 16, fig. 1, Antevs 1914, pl. 5, fig. 1, Frenguelli 1943, fig. 25). Johnston (1893, pp. 175–176, 1895, fig. 2) erected *Thinnfeldia feistmantelii* based on Feistmantel's (1879) large bipinnate fronds from Mt. Victoria (above).

The lectotype could not be located by Fletcher (1971, p. 14) in the Australian Museum, Sydney, and a recent search of the museum's collection failed to locate the specimen (R. Pogson, Australian Museum, 2016, pers. comm., 20th January). A neotype is designated below.

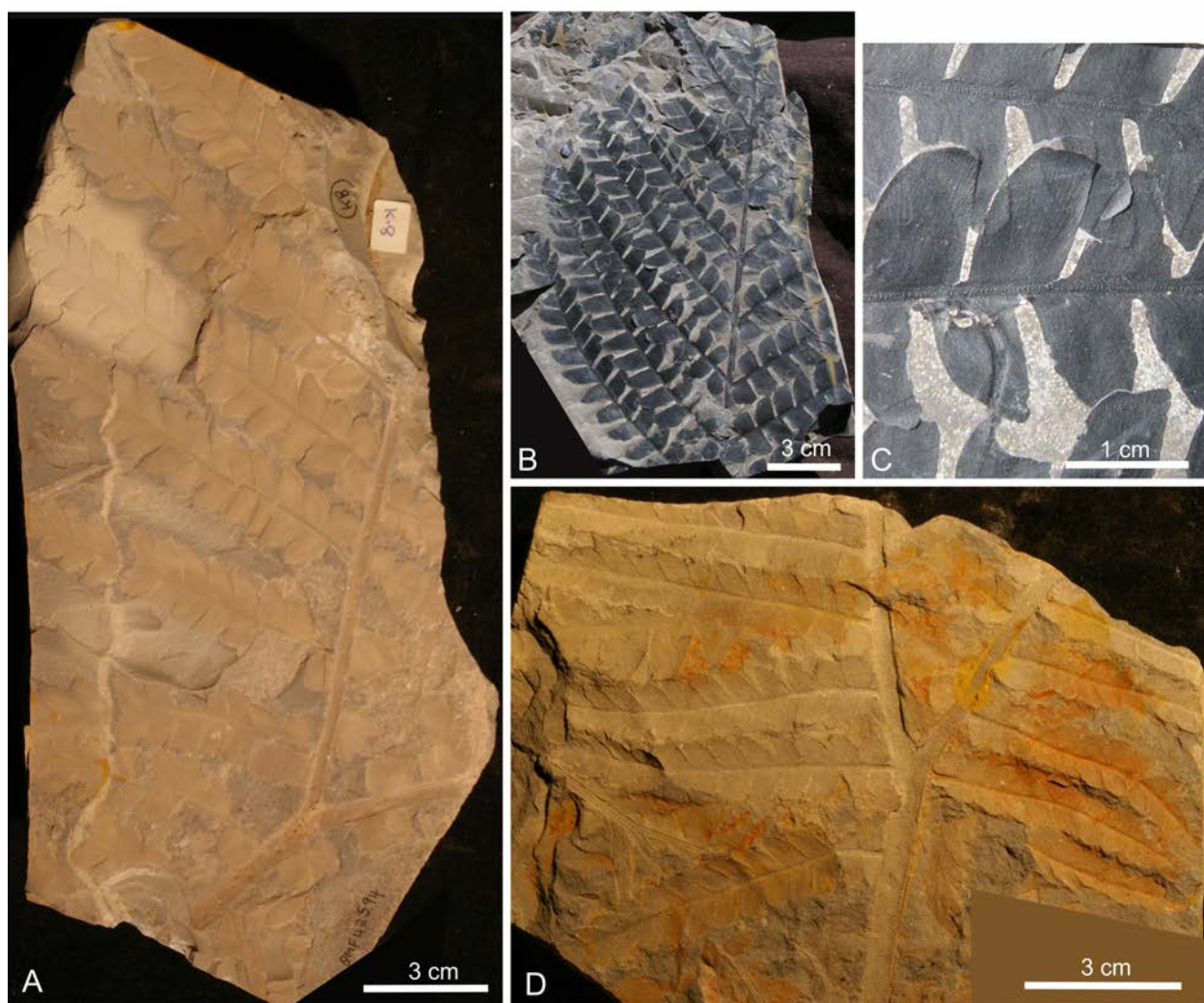


Fig. 13. A–D: *Zuberia feistmantelii* (Johnston 1893) Frenguelli 1943 emend. Artabe 1990. **A:** QMF42594, neotype designated herein; Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); collected by R. Knezour. **B, C:** QMF58727; Callide Mine, near Biloela, Queensland; Callide Basin (lower Rhaetian). **D:** UQF5986; Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian)

Diagnosis. See Artabe (1990, p. 153).

Material. GSQF270, GSQF331, UQF5986 (Fig. 13D): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimens GSQF270 and GSQF331 were figured by Shirley (1898, pl. 10, fig. 2, pl. 11) and assigned to his varieties *Thinnfeldia odontopteroides* var. *triangulata*. and *T. odontopteroides* var. *normalis*, respectively. The latter specimen was figured by Walkom (1917a, pl. 2, figs 1, 2) as *T. feistmantelii*. Hill et al. (1965, pl. 4, fig. 4) figured specimen UQF5986 as *Dicroidium feistmantelii*.

GSQF335: Callide Creek, Queensland; Callide Basin (Upper Triassic, probably lower Rhaetian). Callide Creek is located several hundred metres south of Callide Mine (Dunn Creek area) but the precise collection location along the creek is unknown. The specimen

was recorded but not figured by Walkom (1917a, p. 19).

MVP16093, MVP16099: Leigh Creek, South Australia; coal-bearing strata of the Leigh Creek Coal Measures (Anisian–Norian: Kvitko 1995). Figured by Chapman & Cookson (1926, pl. 20, fig. 9, pl. 21, fig. 10) as *Thinnfeldia feistmantelii*.

QMF42594 (Fig. 13A), neotype designated herein supporting the above-cited lectotype: Blackstone Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

QMF58716–QMF58718, QMF58719a, QMF58719b (SEM stub: Fig. 14A), QMF58719c (TLM slide: Fig. 15A–C), QMF58721, QMF58722, QMF58724a, QMF58724b (SEM stub), QMF58724c (SEM stub), QMF58724d (SEM stub: Fig. 14B), QMF58724e (TLM slide), QMF58724f (TLM slide: Fig. 15D–F), QMF58724g (TLM

slide), QMF58725, QMF58726, QMF58727 (Fig. 13B, C), QMF58728–QMF58730: Callide Mine, near Biloela, Queensland; Callide Basin (Upper Triassic, lower Rhaetian).

UQF64534: Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

UQF82584: Wivenhoe Hill, near Esk, Queensland; Esk Formation, Esk Trough (Anisian).

Occurrence. See Tab. 1.

Description. Frond bipinnate, >300 mm long (incomplete). Rachis bifurcating once, 6 mm wide (near bifurcation). Pinnae linear, opposite to alternate, up to 180 mm long, extending from rachis at >45° but more acutely in distal portion of rachis. Frond commonly having pinnules instead of pinnae distally and near rachis bifurcation. Variation in pinnae morphology greatest between divided rachis segments (i.e. inner pinnae), below rachis bifurcation and in distal portion of rachis. Pinnules 6–(12)–20 mm long, 4–10 mm wide, triangular, rectangular or rhomboidal, bases slightly decurrent to slightly constricted, apices acute, obtuse or slightly retuse. Venation extending from pinna midrib at very acute angle but curving away, commonly bifurcating at least once.

Discussion. Artabe (1990, fig. 2) recognized six species belonging to *Zuberia*. Based on specimens examined herein, *Z. feistmantelii* and *Z. papillata* are regarded as synonymous. Several specimens figured by Anderson & Anderson (1983, pl. 34, 3–18, pl. 35, figs 1, 2, 4–6, 9, pl. 36, fig. 1, pl. 44, figs 17–20, 23, pl. 53, figs 22–25, pl. 59, figs 12–14, pl. 60, figs 1–5, pl. 77, figs 5–16, pl. 80, figs 1, 2, pl. 82, figs 1–5) chiefly as *Dicroidium dubium* subsp. *switzifolium* belong to *Zuberia* but probably not *Z. feistmantelii*.

Townrow (1957) erected *Hoegia papillata* for specimens that megascopically resemble *Zuberia feistmantelii*, the two species being largely distinguished by cuticular characters of doubtful taxonomic significance (Barclay et al. 2007, tab. 1). *Hoegia* has not been widely adopted (Archangelsky 1968, Retallack 1977, Anderson & Anderson 1983, Artabe 1990) and the genus is regarded herein as insufficiently distinguished from *Zuberia*. Townrow (1957) assigned specimen GSQF331 (re-examined herein) to *H. papillata*; the specimen had been

earlier identified as a representative of *Thinnfeldia* by Shirley (1898, pl. 11) and Walkom (1917a, pl. 2, figs 1, 2). It is the near-apical portion of a frond without bifurcation; however, its pinnules resemble those of *Z. feistmantelii*.

In an unpublished thesis, O'Sullivan (1977, pp. 25–26, fig. 38) figured specimens attributable to *Zuberia feistmantelii* from the Callide Mine (Dunn Creek area). His specimens (UQF69920, UQF69924, UQF69925) could not be located during the present study. O'Sullivan also recorded cycadalean (below) and ginkgoalean material. Walkom (1917a) assigned specimen GSQF335 (re-examined herein: from Callide Creek, south of the Callide Mine) to *Thinnfeldia feistmantelii*. It is a small portion of a frond and includes a rachis bifurcation. All pteridospermous fronds recorded from the Callide Basin are attributable to *Z. feistmantelii*, none to *Dicroidium*. Coal was first reported in the basin by Rands (1891) and he identified *T. odontopteroides* from associated strata (repeated by Jack & Etheridge 1892, p. 357), but these specimens were neither figured nor described. As discussed above, both unipinnate and bipinnate fronds were assigned to *T. odontopteroides* at that time.

Cantrill et al. (1995) recorded fragmentary specimens as *Dicroidium zuberi* from the Flagstone Bench Formation, Prince Charles Mountains, East Antarctica (Norian: McLoughlin & Drinnan 1997). Although only unipinnate fragments were identified they considered them to be pinnae from a bipinnate frond. That interpretation seems probable for at least one of their figured specimens (Cantrill et al. 1995, figs 3A) but the remainder are doubtful (Cantrill et al. 1995, figs 3B–D) and may belong to *D. odontopteroides*. Their figured cuticle is from one of the less probable representatives of *Zuberia*. Cantrill et al. (1995) distinguished their specimens, unconvincingly, from *D. odontopteroides* with venation and cuticular characters. Firstly, crenulate anticlinal cell walls are not limited to representatives of *Zuberia*, and can be equally strongly developed in *D. odontopteroides* (e.g. Townrow 1957, figs 5F, 6K, Lele 1962, pl. 1, Bomfleur & Kerp 2010, pl. 5; also Figs 7D, 8 herein). Secondly, “odontopteroid” venation is not necessarily a distinguishing character at specific or generic level. For instance, it is known in representatives of both *Z. feistmantelii* and *D. odontopteroides*; shorter pinnules

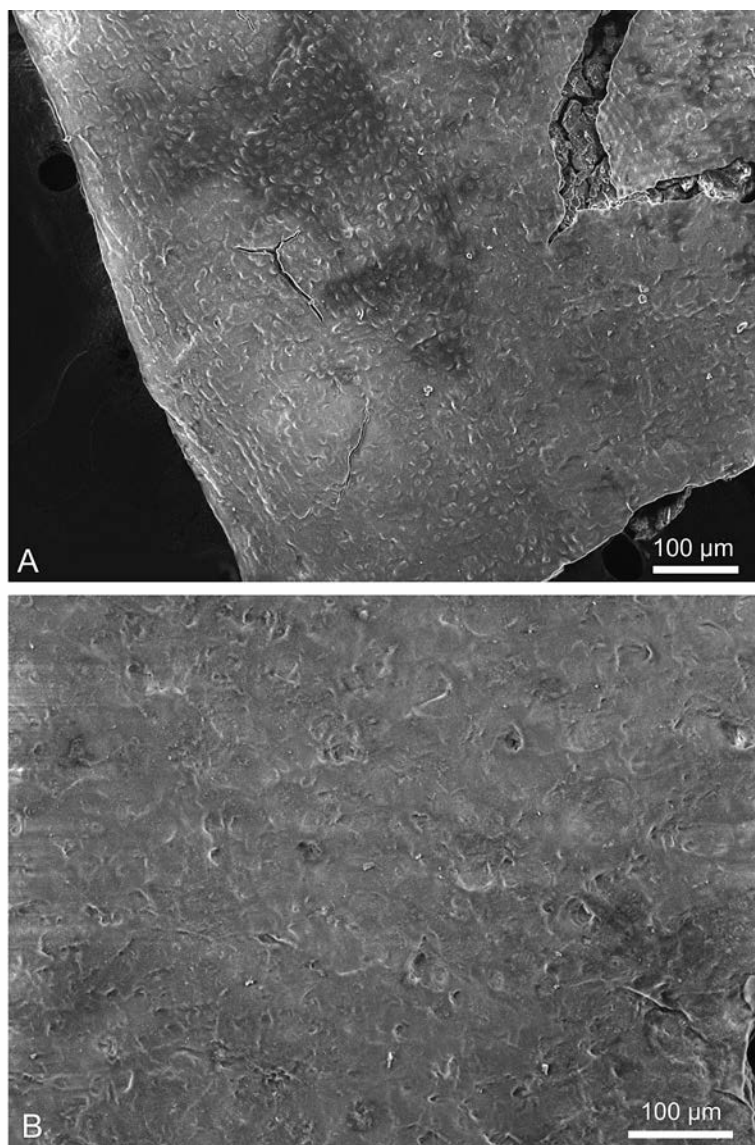


Fig. 14. A–B: *Zuberia feistmantelii* (Johnston 1893) Frenguelli 1943 emend. Artabe 1990; Callide Mine, near Biloela, Queensland; Callide Basin (lower Rhaetian: see text). **A:** QMF58719b (SEM stub), showing papillate and non-papillate areas on pinnule; natural pinnule edge (left). **B:** QMF58724d (SEM stub), showing thick epicellular cutin obscuring cell structure and irregular but non-papillate surface

in the latter species commonly lack a midrib (discussed above). A single small specimen (<30 mm long) was attributed to *D. crassinervis* by Cantrill et al. (1995); its indifferent preservation disallows generic identification. Those authors also recorded the male umkomasiacean fructification *Pteruchus* Thomas 1933 emend. Townrow 1962 from the same location (see Pattemore 2016).

Rees & Cleal (2004) reported three specimens as *Dicroidium feistmantelii* from the ?Upper Triassic–Lower Jurassic Camp Hill Formation, Botany Bay Group at Botany Bay on the Antarctic Peninsula. The specimens are inadequately preserved and devoid of rachis bifurcation and intercalary pinnules. However, the pinnules possibly resemble those of *Zuberia*

zuberi or other species of the genus (see Artabe 1990). Dating of strata at that site and correlation with other nearby locations are based on megaf flora (discussed above). Most specimens indicate an Early Jurassic age but some are suggestive of the latest Triassic (Rees 1993, Rees & Cleal 2004). An outcrop on adjacent Livingston Island comprises undoubtedly Triassic and post-Triassic floral assemblages in close geographic proximity (Barale et al. 1994). Dating and correlation of outcrops of the Botany Bay Group and other coeval strata on the Antarctic Peninsula by Rees (1993), Cantrill (2000) and Rees & Cleal (2004) are generalised and simplistic and do not take into account the structural complexity of the Botany Bay Group rift basins that resulted from Late Triassic

and Early Jurassic lithospheric extension (Storey et al. 1996, Hathway 2000). As discussed above, an upper age limit for the Botany Bay Group is known (Rees 1993) but the lower limit is uncertain and the currently accepted date (Early Jurassic) is based only on megascopic plant remains. It is possible that some strata of the Botany Bay Group previously identified as Lower Jurassic are in fact Upper Triassic. Thus, the specimens attributed to *D. feistmantelii* by Rees & Cleal (2004) could possibly represent the youngest occurrence of *Zuberia*; however, both the identity of the specimens and their precise age require confirmation.

Staining of specimens using safranin in the present study always resulted in one leaf surface colouring much more strongly than the other (staining duration: ca 10 minutes). The strongly coloured surface curled more during drying (resulting in greater fragmentation) and is assumed herein to be the upper leaf surface because some specimens lack stomata on that surface; however, in other specimens stomatal density is comparable on both surfaces. The lighter-coloured surface always included numerous stomata (Fig. 15). The presence or otherwise of papillae appears to be somewhat random, even on an individual pinnule

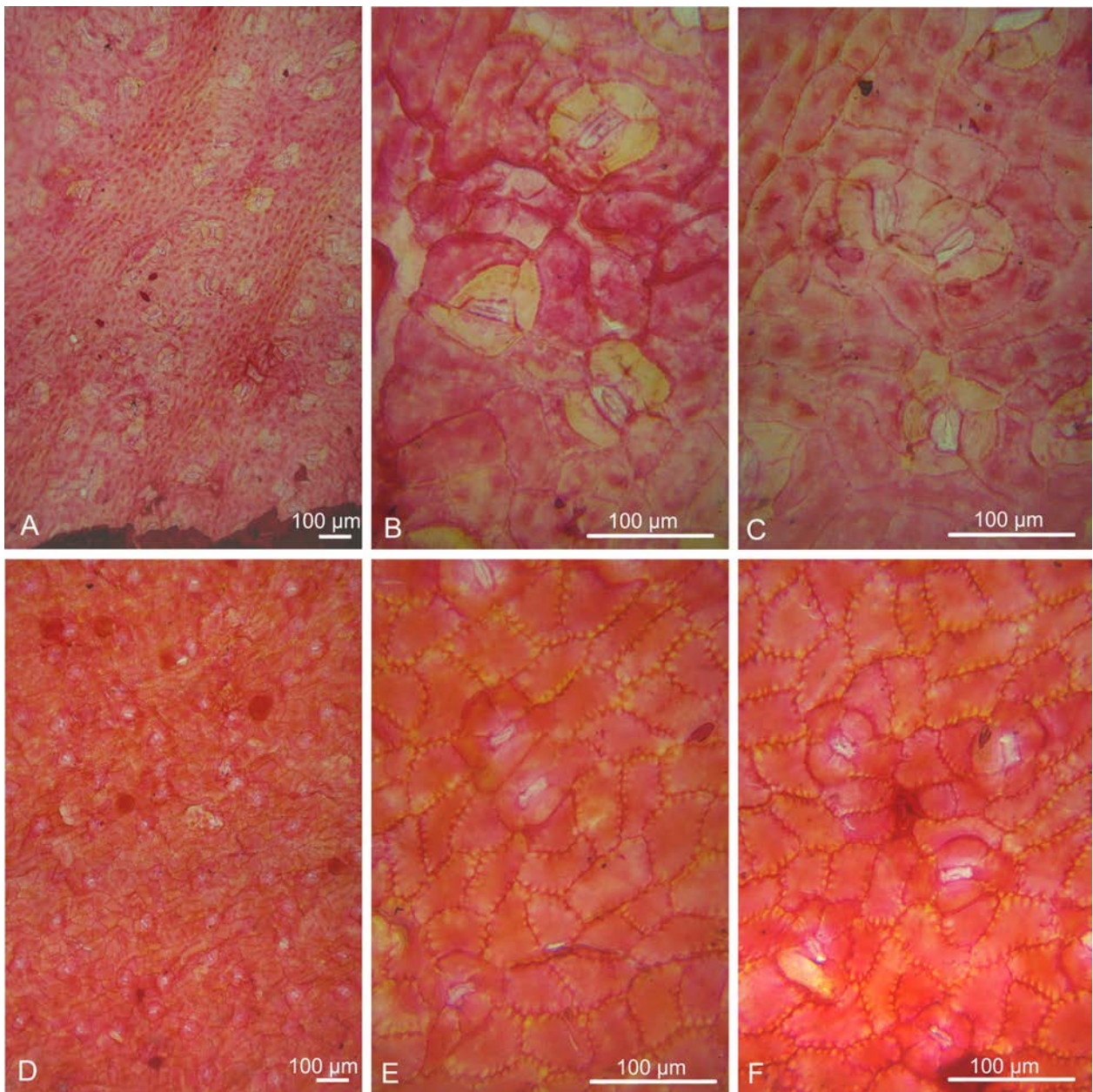


Fig. 15. A–F: *Zuberia feistmantelii* (Johnston 1893) Frenguelli 1943 emend. Artabe 1990; Callide Mine, near Biloela, Queensland; Callide Basin (lower Rhaetian: see text). A–C: QMF58719c (TLM slide), showing anisocytic and stephanocytic stomata and some subsidiary cells that are shared between adjacent stomata. D–F: QMF58724f (TLM slide), showing stephanocytic stomata

(Fig. 14A). No trichome bases were identified. Townrow (1957) figured numerous papillae and stomata (upper/lower leaf surface not distinguished) in specimens that he attributed to *Dicroidium feistmantelii*. For representatives of *Hoegia*, he indicated that stomatal density is approximately the same on both upper and lower leaf surfaces; however, papillae were reported as present in one species of the genus but not in the other. In specimens attributed to *D. zuberi*, Anderson & Anderson (1983, p. 200, pl. 101) recorded papillae and stomata on the lower leaf surface but absent from the upper surface. However, as noted above, many of the specimens they identified as *D. dubium* subsp. *switzifolium* resemble *Zuberia*, and these possibly include figured cuticle (Anderson & Anderson 1983, pl. 99). *Zuberia* exhibits large variation in the position and density of stomata and papillae; this is not unexpected given the potential for environmental influence on those characters (Barclay et al. 2007, tab. 1).

Stomata are commonly stephanocytic although some are anisocytic (3 subsidiary cells: Fig. 15B). Many of those categorised herein as stephanocytic have only 4 subsidiary cells, and their symmetry suggests they may be better identified as staurocytic (following Barclay et al. 2007). Anderson & Anderson's (1983, fig. 6.4) line-drawn figure also indicates staurocytic and stephanocytic stomata in representatives of *Z. feistmantelii*. In some specimens examined in the present study stomata are commonly paired (Fig. 15A, C, E) and, rarely, adjacent stomata share a subsidiary cell (Fig. 15A, C). Pairing of cells was also figured by Anderson & Anderson (1983, pl. 101, fig. 6). However, in most specimens stomatal pairing is rare or absent. It is known that more than one stomatal category can be represented in an individual species or even on the same leaf (Carpenter 2005, Barclay et al. 2007, p. 43).

The range of subsidiary cell patterns identified in *Zuberia feistmantelii* may be useful taxonomically (Barclay et al. 2007, tab. 1); representatives of *Dicroidium* evidently have only stephanocytic stomata. As noted above, the female fructifications that have been variously allied with *Z. feistmantelii* and *D. odontopteroides* differ structurally (Pattemore 2016). Thus, the two fronds are almost certainly not closely related; hence their inclusion in separate genera herein (Tab. 1). *Zuberia feistmantelii* represents a plant that had much larger

fronds (ca 1 m long: Townrow 1957) than any with foliage attributable to *Dicroidium* (three to four times the size of representatives of that genus).

Genus: *Johnstonia* Walkom 1924b

Type species. *Johnstonia coriacea* (Johnston 1888) Walkom 1924b by subsequent designation (Jones & de Jersey 1947a, p. 18).

Type material: see below.

Diagnosis. See Walkom (1924b, p. 79). Jones & de Jersey (1947a, p. 18, pl. 2, figs 1, 4) emended the generic diagnosis based on two specimens that show a second rachis bifurcation. However, as discussed above, one of those specimens (UQF8110) is an unidentifiable fragment and the other (UQF2248) resembles *Dicroidium odontopteroides*; both specimens were re-examined in the present study. *Johnstonia* has been regarded by some authors (e.g. Townrow 1957, 1966, Anderson & Anderson 1983) as synonymous with *Dicroidium*. The genera are treated as distinct herein based on generic diagnostic characters: *Johnstonia* represents a simple leaf, whereas *Dicroidium* has a pinnate structure (Tab. 1).

Johnstonia coriacea

(Johnston 1888) Walkom 1924b

Fig. 16

Synonymy.

- 1886 *Rhacophyllum coriacium* Johnston, pp. 170–171 (not figured).
- 1888 *Rhacophyllum coriacium* Johnston, pl. 26, fig. 9. [basionym]
- 1924b *Johnstonia coriacea* (Johnston) Walkom, pp. 79–81, figs 6–8.
- 1927 *Johnstonia coriacea* Walkom; du Toit, pp. 360–362, text-figs 12D, 13B.
- 1967 *Dicroidium coriacium* (Johnston) Townrow; Jain & Delevoryas, pl. 91, fig. 1.
- 1967b *Dicroidium dutoitii* Townrow, pp. 462–464, figs 1D, 2E, 3B.
- 1977 *Johnstonia coriacea* (Johnston) Walkom 1925; Retallack, micro-fiche frames I23–I25.
- 1977 *Johnstonia dutoitii* (Townrow) Retallack, micro-fiche frame J1.
- 1980 *Johnstonia coriacea* (Johnston) Walkom 1924; Petriella, pl. 2, fig. 6.
- 1982 *Dicroidium coriacium* (Johnston) Townrow; Holmes, fig. 3B–D.
- 1983 *Dicroidium coriaceum* subsp. *coriaceum* Anderson & Anderson, pl. 31, figs 3, 4, pl. 76, figs 1–11.

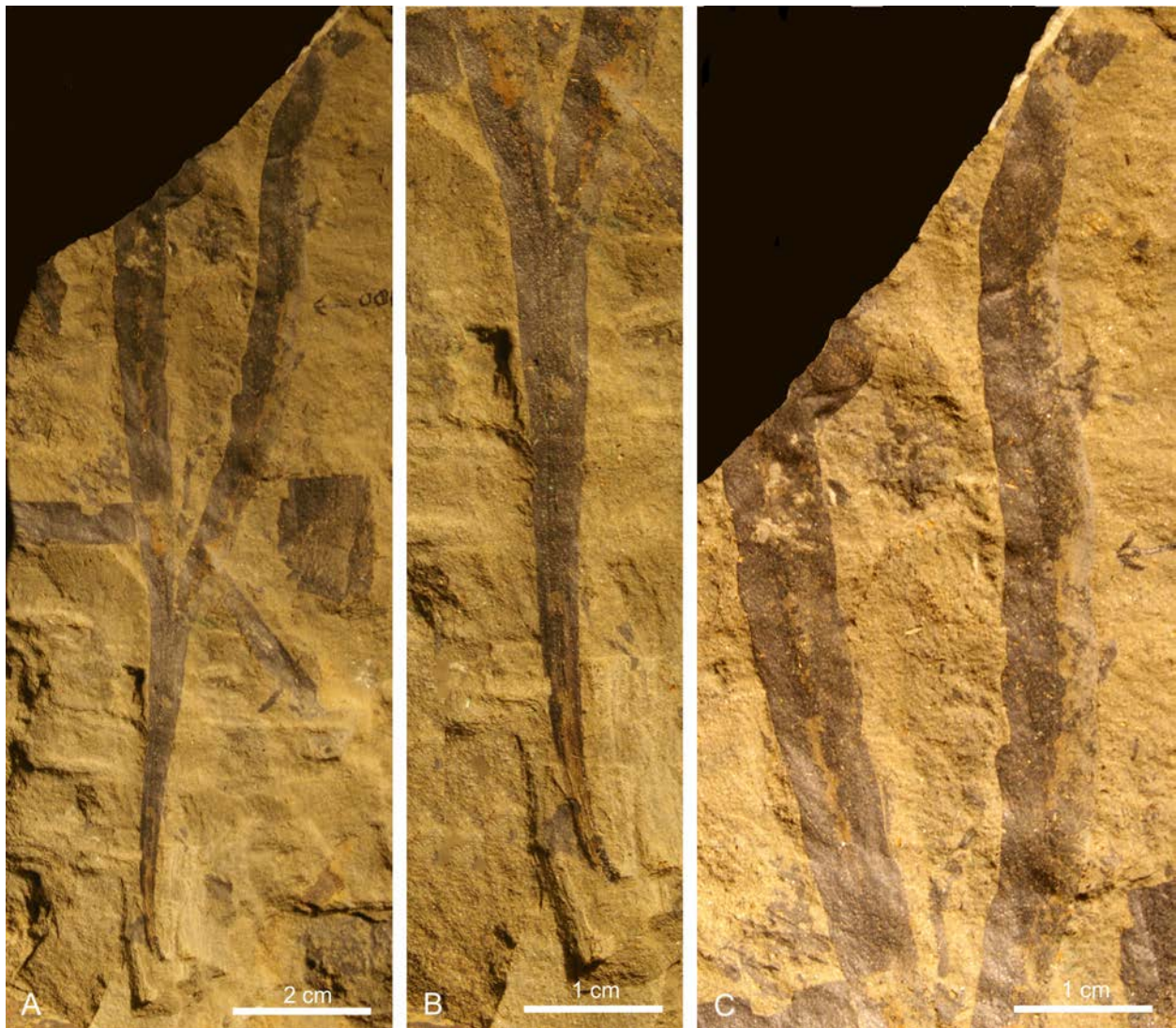


Fig. 16. A–C: *Johnstonia coriacea* (Johnston 1888) Walkom 1924b, UQF82600, neotype designated herein supporting the lectotype (Johnston 1888, pl. 26, fig. 9); Ottaba, north of Esk, Queensland; Esk Formation, Esk Trough (Anisian). A: entire specimen. B, C: optically enlarged basal and apical portions, respectively

- 1983 *Dicroidium coriaceum* subsp. *dutoitii* Anderson & Anderson, pl. 41, figs 1–34, pl. 76, figs 12–36, pl. 85, figs 2–4.
- 2005a “*Dicroidium coriaceum* complex”; Holmes & Anderson, figs 1A, 1B, 2A–C.
- 2006 *Johnstonia coriacea* (Johnston 1887) Walkom 1925; D’Angelo, fig. 1C, 1G.
- 2007 *Johnstonia coriacea* (Johnston) Walkom 1925; Artabe et al., p. 288, fig. 4C, 4D.
- 2011 *Dicroidium dutoitii*; Escapa et al., fig. 7f.
- 2013 *Dicroidium coriaceum* (Johnston) Townrow subsp. *dutoitii* (Townrow) Anderson & Anderson; Chatterjee et al., fig. 4A, 4B.

Type material. Holotype (Johnston 1888, pl. 26, fig. 9) by effective original designation [ICN, Article 9.1, Note 1]; collected from Lord’s Hill, New Town, Hobart, from strata associated with Upper Triassic coal measures of the Tasmania Basin (Carnian–Norian; Reid et al. 2014). The specimen is held by the Tasmanian

Museum but it was unable to be located by Retallack (1977); hence, a neotype is designated below.

Diagnosis. See Johnston (1886, p. 170) and Walkom (1924b, p. 79).

Material. UQF82600 (Fig 16: neotype, designated herein) supporting the holotype (Johnston 1888, pl. 26, fig. 9): Ottaba, north of Esk, Queensland; Esk Formation, Esk Trough (Anisian).

Occurrence. See Tab. 1.

Description. Leaf simple, bifurcating once, 145 mm long (complete), 6–7 mm wide above bifurcation. Below bifurcation, lamina gradually narrowing to short petiole (ca 3 mm long). Margin entire but slightly sinuate locally. Apex acutely pointed. Midrib prominent, 1.1 mm wide basally, ca 0.6 mm above bifurcation but

narrowing distally. Secondary veins arising very acutely from midrib and curving away toward margin, commonly bifurcating once.

Discussion. Townrow (1967b) erected *Dicroidium dutoitii* based on entire to slightly sinuate specimens from Antarctica (Middle and Upper Triassic Lashly Formation: Pattemore et al. 2015a, p. 707) and South Africa (Carnian Molteno Formation) that resemble *Johnstonia coriacea* except for their greater leaf width (10–15 mm). No other characters separate those species. Retallack (1977) recombined *D. dutoitii* with *Johnstonia*, regarding its morphology as intermediate between that of *J. coriacea* and *D. odontopteroides*; however, his line-drawn figure of *J. dutoitii* is strongly crenate, unlike the type specimen of the species (slightly sinuate: du Toit 1927, text-fig. 12D). It is unclear why Retallack's figure is so strongly crenate as most material that he included in the species is only slightly sinuate. He did include a strongly pinnatifid specimen that was assigned to *D. odontopteroides* by Jain & Delevoryas (1967, pl. 90, fig. 3). The specimen represents a small apical portion of a frond, clearly attributable to *D. odontopteroides*. Thus, Retallack's (1977) interpretation of *J. dutoitii* as pinnatifid is unsupported by the type material and the species is regarded herein as synonymous with *J. coriaceae*; neither is pinnate. Gnaedinger & Herbst (2001) assigned indifferently preserved specimens to *J. dutoitii* from the Upper Triassic La Ternera Formation in the Cerro La Ternera area (Region 3), northern Chile that appear to be a admixture of unipinnatifid and slightly sinuate but simple fronds.

Walkom's (1924b, figs 9, 10) figured specimens that were assigned to his species *Johnstonia dentata* and to his recombination *J. trilobita* (discussed above) are probably within the natural variation of *Dicroidium odontopteroides*. A specimen recorded by Jones & de Jersey (1947a, pl. 2, fig. 5b) as *J. trilobita* (now catalogued as UQF44023: re-examined herein) was evidently assumed to constitute the two distal portions of a bifurcated unipinnate frond (bifurcation not preserved) but it surely represents adjacent pinnae of a frond belonging to *D. superbum*. Several other specimens assigned by Jones & de Jersey (1947a) to various species of *Johnstonia* are considered doubtful representatives of the genus (UQF8184, UQF8189, UQF8464,

UQF8465: all re-examined herein; also UQF8186 which was incorrectly identified as "UQF8136" by those authors and figured by Hill et al. 1965, pl. 4, fig. 7). The specimens are insufficiently preserved for confident assignment; some may be representatives of *D. odontopteroides*, others are probably pinnae of *D. superbum*. Retallack (1980b) recorded *Johnstonia* from the Ladinian of the South Island, New Zealand; however, his fragmentary specimens probably belong to *D. odontopteroides*. The specimen identified as "*D. coriaceum* complex ... intergrading with shorter pinnuled forms of the *D. odontopteroides* complex" by Holmes & Anderson (2005a, fig. 2E) is representative of *D. odontopteroides*; it does not resemble the holotype of *J. coriaceae* (Johnston 1888, pl. 26, fig. 9).

Townrow (1957) recombined *Johnstonia coriacea* with *Dicroidium* but his figured specimens are unlike the type specimen of the species and are attributable to *Dicroidium odontopteroides*. Bomfleur & Kerp's (2010) figured specimens, identified as *D. coriacea*, are insufficiently preserved for generic assignment; they are possibly pinnae belonging to *D. dubium* or the apical portions of a frond attributable to *D. odontopteroides*. Likewise, Archangelsky's (1968) specimens figured as *D. coriacea* are variously representative of *D. odontopteroides* and *J. coriacea*. Thus, the cuticle figured as *D. coriacea* by the above authors (i.e. Townrow 1957, Archangelsky 1968, Bomfleur & Kerp 2010) doubtfully represent that species.

The only figured cuticle to be extracted from a bona fide representative of *Johnstonia coriacea* was extracted from a specimen from the Carnian of South Africa (BP/2/105: Anderson & Anderson 1983, pl. 41, fig. 3, pl. 107, figs 1, 2). Their figures indicate that stomata are stephanocytic and located on both upper and lower leaf surfaces. The epicellular layer appears to have been papillate but not strongly and perhaps not consistently. However, the limited available data precludes reliable comparison. In contrast, Bomfleur & Kerp's (2010, p. 84, pl. 9, figs 4–11) figured cuticle, albeit unreliably attributed as noted above, is not papillate, whereas Archangelsky (1968, p. 507) indicated that the subsidiary cells are papillate (also based on unreliably identified specimens).

Townrow's (1957) inclusion of *Johnstonia coriacea* in *Dicroidium* was supported by

Archangelsky (1968) and Anderson & Anderson (1983). However, Retallack (1977) disagreed, regarding the leaf as sufficiently megascopically distinct from *Dicroidium*. The latter genus comprises fronds that have a pinnate structure (as diagnosed by Townrow 1957), whereas *Johnstonia coriacea* is simple (apropos of Walkom 1924b). Retallack (1983) recognised other species of *Johnstonia* (unipinnatifid) having characters that probably fall within the natural variation of *D. odontopteroides* (above). Thus, *J. coriacea* is adopted in the present study because the leaf is not pinnate. Furthermore, no fructification has been allied with the species to support its inclusion in *Dicroidium* (Tab. 1).

Genus: *Xylopteris*

Frenguelli 1943 emend. nov.

Type species. *Xylopteris elongata* (Carruthers 1872) Frenguelli 1943 emend. nov. by original designation (Frenguelli 1943, p. 318); see also discussion by Menendez (1951, p. 224). Frenguelli (1943) noted that the species was the most widely known and characteristic of the genus. Type material: see below.

Emended diagnosis. Frond unipinnate or bipinnate. Rachis bifurcating once, commonly having distinct central vein but may be indistinct or absent in larger fronds (particularly below rachis bifurcation). Pinna-rachis and pinnules narrowly linear, entire, opposite to alternate, univeined.

Discussion. Frenguelli's (1943, p. 324) generic diagnosis included forked pinnules, presumably based on Carruthers's (1872, p. 355, pl. 27, fig. 1) erroneous interpretation of the type species (corrected by Townrow 1962). Stipanovic et al. (1996, p. 155) emended the generic diagnosis, including multiple rachis bifurcations and tripinnate fronds. However, those authors were apparently unaware of Townrow's (1962) re-evaluation of the lectotype of *Xylopteris elongata* (below) and the subsequent contribution to the species by Anderson & Anderson (1983). Tripinnate specimens attributed to *X. tripinnata* are shown herein to belong to *Dicroidium superbum*. Thus, the diagnostic emendation of *Xylopteris* by Stipanovic et al. (1996) is not adopted and Frenguelli's (1943) diagnosis is emended.

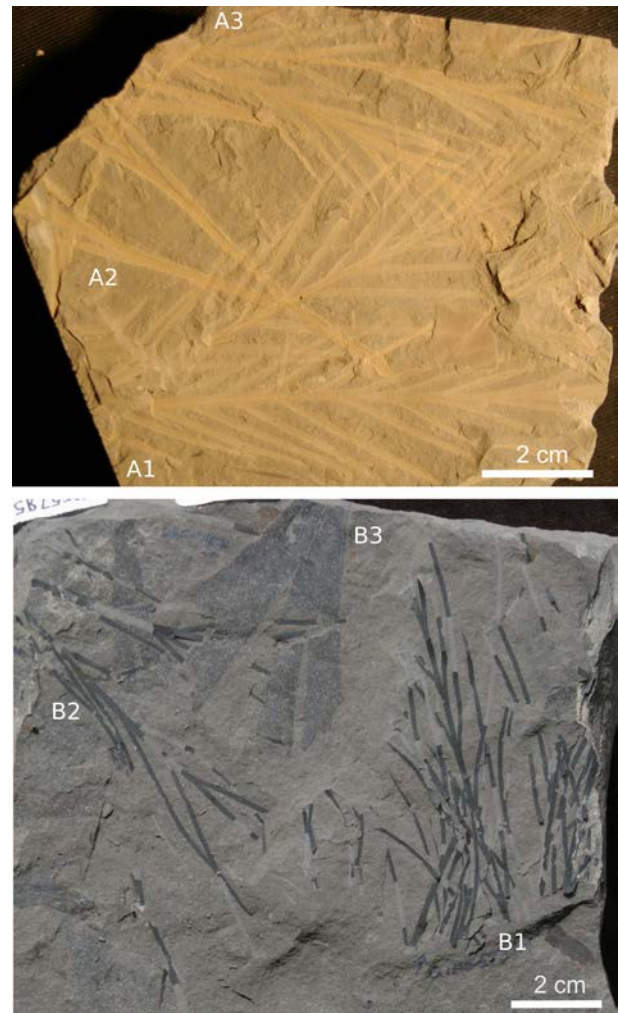


Fig. 17. A1, A3: *Xylopteris elongata* (Carruthers 1872) Frenguelli 1943 emend. nov., UQF64471b and UQF82601b, respectively; Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). A2: *Xylopteris argentina* Frenguelli 1943, UQF82602b. B1, B2: *Xylopteris elongata* (Carruthers 1872) Frenguelli 1943 emend. nov., QMF57849a and QMF57851a, respectively; Meandu Mine, near Nanaingo, Queensland; Tarong Basin (upper Carnian). B3: *Sphenobaiera* sp., QMF57850

Xylopteris elongata (Carruthers 1872)

Frenguelli 1943 emend. nov.

Figs 17(A1, A3, B1, B2), 18

Synonymy. The following synonymy list is limited to figured specimens that are important to the discussion herein. See synonymy listings provided by Townrow (1962) and Retallack (1977).

- 1872 *Sphenopteris elongata* Carruthers, p. 355, pl. 27, fig. 1. [basonym: figure inaccurate, see text].
- 1909 *Stenopteris rigida* Dun, pp. 313–314, pl. 50, figs 1, 2.
- 1943 *Xylopteris elongata* Carr.; Frenguelli, pp. 324–325, figs 30, 31.
- 1962 *Xylopteris elongata* (Carruthers) Frenguelli; Townrow, pp. 123–127, text-fig. 1A–F.

- 1967 *Xylopteris rigida* (Dun) Jain & Delevoryas, p. 573, pl. 91, figs 3–5.
- 1977 *Xylopteris elongata* (Carruthers) Frenguelli 1943; Retallack, micro-fiche frame J8.
- 1977 *Xylopteris elongata* var. *elongata* (Carruthers) Frenguelli 1943; Retallack, micro-fiche frames J9–J10.
- 1977 *Xylopteris elongata* var. *rigida* (Dun) Stipanovic & Bonetti; Retallack, micro-fiche frames J11–J12.
- 1982 *Dicroidium elongatum* (Carruthers) Archangelsky; Holmes, p. 10, fig. 5A.
- 1983 *Dicroidium elongatum* forma *elongatum* Anderson & Anderson, pl. 38, figs 10–15, pl. 40, figs 8–12, pl. 46, figs 2–15, pl. 51, fig. 4, pl. 67, figs 1–9, pl. 72, figs 5–12.
- 1983 *Dicroidium elongatum* subsp. *matatifolium* Anderson & Anderson, pl. 38, figs 7–9, pl. 40, figs 1–7, pl. 45, figs 7–31, pl. 51, figs 1–3, pl. 63, figs 1–21, pl. 72, figs 1–4.
- 2007 *Dicroidium odontopteroides*; Bomfleur et al., fig. 2(3).
- 2010 *Dicroidium elongatum* (Carruthers) Archangelsky; Bomfleur & Kerp, pp. 69, 70, 73, pl. 1, figs 1, 3.
- 2011 *Dicroidium elongatum*; Escapa et al., fig. 7c.
- 2011b *Dicroidium elongatum*; Bomfleur et al., fig. 3g.

Type material. Lectotype subsequently designated by Townrow (1962, p. 123, text-fig. 1) and selected from specimens originally described by Carruthers (1872). The material is held by the Natural History Museum, London and was collected from the Tivoli Mine, Ipswich, Queensland (Carnian–lowermost Norian Ipswich Basin).

The Tivoli Mine, one of the earliest coal mining operations in the Ipswich Coal Measures (1866 to ca 1882: Whitmore 1981), was located ca 4 km northeast of Ipswich and apparently exploited the Tivoli Seam of the Tivoli Formation (The Brisbane Courier 1871, p. 3, Whitmore 1981, 1985). As noted above, Townrow (1962) re-examined the type specimen and considered Carruthers's (1872, pl. 27, fig. 1) line-drawn interpretation inaccurate. In particular, there is no evidence of more than one rachis bifurcation, nor for the forking of pinnules (Townrow 1962, text-fig. 1). Thus, the diagnoses by Carruthers (1872) and Jones & de Jersey (1947a) are inaccurate (the latter authors repeating Carruthers's error). Stipanovic et al. (1996) were apparently unaware of Townrow's (1962) contribution to the species.

An emended diagnosis is proposed below based on Townrow's (1962) description of the type material and specimens examined herein. Baldoni's (1980) description chiefly concerns the cuticle; her circumscription of megascopic

material is inadequate for species recognition. Retallack (1977) and Anderson & Anderson (1983) provided brief descriptions; however, the latter authors greatly expanded the diagnostic characters encompassing the species (discussed below).

Emended diagnosis. Frond unipinnate, >100 mm long. Rachis 2–4 mm wide, ca 0.5 mm wide distally. Pinnules commonly >60 mm long, 1–1.5 mm wide basally and ca 0.8 mm wide distally, at least 4 on either side of rachis (commonly many more), borne above and below rachis bifurcation. Pinnule apices abruptly rounded to acutely pointed.

Material. QMF57849a (Fig. 17B1), QMF57849b (SEM stub: Fig. 18A, 18B), QMF57849c (TLM slide: unprocessed cuticle), QMF57851a (Fig. 17B2), QMF57851b (TLM slide: Fig. 18F, G), QMF57851c (TLM slide: Fig. 18C–E), QMF57851d (TLM slide), QMF57852, QMF57855, QMF57864, QMF57865, QMF57874, QMF57882: Meandu Mine, near Nanango, Queensland; Tarong Basin (upper Carnian), Queensland, Australia.

UQF20631a/b (part and counterpart): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

UQF64471a and counterpart UQF64471b (Fig. 17A1), UQF64473, UQF64481, UQF64723, UQF82601a and counterpart UQF82601b (Fig. 17A3): Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

Occurrence. See Tab. 1.

Discussion. The lectotype is unipinnate and univeined (Townrow 1962). The cuticle figured herein (Fig. 18) from the Carnian Tarong Basin resembles that identified from Carruthers's (1872) collection (Townrow 1962, text-fig. 1) from the Tivoli Formation, Ipswich Basin. Stomata are stephanocytic, commonly having two prominent lateral subsidiary cells and two to four subsidiary cells positioned longitudinally. All epidermal cells and stomata are consistently aligned with the longitudinal direction of the pinnule or rachis, no epidermal characters distinguish pinnule and rachis nor upper and lower leaf surfaces. SEM and TLM images (Fig. 18) show no indication of secondary venation. Safranin staining (duration: ca

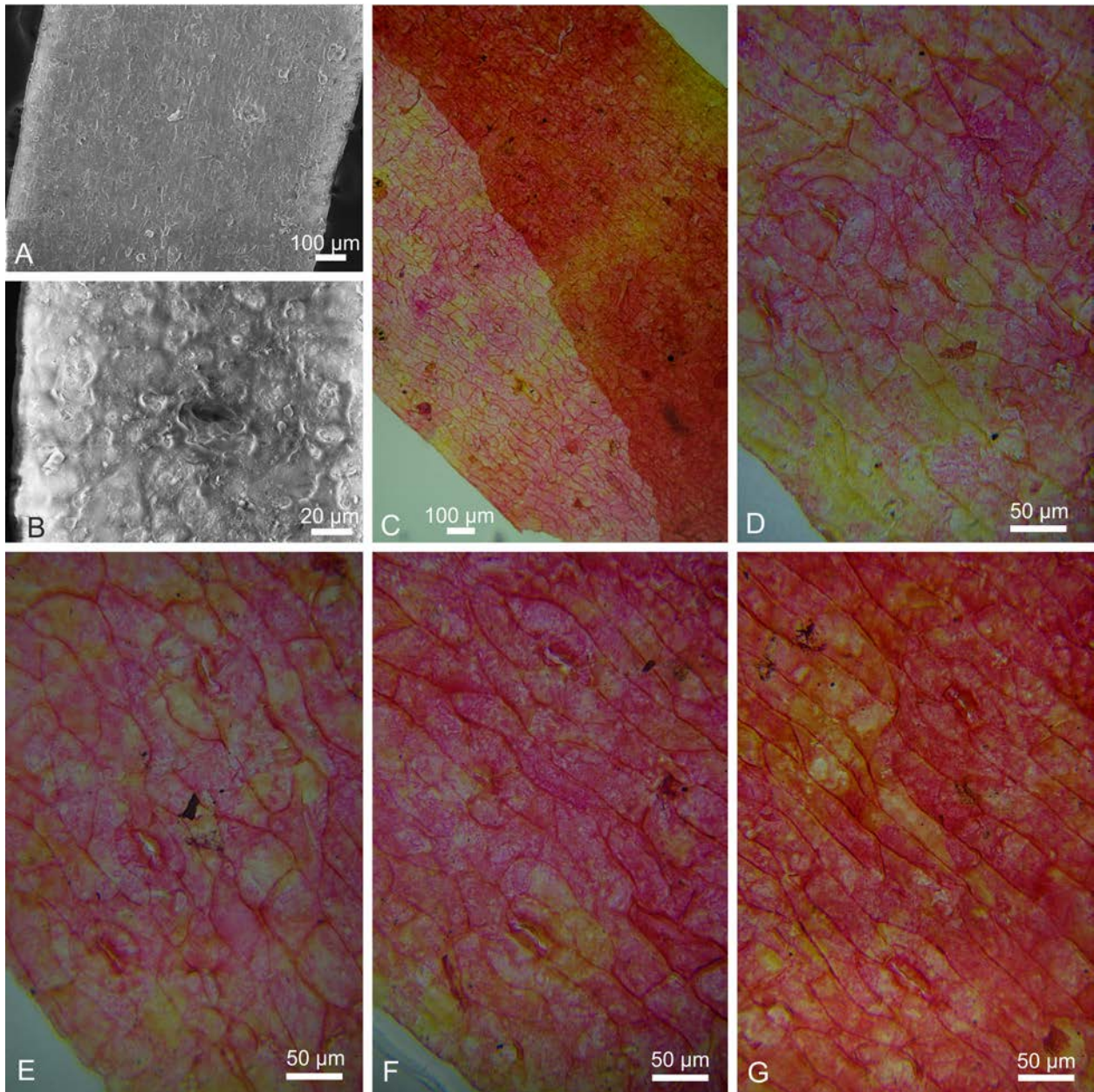


Fig. 18. A–G: *Xylopteris elongata* (Carruthers 1872) Frenguelli 1943 emend. nov.; Meandu Mine, near Nanango, Queensland; Tarong Basin (upper Carnian). **A, B:** QMF57849b (SEM stub). **C–E:** QMF57851c (TLM slide). **F, G:** QMF57851b (TLM slide). **A:** full pinnule width, showing thick and irregular epicellular cuticle obscuring underlying cell structure. **B:** stoma (specimen edge not natural). **C:** showing full pinnule width; upper darker portion comprises superimposed upper and lower epidermis; lower lighter area shows single epidermal layer. **D–G:** stomata and cell alignment with longitudinal axis of pinnule

6 minutes) commonly coloured both upper and lower surfaces of pinnules equally, but in some cases a slight difference in degree of colouring was observed between those surfaces. Thus, the thickness of epicellular cutin was probably more or less equal on both upper and lower leaf surfaces. The epicellular surface is rough but not papillate (Fig. 18). Likewise, the cuticle from Carruthers's (1872) collection is not papillate (Townrow 1962, p. 126).

Cuticular specimens from the Tarong Basin were easily removed mechanically from the rock surface. Microscopic examination

of unprocessed cuticle (i.e. not chemically treated: TLM slide QMF57849c) with a strong light source shows a distinctly darker central region laterally, extending for at least half of the entire width of rachides and pinnules but becoming abruptly lighter near margins. The central portion probably contained a sub-circular vascular bundle, suggesting that the rachis and pinnules were possibly elliptical (or winged) in cross-section prior to compression.

Archangelsky (1968) included *Xylopteris* in *Dicroidium* based on cuticular resemblance. Retallack (1977) disagreed with Archangelsky's

proposal, regarding the genera as easily distinguished. Anderson & Anderson (1983) included a large number of specimens in *D. elongata* (= *X. elongata*) that bear no resemblance to the lectotype of the species. Most of those incorrectly assigned specimens were identified as *D. elongata* f. *rotundipinnulium* and *D. elongata* f. *spinifolium*; they have been reallocated to *D. superbum* in the present study. As discussed above, inclusion of those specimens in *X. elongata* has exaggerated a putative morpho-continuum between *Xylopteris* and *Dicroidium*.

Other specimens figured as *Dicroidium elongata* by Anderson & Anderson (1983) resemble *D. odontopteroides* (see above synonymy for that species). Although it is arguable that some of those specimens have irregular pinnule margins (hence, possibly better attributed to *D. dubium*), they surely do not resemble the lectotype of *Xylopteris elongata*.

Retallack (1977) recognised two varieties of *Xylopteris elongata*, one having closely spaced pinnules and the other widely spaced pinnules (>4 pinnule widths between adjacent pinnae). Baldoni (1980) identified the widely spaced forms as a separate species, *X. rigida* (Dun 1909) Jain & Delevoryas 1967. Dun (1909) erected *Sphenopteris rigida* based on specimens from the Lower–Middle Triassic (?Olenekian–Anisian: Totterdell et al. 2009, fig. 2) Napperby Formation of the Gunnedah Basin, New South Wales. Jain & Delevoryas (1967) recombined the species with *Xylopteris* but they were apparently unaware of Townrow's (1962) reassessment of the type species and thus considered Dun's (1909) and their own material to differ from that species. Retallack (1977) regarded *X. rigida* as a junior synonym of *X. elongata*. Baldoni (1980) adopted *X. rigida* based on cuticular characters; however, her sample sizes were small and the identified distinguishing characters have limited taxonomic value (following Barclay et al. 2007, tab. 1). Her figured megascopic specimens assigned to *X. rigida* and to *X. elongata* have not been included in the above synonymy as they are insufficient for confident assignment. Specimen QMF52275 (re-examined herein) was reported from Dinmore Quarry, Queensland (upper Tivoli Formation, Brassall Subgroup, Ipswich Basin: Carnian–lowermost Norian) by Anderson et al. (2008) and has a stem with several attached fronds. The fronds were attributed to

Dicroidium elongata but they are not univeined and have strongly lobed pinnules and are thus attributed herein to *D. superbum*. They do not resemble the lectotype of *X. elongata*.

Bomfleur & Kerp (2010) included unipinnate and bipinnate fronds in *Dicroidium elongata* (= *Xylopteris elongata*) essentially following Anderson & Anderson (1983). They also adopted *D. spinifolia* (Tenison-Woods 1884) Anderson & Anderson 1970 for bipinnate fronds but suggested that they could distinguish bipinnate specimens of the two species based on the cuticle (Bomfleur & Kerp 2010, p. 70). However, the megascopic specimens that they assigned to *D. spinifolia* belong to *D. superbum*, thus accounting for the differing cuticle. Moreover, their cuticular figures suggest the presence of secondary venation (Bomfleur & Kerp 2010, pl. 13). The cuticle assigned to *D. elongata* (Bomfleur & Kerp 2010, pl. 2) appears to be from a bipinnate frond (Bomfleur & Kerp 2010, caption for pl. 2, fig. 1) and as such it is probably representative of *X. spinifolia*.

Douglas (1969) erected *Xylopteris difformis* based on specimens from the Lower Cretaceous Otway Group (Duddy 2003, fig. 9.2), Victoria. His designated holotype is preserved as a carbonaceous compression in a core sample (MVP167984, formerly GSV60320: Douglas 1969, fig. 1.34, pl. 10, fig. 1; re-examined herein). The leaves are incomplete, <50 mm long, narrow with a wide midrib, and venation (or striation), where visible, is subparallel to the midrib. The latter character differs from Gondwanan Triassic species of *Xylopteris* (univeined). Furthermore, the leaves are basally expanded and emerge from a common point (perhaps a remnant of a small tuft), suggesting that they may be from a subarborescent lycophyte.

Xylopteris spinifolia

(Tenison-Woods 1884) Frenguelli 1943

Fig. 19

Synonymy. The following synonymy list is limited to figured specimens that pertain to the discussion herein. See also Retallack's (1977) synonymy list.

- 1884 *Trichomanides spinifolium* Tenison-Woods, p. 95, pl. 3, fig. 7. [basionym]
- 1917a *Stenopteris elongata* (Carruthers); Walkom, pl. 1, fig. 1, pl. 6, fig. 3.
- 1947a *Stenopteris spinifolia* (Tenison-Woods) Seward; Jones & de Jersey, text-fig. 17, pl. 2, fig. 6, pl. 3, fig. 2.

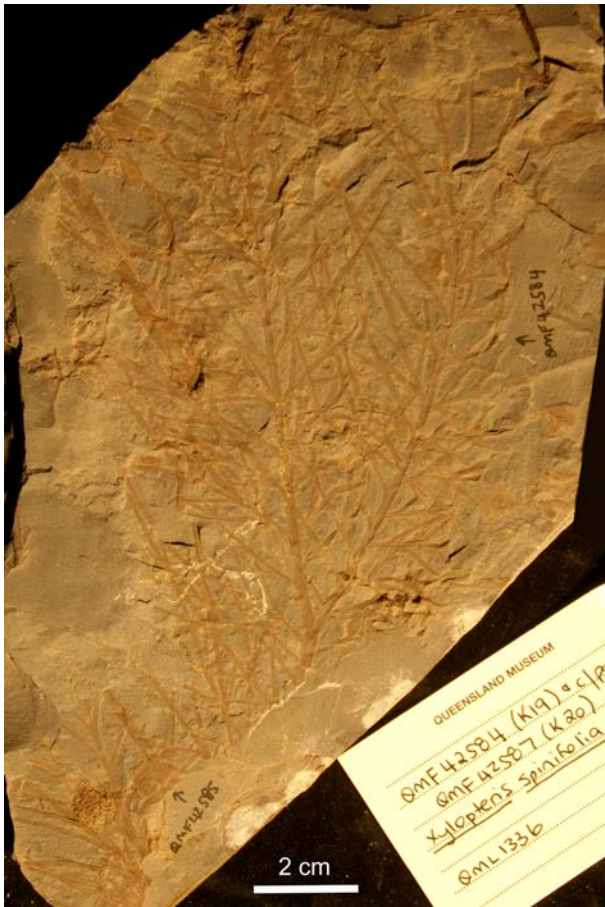


Fig. 19. *Xylopteris spinifolia* (Tenison-Woods 1884) Fren-guelli 1943, QMF42584a; Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Collected by R. Knezour

- 1977 *Xylopteris spinifolia* (Tenison-Woods) Fren-guelli 1943; Retallack, micro-fiche frames J13–J14.
- 1982 *Dicroidium spinifolium* (Tenison-Woods) Ander-son & Anderson; Holmes, fig. 5B, C (only).
- 1983 *Dicroidium elongatum* forma *remotipinnulum* Anderson & Anderson, pl. 48, figs 25–27.
- 1983 *Dicroidium elongatum* forma *spinifolium* Anderson & Anderson, pl. 46, figs 16–21, pl. 47, figs 1–4, 6.
- 2005a *Dicroidium elongatum* (Carruthers) Archangel-sky 1968; Holmes & Anderson, pp. 8–9, figs 19, 20A.

Type material. Holotype (Tenison-Woods 1884, p. 95, pl. 3, fig. 7) by effective original designation [ICN, Article 9.1, Note 1]; purportedly collected from Rosewood, west of Ipswich, Queensland. The strata at that locality are Early–Middle Jurassic in age, being part of the Clarence–Moreton Basin (Fig. 2). As discussed above, Tenison-Woods’s (1884) collection from the Rosewood area is almost certainly com-promised, representing an admixed Trias-sic/Jurassic flora (at least). Thus, his figured specimen (SUM33, Macleay Museum, The

University of Sydney; Retallack 1977) may not be from the reported location or is possi-bly not a genuine representative of the genus; however, based on Tenison-Woods’s figure and description the former explanation seems probable. The specimen has been neither fig-ured nor described since Tenison-Woods’s time and remains a doubtful basis for a species that otherwise includes Triassic material.

Diagnosis. See Tenison-Woods (1884, p. 95).

Material. GSQF266, UQF8200, UQF20632a/b (part and counterpart): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen GSQF266 was figured by Shirley (1898, pl. 10, fig. 3) as *Trichomanides elon-gata* (Carruthers 1872) Jack in Jack & Ethe-ridge 1892 and described by Walkom (1917a, pp. 40–41) as *Stenopteris elongata* (Carruthers 1872) Seward 1903. The specimen comprises the distal portions of several fronds that are mostly unipinnate, but pinnules attached to two lower pinnae indicate that the fronds are bipinnate, albeit poor examples. Specimen UQF8200 (formerly S42 of Simmonds’s col-lection) was figured by Walkom (1917a, pl. 1, fig. 1) as *S. elongata* and by Jones & de Jersey (1947a, pl. 2, fig. 6) as *S. spinifolia*.

QMF42584a/b (Fig. 19): Blackstone Hill, Ipswich; Blackstone Formation, Brassall Sub-group, Ipswich Basin (Carnian–lowermost Norian). Specimen QMF42584b is also cata-logued as QMF42587 (counterpart).

UQF18863a/b (part and counter-part), UQF20619, UQF20622, UQF20623, UQF20632a/b (part and counterpart), UQF43867 (previously S41 of Simmonds’s collection): Denmark Hill, Ipswich; Black-stone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen UQF43867 was figured by Walkom (1917a, pl. 6, fig. 3) and Jones & de Jersey (1947a, pl. 3, fig. 2) as *Stenopteris elongata* and *Stenopteris spinifolia*, respectively.

UQF64484, UQF64744a/b (part and counter-part): Dinmore Quarry, Dinmore, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

Occurrence. See Tab. 1.

Description. Frond bipinnate, >130 mm long. Rachis bifurcating, <2.2 mm wide basally. Pinnae opposite to alternate, up to 50 mm long,

arising from rachis at $<50^\circ$. Pinna-rachides and pinnules ca 1 mm wide. Pinnules linear with acutely pointed apices, opposite to subopposite, <13 mm long, inclined to pinna-rachis at ca 30° . Pinnae and pinnules univeined.

Discussion. Despite doubts regarding the collection location of the type specimen, circumscription of the species herein follows Tenison-Woods's (1884) diagnosis. Anderson & Anderson (1970) recombined the species with *Dicroidium*. Bomfleur & Kerp (2010) emended the diagnosis based on specimens from the Upper Triassic of North Victoria Land, Antarctica. However, as noted above, their specimens are representative of *D. superbum*, which was hitherto poorly understood. Representatives of *D. superbum* commonly have linear pinnules positioned distally on pinnae (somewhat resembling those of *Xylopteris*) but the pinnules are generally not linear in the basal portion of pinnae. As noted above, the cuticle figured by Bomfleur & Kerp (2010, pl. 2) as *D. elongata* probably belongs to *X. spinifolia* as it appears to be from a bipinnate frond (Bomfleur & Kerp 2010, caption for pl. 2, fig. 1).

Anderson & Anderson (1983, p. 116) erected forma *Dicroidium elongata* f. *spinifolium* based on Tenison-Woods's (1884, pl. 3, fig. 7) figured specimen (the type of *Xylopteris spinifolia*) but their circumscription is inconsistent with the diagnoses of both *X. elongata* (= *D. elongata*) and *X. spinifolia*, encompassing a set of characters resembling those of *D. superbum*. Inadequately preserved specimens attributed to *Xylopteris* by Ottone (2006, fig. 2A, C) from the Middle to Upper Triassic of the Rincón Blanco Group in San Juan Province, Argentina have broad pinnules (up to 3 mm wide) and possibly represent the apical portions of fronds belonging to *D. superbum*.

Order: ?**Peltaspermales**

Family: Uncertain

Genus: ***Paraxylopteris***

Pattemore & Rigby 2005

Type species. *Paraxylopteris queenslandensis* by original designation (monotypic).

Type material: see below.

Diagnosis. As for species (monotypic genus).

Paraxylopteris queenslandensis

Pattemore & Rigby 2005

Figs 20, 21

Synonymy.

2005 *Paraxylopteris queenslandensis* Pattemore & Rigby, pp. 336–337, fig. 6A, B.

Type material. Holotype (QMF42425a/b, part and counterpart: Fig. 20) by original designation (Pattemore & Rigby 2005, pp. 336–337, fig. 6); collected from Dinmore Quarry, Ipswich, Queensland (upper Tivoli Formation, Brassall Subgroup, Ipswich Basin: Carnian–lowermost Norian).

Diagnosis. See Pattemore & Rigby (2005, p. 336).

Material. QMF42425a/b (holotype, part and counterpart: Fig. 20), QMF58778a/b (part and counterpart: Fig. 21): Dinmore Quarry, Ipswich, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen QMF42425b



Fig. 20. *Paraxylopteris queenslandensis* Pattemore & Rigby 2005, QMF42425a, holotype; Dinmore Quarry, Ipswich, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Collected by R. Knezour

(counterpart to QMF42425a) was originally numbered as QMF42515.

Occurrence. As for material listed above; unknown elsewhere.

Description. Frond unipinnate, ca 70 mm

long. Rachis linear, leaf-like, <2.5 mm wide, having prominent midrib, ?bifurcating. Pinnales arising very acutely (<20°), subopposite to alternate, univeined. Fertile portion of frond limited to oval-shaped area (<25 mm long, <10 mm wide) centred on rachis. Numerous

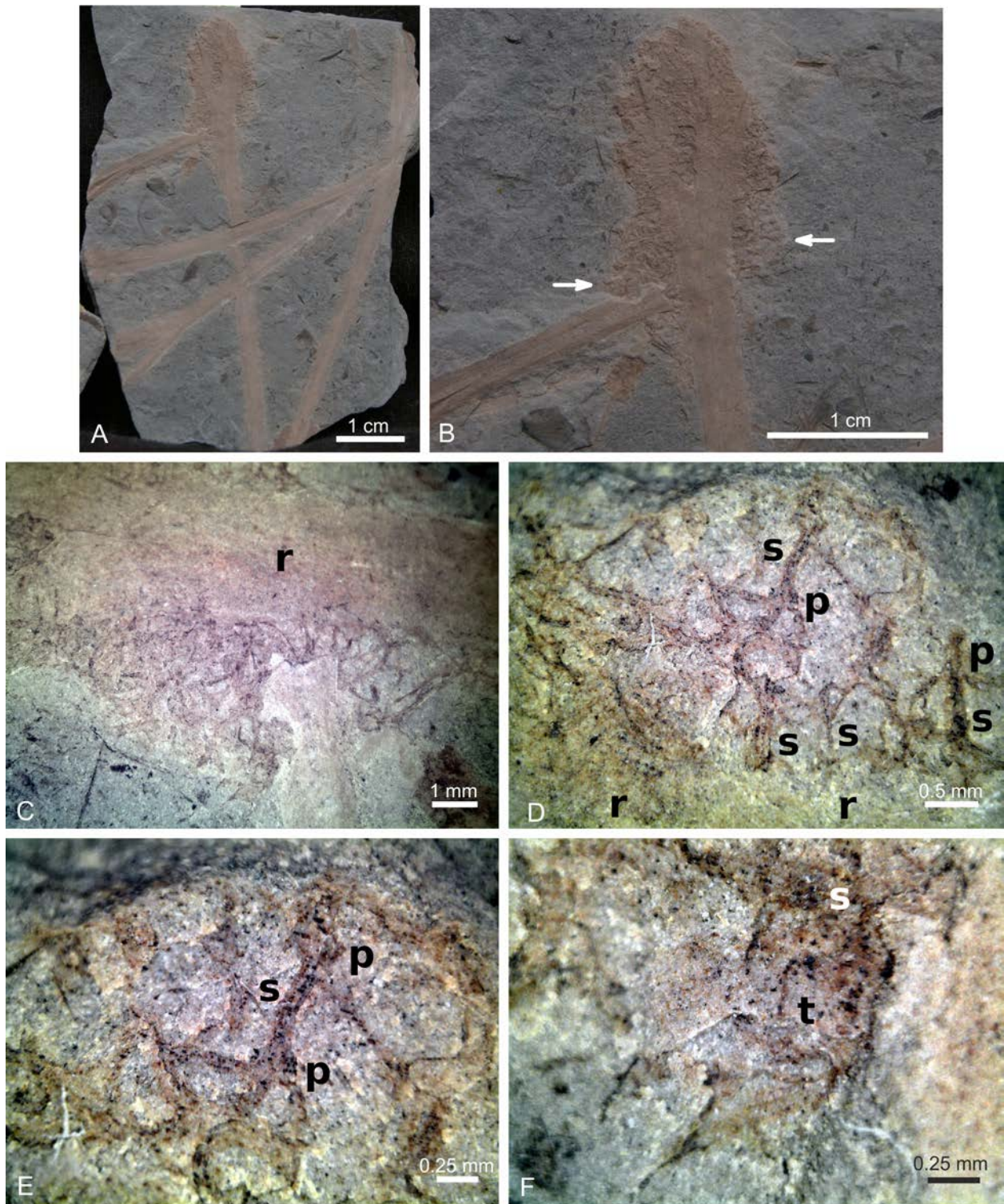


Fig. 21. A–F: *Paraxyleopteris queenslandensis* Pattemore & Rigby 2005, QMF58778b; Dinmore Quarry, Ipswich, Queensland; upper Tivoli Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). **B:** left arrow indicates position of images C and F; right arrow indicates position of images D and E. Key: **p** – point of branching; **r** – rachis; **s** – hair-like structure; **t** – blade (?sac). Collected by R. Knezour

very small hair-like (<0.13 mm wide, length probably >3 mm) structures arising from rachis and pinnules in an unclear arrangement; each hair-like structure having at least one pair of opposite branches. Fertile structures bearing uncertain number of small leaf-like blades or ?sacs (1.25 mm long, 0.6 mm wide), mounted ?bilaterally. Specimens not carbonaceous.

Discussion. The specimens described above are the only known representatives of the genus. Both specimens resemble *Xylopteris argentina* Frenguelli 1943 except for their fertile structures. Non-fertile fronds attributable to the latter are preserved on slabs adjacent to both fertile specimens (Figs 20, 21). *Xylopteris argentina* is common in strata at Dinmore Quarry (Pattemore & Rigby 2005). Other non-fertile specimens from the site were examined herein (UQF82579a/b, UQF82602a/b: the latter, Fig. 17A2) but are not described separately in the present study (see description by Pattemore & Rigby 2005, p. 335). *Xylopteris argentina* is distinguished from *X. elongata* based on the number of pinnules on each side of the rachis (the latter having >4: Retallack 1977, micro-fiche slides, J7–J8); see Fig. 17A1–3 herein. Frenguelli (1943) erected *X. argentina* based on Kurtz's (1921) variety *X. elongata* var. *argentina* but Frenguelli has priority at species level (ICN, Article 11.2). A report of more than one rachis bifurcation (Stipanovic et al. 1996, pp. 156–158, fig. 30) in fronds attributable to *X. argentina* is a doubtful interpretation. That character is otherwise unknown in the genus. As noted above, Stipanovic et al. (1996) largely based their view of the genus on an erroneous description of the lectotype of *X. elongata* [type species].

Cuticle belonging to *Xylopteris argentina* (Anderson & Anderson 1989, pls 3–6) resembles that of *X. elongata* (Fig. 18). It is known only from three South African specimens, all from one locality (Little Switzerland, western KwaZulu-Natal: Carnian Molteno Formation). Cuticle that was line-drawn by Anderson & Anderson (1983, fig. 6.6) as *D. elongatum* subsp. *argentinum* was from a specimen that they attributed elsewhere to *D. elongatum* subsp. *elongatum* (BP/2/1368: Anderson & Anderson 1983, pl. 38, fig. 16, pl. 105, figs 1–3, 5, 6 and fig. 6.5 on p. 201). Baldoni (1980) described but did not figure cuticle (lacking stomata) from a specimen attributed to *X. argentina*.

The fertile portion of the frond is laterally centred on the rachis in both specimens and comprises numerous hair-like structures that arise in an unknown arrangement, presumably from one side of the rachis. Those small structures are branched oppositely (Fig. 21D, E); thus, their interpretation as fungal hyphae is improbable. They are unlike the filiform structures in representatives of *Osmundopsis* Harris 1931 emend. Harris 1961, which are bi- and tri-pinnate and lack laminae (Harris 1961, Holmes 2001b).

The specimens do not structurally resemble *Pteruchus*, which has dedicated pinnate fructifications (Pattemore 2016). *Paraxylopteris queenslandensis*, an apparently otherwise unmodified vegetative frond, is tentatively placed here in the Peltaspermales based on the long-recognised association of *Xylopteris* with other pteridosperms of the Gondwanan Triassic (Frenguelli 1943, Archangelsky 1968, Retallack 1977). *Xylopteris* has been closely allied with *Dicroidium* (Archangelsky 1968, Retallack 1977, Anderson & Anderson 1983); however, the evidence for that association is limited to bifurcating rachides and stephanocytic stomata in representatives of both genera. The small size of the fertile parts suggests that they represent rudimentary male pteridosperm fructifications; however, interpretation as fertile fern fronds cannot be discounted. No probable female fructification has been identified.

Order: Ginkgoales

Discussion. Three genera have mainly been used for ginkgoalean leaf specimens from the Gondwanan Triassic: *Ginkgoites* Seward 1919, *Baiera* Braun 1843 emend. Florin 1936 and *Sphenobaiera* Florin 1936 emend. Harris & Millington 1974. Ginkgoalean reports from the Gondwanan Triassic were summarised by Barboni & Dutra (2015).

Ginkgoaleans are unrecorded from the Lower and Middle Jurassic of Queensland. Gould (1974) first noted their absence from the Walloon Coal Measures in Queensland. Similarly, Birkenmajer & Ociepa (2008, p. 86) observed that ginkgoaleans are absent from the Hope Bay flora in Antarctica (?uppermost Triassic–Lower Jurassic: discussed above). The numerous studies cited herein concerning the Lower and Middle Jurassic of Australia, New Zealand and Antarctica suggest that ginkgoaleans were absent from all those regions (i.e. much of

Eastern Gondwana: Fig. 23) through that interval; however, that is not true for Western Gondwana (Zamuner et al. 2001, Gnaedinger 2012).

Ginkgoites was established for fossilised leaves resembling those of *Ginkgo biloba* L. but lacking confirmatory fructifications (Seward 1919). *Baiera*, based on German Jurassic material (Bauer et al. 2013), resembles *Ginkgoites* but differs in having several deeply divided leaf segments (Florin 1936, Harris & Millington 1974, pp. 29–30). Early confusion regarding differentiation of the genera (Seward 1919, Harris 1935) was addressed by Florin (1936), whose diagnostic emendation of *Baiera* was adopted by Bauer et al. (2013). Harris & Millington (1974, p. 4) chose not to use *Ginkgoites*, instead referring the fossil material to *Ginkgo*. However, recent changes regarding the treatment of fossil taxa (ICN: Zijlstra 2014) suggests Florin's (1936) approach is preferable.

Czekanowskia Heer 1876 has been reported from Gondwana (e.g. Frenguelli 1946, Jones & de Jersey 1947a); however, Samylina & Kiritchkova (1991, 1993) established that czekanowskians are restricted to the Northern Hemisphere, reaching maximum dispersal during the Jurassic. The leaves broadly resemble those of other ginkgoaleans but are distinguished by their epidermal structure (Samylina & Kiritchkova 1993).

Family: **Ginkgoaceae** Engler in Engler & Prantl 1897

Genus: ***Sphenobaiera*** Florin 1936 emend. Harris & Millington 1974

Type species. *Sphenobaiera spectabilis* (Nathorst 1906) Florin 1936 by original designation, based on specimens from Stabbarp, Sweden (Rhaetian: Florin 1936). The type species is known exclusively from that locality and from coeval strata in Jameson Land, Greenland (Pott & McLoughlin 2011, pp. 1025, 1038).

Diagnosis. See Harris & Millington (1974, p. 39).

Discussion. *Sphenobaiera* was established on specimens previously assigned to *Baiera* and on additional material from Franz Josef Land (Florin 1936), northern Barents Sea. Franz Josef Land (a group of islands) includes Triassic–Cretaceous strata (Dibner 1998); however, it seems that Florin's (1936) specimens

(from five locations on three islands) are probably an admixture of Upper Jurassic and Lower Cretaceous material (Newton & Teall 1897, 1898, Koettlitz 1898, Smelror 1986, Dibner 1998, Dypvik et al. 1998, Solheim et al. 1998). Numerous specimens have since been referred to *Sphenobaiera* from the Permian through Cretaceous with a global distribution (Taylor et al. 2009). The genus is characterised by the lack of a distinct petiole (or significantly reduced lamina) which is offset from the remainder of the leaf lamina. The generic emendation by Harris & Millington (1974) added “leaves shed separately”, thereby better distinguishing the genus from czekanowskian foliage. *Sphenobaiera*-like leaves have been affiliated with a range of fructifications, including some with organic connection (Harris 1935, Archangelsky 1965, Harris & Millington 1974, Kirchner & van Konijnenburg-van Cittert 1994, Retallack 1981, Zhou 1997, Anderson & Anderson 2003).

***Sphenobaiera* sp.**

Figs 17B3, 22A

Material. QMF57838, QMF57845 (Fig. 22A), QMF57850 (Fig. 17B3), QMF57853, QMF57868 and QMF57883: Meandu Mine, Queensland; Tarong Basin (upper Carnian).

Description. Largest specimen 90 mm long, 65 mm wide (almost complete). Leaves cuneate, lamina divided at least once into lanceolate segments; medial division deep (two-thirds of leaf length), others ca half the length of leaf; not exceeding four segments per leaf. Apices slightly retuse or ragged (?damaged). Leaf base gradually reduced to 3 mm wide; no indication of distinct petiole. Venation parallel: density, ca 20 veins per 10 mm but unclear in all but one specimen (QMF57838). Vein bifurcation indeterminate due to indifferent preservation.

Discussion. The leaf morphology and venation density resemble that of specimens assigned by Holmes and Anderson (2007) to their species *Sphenobaiera densinerva*, except that the specimens from the Tarong Basin are not petiolate. Holmes & Anderson's figured specimens have significantly reduced laminae basally and are probably better placed in *Baiera* (following Florin 1936, Harris & Millington 1974, Bauer et al. 2013). Several ginkgoalean specimens lacking a distinct petiole

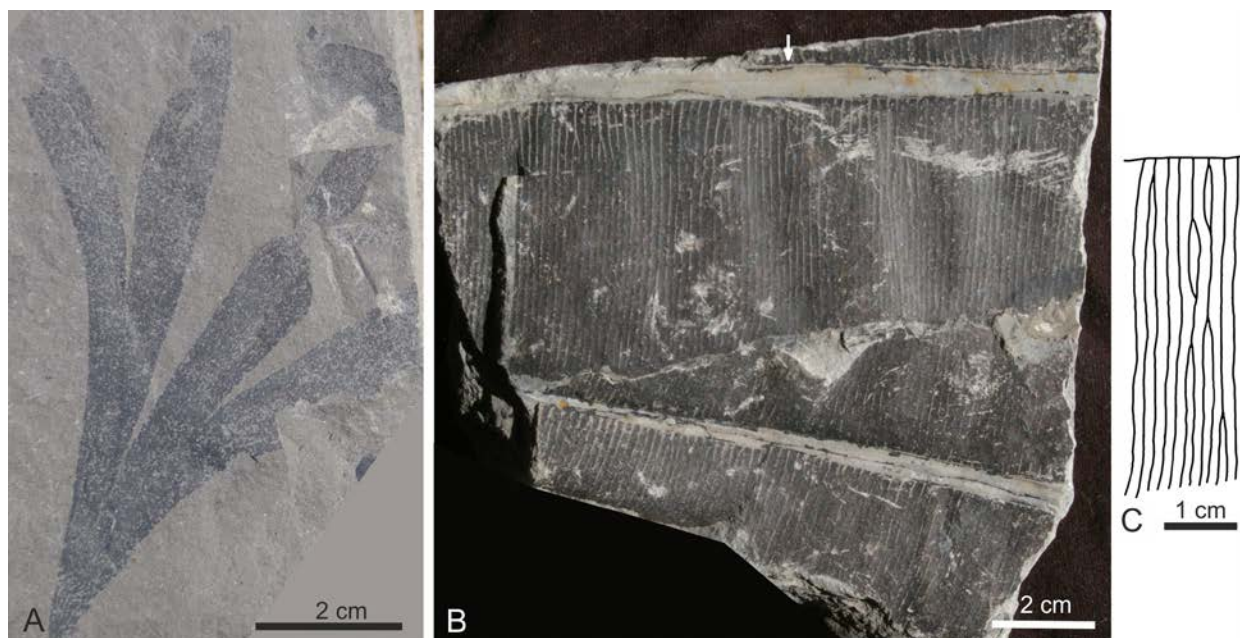


Fig. 22. **A:** *Sphenobaiera* sp., QMF57845; Meandu Mine, near Nanango, Queensland; Tarong Basin (upper Carnian). **B, C:** *Nilssononia taeniopteroides* Halle 1913, QMF58715; Callide Mine, near Biloela, Queensland; Callide Basin (lower Rhaetian). Arrow indicates position of venation shown in camera lucida image, C

were figured by Walkom (1917b, 1924a, 1928) from the Anisian–lowermost Norian of south-east Queensland but their leaves are divided into more segments than those described above.

Jones & de Jersey (1947a) recombined *Baiera tenuifolia* Johnston 1888 with *Czekanowskia* and included additional material from the Ipswich Basin (UQF2037: re-examined herein; also figured by Hill et al. 1965, pl. 9, fig. 2). The specimen has many more divided leaf segments and each segment is much narrower than in the specimens described here. Other ginkgoalean specimens, figured by Jones & de Jersey (1947a) and Hill et al. (1965), are either petiolate or have undivided laminae.

Anderson and Anderson (1989) erected *Sphenobaiera sectina* and *S. helvetica* with specimens from the Carnian of South Africa. Representatives of both species broadly resemble the specimens described herein but their vein density is appreciably lower (about half).

Class: **Cycadopsida**

Order: **Cycadales**

Family: **Beaniaceae** Meyen 1984

Discussion. The family name is derived from the name of the female cone, *Beania* Carruthers 1869 emend. Harris 1964. Representatives of

Beania, *Nilssonia* (below), and other genera have been recognised as belonging to the same plant (Harris 1964, p. 164, Meyen 1984, Pant 1987, Jones 1993), as was originally suggested by Seward (1917, p. 568).

Genus: **Nilssonia** Brongniart 1825b

Type species. Brongniart (1825a, p. 218, 1825b, pl. 12, figs 3–5) erected *Nilssonia elongata* and *N. brevis* with specimens from the Lower Jurassic of Sweden (Pott et al. 2007a, p. 199). A third species was not definitely included in the genus (*Nilssonia? aequalis*: Brongniart 1825a, p. 219, pl. 12, fig. 6) and is now known to be bennettitalean (Pott & McLoughlin 2009, pp. 125–129). The type of *N. elongata* was assigned by Nathorst (1909) to his *N. brevis* f. *elongata*; thus effectively designating *N. brevis* as the type species (confirmed by Seward 1917, p. 566).

Diagnosis. Generic diagnostic characters were summarised by Harris (1964, p. 32).

***Nilssonia taeniopteroides* Halle 1913**

Fig. 22B, C

Synonymy.

1913 *Nilssonia taeniopteroides* Halle, pp. 47–50, text-fig. 11, pl. 5, pl. 6, fig. 1–7. [basionym]

1977 *Nilssonia crassinervis*; O'Sullivan (unpubl.), p. 25, fig. 38d.

- 1980 *Nilssonia ametra* Webb (unpubl.), pp. 90–93, text-figs 18e, 18f, 21a–d, pl. 11, figs 1, 2, 4, 5, 7, pl. 29, figs 1–5.
- 1989 *Nilssonia taeniopteroides* Halle 1913; Gee, pp. 184–185, pl. 6, fig. 49.
- 2004 *Taeniopteris taeniopteroides* (Halle) Rees & Cleal, pp. 48–50, text-fig. 5a–d, pl. 15, figs 1–4.
- 2008 *Nilssonia taeniopteroides* Halle; Birkenmajer & Ociepa, pp. 55–57, figs 28, 29.

Type material. Lectotype (Halle 1913, text-fig. 11b, pl. 5) designated subsequently by Gee (1989, p. 185); collected from the ?Upper Triassic–Lower Jurassic Mount Flora Formation, Botany Bay Group (included in the Botany Bay Group basins: Hathway 2000) at Hope Bay, Antarctic Peninsula. Further detail provided by Rees and Cleal (2004, p. 49).

Diagnosis. See Halle (1913, pp. 47–50).

Material. QMF58715: Callide Mine, near Biloela, Queensland; Callide Basin (Upper Triassic, lower Rhaetian).

Occurrence. Lower Rhaetian of the Callide Basin, Queensland. ?Upper Triassic–Lower Jurassic, Botany Bay Group, Antarctic Peninsula (Botany Bay Group basins: Hathway 2000).

Description. Leaf simple, entire, ca 100 mm wide; midrib 2–6 mm wide. Secondary veins arising almost perpendicularly to midrib, extending almost straight to margin. Veins commonly bifurcating once, rarely twice, ca 8 veins/10 mm, rarely merging. Although faint and only locally present, secondary venation over midrib indicates dorsal attachment of lamina.

Discussion. O’Sullivan (1977, fig. 38d) and Webb (1980, pl. 11, figs 1, 2) figured specimen UQF69922 from lower Rhaetian strata of the Callide Mine (Dunn Creek area), Callide Basin, Queensland. Indifferently preserved cuticle was extracted from the specimen by Webb (1980, text-fig. 21, pl. 29, figs 1–5); it is the only record of cuticle belonging to *Nilssonia taeniopteroides*. Stomata are unaligned and restricted to the lower leaf surface; cells on the upper surface are strongly aligned. Webb’s (1980, text-fig. 21) line-drawn figure suggests the stomata are actinocytic (Barclay et al. 2007, fig. 3). Available epidermal characters, albeit limited, are consistent with Harris’s (1964) figured specimens from the Middle Jurassic of Yorkshire that were assigned to various species of the genus. Representatives

of *Nilssonia* from the Upper Triassic of Austria (Pott et al. 2007a, pls 3, 5) have actinocytic stomata.

Nathorst (1909) erected *Nilssoniopteris* based on *Nilssonia tenuinervis* Nathorst 1880, its lectotype from the Yorkshire Middle Jurassic being designated only recently (Cleal et al. 2006). Cuticle belonging to the type species of *Nilssoniopteris* (Nathorst 1909, pl. 7, fig. 21, Cleal et al. 2006, fig. 1A–C) has strongly crenulate anticlinal cell walls, unlike that of Webb’s (1980, text-fig. 21, pl. 29, figs 1–5) figured cuticle (smooth). Pott et al. (2007b) identified *Nilssoniopteris* from the Carnian of Austria having smooth anticlinal walls; they suggested that their specimens represent an early evolutionary stage in the bennettitaleans, prior to the development of crenulate anticlinal cell walls in that group. That is an improbable explanation because cell wall crenulation is predominantly influenced by environmental conditions, not genetic factors (Barclay et al. 2007, tab. 1). Thus, that character is not useful in distinguishing *Nilssoniopteris* and *Nilssonia*. Likewise, both genera include species variously having amphistomatic or hypostomatic leaves (Cleal et al. 2006, Pott et al. 2007a, b). Syndetocheilic stomatal development has been assumed in representatives of *Nilssoniopteris* (e.g. Harris 1969, Cleal et al. 2006, Pott et al. 2007b), but that is questionable because preserved stomatal ontogeny is unrecorded in specimens assigned to the type and other species of the genus; thus, that presumed ontogenetic pathway is speculative (see Baranova 1987, pp. 56–57). Stomatal apparatuses in representatives of *Nilssoniopteris* are diacytic (Pott et al. 2007b) or laterocytic (Harris 1969, Pott et al. 2007b, pl. 2, fig. 6); those of the type species are less clear but are probably laterocytic (type specimen: Cleal et al. 2006, fig. 1A, B). As noted above, the only recorded cuticle from a representative of *Nilssonia taeniopteroides* conforms with that of other species of *Nilssonia*, suggesting that vein bifurcation is not a reliable basis for distinguishing *Nilssonia* and *Nilssoniopteris* (cf. Pott et al. 2007a, b).

Webb (1980) assigned specimens from the Callide Basin (UQF23851, UQF69922, UQF71058, UQF71059) to his unpublished species “*Nilssonia ametra*”; none could be located during the present study. *Nilssonia dissita* Webb in Holmes et al. (2010) was based on specimens from the Anisian Esk Trough, Queensland and Nymboida Coal Measures,

New South Wales. The species has a much narrower midrib than the specimen described here. Unlike *N. dissita*, Webb (1980) identified veins that bifurcate then merge in his specimens from the Callide Basin; this character is confirmed in the present study (Fig. 22C) and was also observed by Halle (1913, p. 49) and Rees & Cleal (2004, p. 50) in specimens from the ?Upper Triassic–Lower Jurassic of the Botany Bay Group on the Antarctic Peninsula (locality and geology discussed previously).

The study specimen includes two partially overlapping leaf fragments (Fig. 22B). The lamina are dorsally attached to the midrib, despite the venation over the midrib being very faint and only visible in places; likewise, this can also be seen in Gee's (1989, pl. 6, fig. 49) figured specimen. It appears that the cleavage plane had a tendency to pass through the midrib rather than consistently follow the lamina over the midrib's upper surface. Webb (1980) referred to this as "splitting", and it was observed in most of his specimens to some extent. He interpreted this as partial separation of lamina over the midrib. Halle (1913, p. 49) regarded this as a projection of the midrib. However, the lamina were probably domed (i.e. raised) over the midrib and thus, as noted above, the variously faint or locally absent venation over the midrib that has been observed in several specimens is probably a result of the cleavage plane (i.e. not a partial or inconsistent separation of lamina).

DISCUSSION

VICTORIAN TRIASSIC

Specimens recorded by Chapman (1927) and numerous other undescribed specimens held in the Victoria Museum from two Victorian localities are re-examined herein: viz., Old Nuggetty Gully, Yandoit Hill and the Council Trench, south of Bald Hill, Bacchus Marsh (Douglas 1988, fig. 7.1, Duddy 2003, p. 241). The precise age(s) of Mesozoic strata at those sites is conjectural.

The weathered fossiliferous beds of the Council Trench disconformably overlie Permian strata and are very limited in extent (David & Browne 1950, Duddy 2003). Chapman (1927) suggested that megaflores in the Council Trench resembled that of the Ipswich

Basin. However, the remains are fragmentary and a Triassic dating remains unconfirmed (Douglas 1969, 1988, Duddy 2003). The fossil flora from Yandoit Hill was also suggested to resemble that of the Ipswich Basin (Douglas 1969, 1988) but the specimens are even more fragmentary than those from the Council Trench. Various attempts to date strata in the Council Trench have been inconclusive, and fission track analysis of a weathered sandstone provided poor age resolution, including the possibility of post-Triassic deposition (Duddy 2003). A Triassic dating of the Yandoit Hill specimens is evidently based on nothing more than cuticular comparison with specimens from the Ipswich Basin (Douglas 1969, Duddy 2003).

Douglas (1969) identified leaf fragments as *Xylopteris* sp. A from Yandoit Hill, Victoria. All specimens are <10 mm long and were assumed to be from a pinnate leaf. He was unable to draw definitive cuticular comparisons with various species of the genus; his specimens possibly resemble those assigned to *Stenopteris elongata* Carruthers 1872 by Walkom (1919a, pl. 1, fig. 10, pl. 3, fig. 5) from the Lower Cretaceous Burrum Coal Measures, Maryborough Basin, Queensland, and those referred to *Xylopteris elongata* by White (1969) from the Orallo Formation (Lower Cretaceous), Surat Basin, Queensland. Three of Walkom's (1919a) specimens, re-examined herein (GSQF773, GSQF798, GSQF1146), probably represent subarborescent lycophytes, being very small and having multiple bifurcations. Attributions to *Xylopteris* and *Stenopteris* from the Australian post-Triassic (Walkom 1919a, Douglas 1969, White 1969) were probably influenced by the incorrect interpretation of the lectotype of *X. elongata* by Carruthers (1872); as noted above, he identified multiple bifurcations in the frond but Townrow (1962) established that it includes only one bifurcation.

Douglas (1969) tentatively attributed very small leaf fragments lacking secondary venation to *Rienitsia lobata* Jones & de Jersey 1947a from Yandoit Hill, based only on cuticular resemblance to specimens described from the Ipswich Basin by Jones & de Jersey (1947a, pp. 41–45). Walkom (1932) established *Rienitsia* on the basis of fertile fern fronds from the Triassic of the Sydney Basin. Jones & de Jersey (1947a) erected *Rienitsia lobata* with sterile material from the Ipswich Basin and

Table 2. Notes on key specimens examined herein from the Mesozoic of Bacchus Marsh, Victoria

Specimen No.	Identification by Chapman (1927)	Notes
MVP16065	<i>Thinnfeldia odontopteroides</i> Morris 1845 Chapman (1927, pl. 11, fig. 19)	Small fragment (16 mm long) with 1 complete and 3 incomplete pinnules. Venation <i>Cladophlebis</i> -like
MVP16077	<i>Thinnfeldia feistmantelli</i> Johnston 1895 Chapman (1927, pl. 12, fig. 30)	Small fragment (10 mm long) with 4 pinnules. Distal portion of pinnules either missing or partially obscured by sediment; thus, rhomboidal shape described by Chapman (1927, p. 132) is uncertain. Venation unclear. Too poor for confident identification
MVP16058	<i>Thinnfeldia lancifolia</i> Morris 1845 Chapman (1927, pl. 11, fig. 20)	Fragment of single pinnule (9 mm long). Insufficient for confident identification. Probably a fern pinnule
MVP16083	<i>Thinnfeldia lancifolia</i> Morris 1845 Chapman (1927, pl. 11, fig. 21)	Single incomplete pinnule (20 mm long, 5 mm wide). Venation faint, <i>Cladophlebis</i> -like
MVP16068	<i>Stachyopitys</i> sp. cf. <i>S. annularoides</i> Shirley 1898 Chapman (1927, pl. 11, fig. 25)	Complex structure (9 mm long, 4 mm wide) with linear attachments (3 mm long, ca 0.7 mm wide) radiating from one end of a short “stalk”. Distal portion of “stalk” includes subcircular objects. Does not resemble <i>Stachyopitys</i> nor <i>Pteruchus</i> . Probable representative of <i>Williamsonia</i> Carruthers 1870. Resembles “?equisetaceous sheath” figured by Walkom (1919a, pl. 3, fig. 8) from the Lower Cretaceous Burrum Coal Measures, Queensland (GSQF761: examined herein); also cf. Harris (1969, fig. 60B)
MVP16080	<i>Ginkgoites digitata</i> Brongniart 1828 Chapman (1927, pl. 11, fig. 29)	Specimen ca 15 mm long, <5 mm wide, with prominent and wide longitudinal ridges but no venation. Fan shaped in gross form but otherwise unlike ginkgoalean foliage. Possibly equisetalean
MVP16062 (paratype)	<i>Ginkgoites darleyensis</i> Chapman 1927 Chapman (1927, pl. 12, fig. 32)	Indifferently preserved, 15 mm long, venation unclear. Too poor for assignment, possibly a stem fragment
MVP16064 (paratype)	<i>Ginkgoites darleyensis</i> Chapman 1927 Chapman (1927, pl. 12, fig. 33)	Specimen 13 mm long. Chapman's figured venation not visible. Not ginkgoalean; possibly a branching stem
MVP16067 (holotype)	<i>Ginkgoites darleyensis</i> Chapman 1927 Chapman (1927, pl. 12, fig. 34)	Specimen 17 mm long, 1–2 mm wide. No venation visible. General form not indicative of ginkgoalean affiliation; probably a clubmoss

Herbst (1977) recombined the species as *Dejersya lobata* [type species]. Douglas (1969) also attributed several specimens from the Victorian Lower Cretaceous to his species *Rienitsia variabilis*, later recombined as *Rintoulia variabilis* [type species] by McLoughlin et al. (2002); for further discussion see Pattemore et al. (2015a, p. 709). Douglas (1969) incorrectly applied the term “haplocheilic” in his descriptions of both *Xylopteris* and *Reinitsia* cuticle, thus biasing his epidermal characterisation toward the gymnosperms (Pattemore et al. 2015, p. 697). Moreover, his limited cuticular comparisons are insufficient for reliable identification (Pattemore et al. 2015a, based on Barclay et al. 2007).

Chapman's (1927) specimens from the Council Trench (Tab. 2) and numerous others examined herein from that locality and Yandoit Hill (MVP specimens) bear scant resemblance to Triassic floral assemblages. Despite the above noted fission track results, the most convincing megascopic comparisons are with the flora from the Lower Cretaceous Burrum Coal Measures, Queensland.

UMKOMASIACEAE

Archangelsky (1968) regarded *Xylopteris* and *Zuberia* as junior synonyms of *Dicroidium* based only on the similarity of cuticle and/or pinnules in some species. Anderson & Anderson (1983) went considerably further, suggesting that a continuum of morphological characters exists among species of those genera and that it resulted from sympatric speciation. That view evidently resulted from a misunderstanding of the characters encompassing *D. superbum*. Numerous specimens attributable to *D. superbum* were in fact misidentified by Anderson & Anderson (1983) and many other authors. The species and its lectotype have hitherto been inaccurately and inadequately depicted in publications. Its representatives possess pinnules varying among linear, oblanceolate, obovate, oblong, lobed or unlobed. Pinnules can be sufficiently narrow that they resemble those of *Xylopteris*.

Anderson & Anderson's (1983) postulated morpho-continuum among fronds of the

Umkomasiaceae was further emphasised by their greatly expanded circumscriptions of *Xylopteris elongata* (included in *Dicroidium* by them) and *D. dubium*. Their concept was apparently strongly influenced by the above-noted misidentifications and effectively encompassed morphological characters representing subsets of *Xylopteris*, *Dicroidium* and *Zuberia*.

As described previously, the lectotype of *Xylopteris elongata* is unipinnate, univeined, and has long and very narrow pinnules. However, Anderson & Anderson (1983) included bipinnatifid and bipinnate fronds with lobed and multiveined pinnules. Specimens having such additional characters were chiefly assigned to *Dicroidium elongata* forma *rotundipinnulium* and *D. elongata* forma *spinifolium*, but they belong to *D. superbum*. The circumscription of *D. dubium* was enlarged so as to include unipinnate and bipinnate fronds, thereby embracing characters common to *D. odontopteroides* and species of *Zuberia*. Fronds belonging to the latter genus were chiefly included in *D. dubium* subsp. *helvetifolium* and *D. dubium* subsp. *switzifolium*. However, as discussed above, the host plants of *Z. feistmantelii* and *D. odontopteroides* are almost certainly generically distinct based on allied fructifications and wood (Tab. 1).

Genuine representatives of *Xylopteris*, both megascopic and microscopic, show no suggestion of secondary venation. A continuum of characters between *Xylopteris* and *Dicroidium* should at least evidence the emergence of a rudimentary secondary vascular system in *Xylopteris*, but that has not been demonstrated. Anderson & Anderson (1983) simply misidentified narrow pinnules belonging to *D. superbum* as those of *X. elongata* and considered them to show a linkage among species of the two genera; hence their inclusion of *Xylopteris* in *Dicroidium*. Furthermore, neither wood nor fructification has been allied with *Xylopteris* to support its inclusion in *Dicroidium* (Tab. 1); on the contrary, *Paraxylopteris queenslandensis* (allied with *X. argentina*) indicates that the host plants of *Xylopteris* and *Dicroidium* were probably not closely related.

Thus, the putative continuum linking representatives of *Dicroidium*, *Xylopteris* and *Zuberia* is regarded as an artificial construct resulting from (1) specimen misidentification and (2) enlargement of circumscriptions well beyond what can be justified based on the respective

type material. Moreover, that hybridisation could produce such a morphological continuum in the gymnosperms has been shown to be improbable (Pattemore et al. 2015a, p. 698).

DECLINE OF THE UMKOMASIACEAE

The umkomasiaceans were widely distributed in the Gondwanan Triassic (Retallack 1977, Anderson & Anderson 1983, 2003, pp. 243, 251, 257); however, *Dicroidium*, *Johnstonia*, and *Xylopteris* evidently became extinct during the Norian (Tab. 1). Although the Gondwanan megafloral record is considerably less well represented in the Rhaetian than in the Anisian–Norian, it appears that *Zuberia* may have been the only umkomasiacean lineage to have survived into the Rhaetian. Representatives of the genus probably did not persist post-Triassic, indicating that bona fide umkomasiacean fructifications are entirely pre-Jurassic (Pattemore 2016).

The palynofloral record in Australasia connotes a substantial change in plant assemblages and the decline of the umkomasiaceans near the end-Triassic (de Jersey & McKellar 2013). The dispersed pollen genera *Alisporites* Daugherty in Daugherty & Stagner 1941 and *Falcisporites* Leschik 1956 emend. Klaus 1963 have been widely used as indicative of umkomasiacean abundance. Balme (1995) confidently allied *Falcisporites* with *Pteruchus*. However, a correlation between *Alisporites* and the umkomasiaceans is dubious, its stratigraphic representation extending well beyond that of undoubted umkomasiacean megascopic specimens (Pattemore et al. 2015a, pp. 692–694). Furthermore, those pollen genera are difficult to distinguish without good preservation. Thus, despite palynology suggesting a substantial decline in umkomasiacean abundance near the close of the Triassic, it provides insufficient evidence to confidently determine rates of decline or precise dating of species extinction.

The Triassic–Jurassic boundary (TJB) marks a major extinction event that correlates with elevated levels of atmospheric carbon dioxide (Ruhl et al. 2011, Bachan et al. 2012, Bartolini et al. 2012, Ritterbush et al. 2015, Guex 2016). The extinction began prior to the TJB, with species diversity reaching a minimum near the boundary (Guex 2016, fig. 2.4) and resulting in an estimated 80% to more than 95% termination of plant species in parts

of the Northern Hemisphere (McElwain et al. 1999, 2009).

The Lower and Middle Jurassic of Eastern Gondwana (Fig. 23) preserve floral assemblages that are remarkably different from those of the Triassic. The Middle Jurassic Walloon Coal Measures, Queensland, are dominated by ferns. The fragmentary state of other plants (chiefly lycopods, conifers, and bennettitaleans) indicates that they probably represent an upland floral assemblage that underwent significant transportation prior to deposition. By contrast, ferns dominate strata that accumulated very close to coal-forming paludal environments. Elsewhere in the Lower and Middle Jurassic of Eastern Gondwana, assemblages have greater and somewhat more evenly balanced floral diversity (ferns, lycopods, conifers, cycads, and bennettitaleans). Ginkgoaleans existed in

Eastern Gondwana until near the close of the Triassic (Callide Basin: O'Sullivan 1977, fig. 38a) but they were evidently absent below ca 60°S palaeolatitude during the Early and Middle Jurassic (Fig. 23).

Dicroidium odontopteroides is one of the most abundant plants associated with Triassic coal measures of Eastern Gondwana, being common in the lower Norian (e.g. Ipswich Basin), but it has not been reliably recorded above the Norian. Thus, the umkomasiaceans evidently began their decline at some point within the middle or late Norian. The rate of decline is not clear, but it possibly indicates that the cause(s) of the end-Triassic extinction (e.g. climate change resulting from volcanism: Ritterbush et al. 2015 and references therein) had a longer lead-time than has been previously acknowledged.

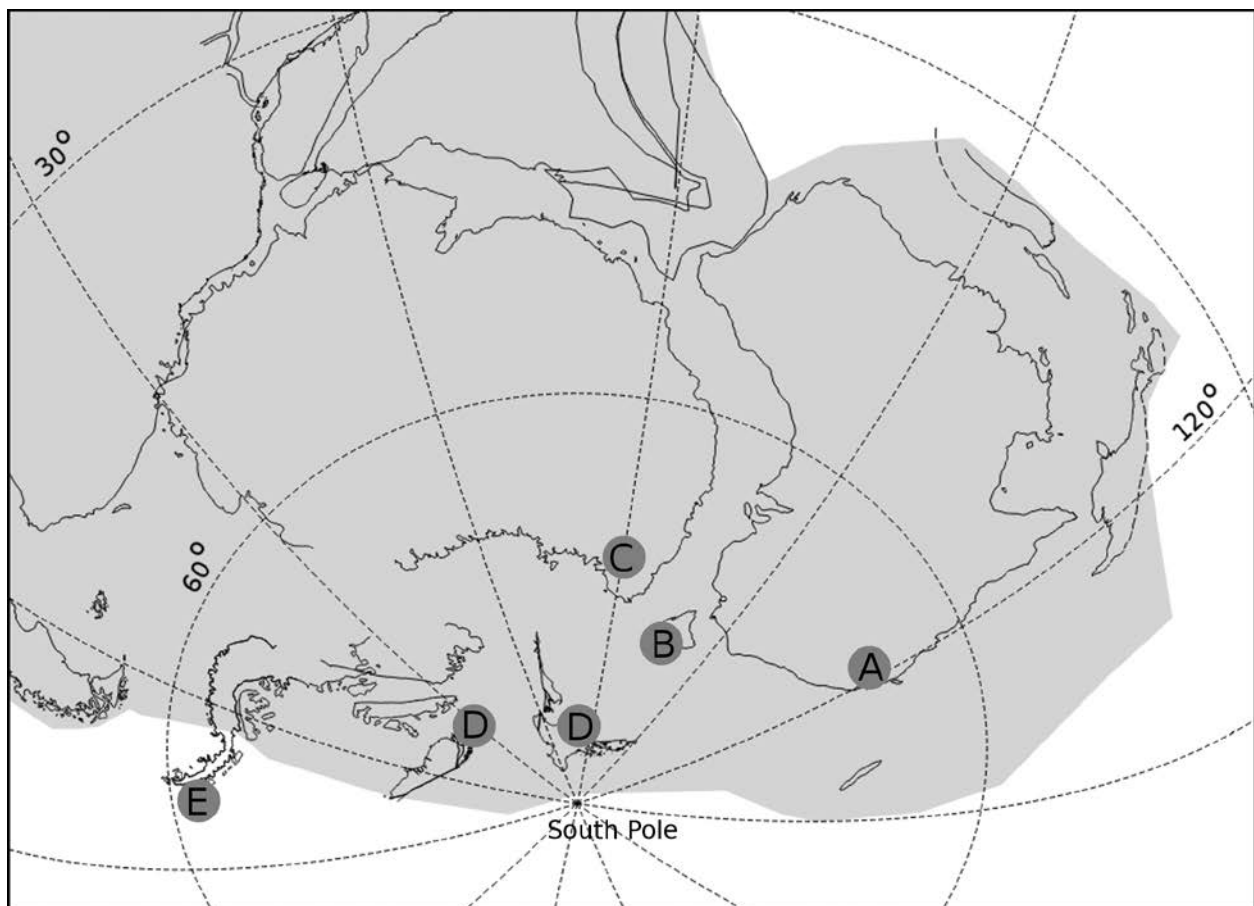


Fig. 23. Eastern Gondwana (grey) during the Early and Middle Jurassic, showing key Australasian and Antarctic megascopic plant locations. **A:** southeast Queensland; numerous sites in the Clarence-Moreton and Nambour basins (Lower and Middle Jurassic: Fig. 2 herein). **B:** Lune River area, southern Tasmania (Lower Jurassic: Calver 2009, Cook et al. 2012). **C:** Shafer Peak and other sites, North Victoria Land, Antarctica (Lower Jurassic: Bomfleur et al. 2011a). **D:** several sites, North and South Islands, New Zealand; Murihiku Terrane (Middle Jurassic: Thorn 2001, Pattemore et al. 2014, 2015a). **E:** Hope and Botany bays and other sites, Antarctic Peninsula; Botany Bay Group basins (?uppermost Triassic–Lower Jurassic: Hathway 2000, Rees & Cleal 2004, Birkenmajer & Ociepa 2008, and references therein). Palaeogeographic reconstruction based on Toarcian but represents a suitable approximation for much of the Early and Middle Jurassic period in Eastern Gondwana. Modified from Pattemore et al. (2014, fig. 9) and based on Seton et al. (2012). For representation of palaeogeography at approximately the Triassic/Jurassic transition see Seton et al. (2012, fig. 18) and Torsvik & Cocks (2013, fig. 19)

CONCLUSIONS

1. Fructifications allied with species of *Zuberia* and *Dicroidium* differ structurally, indicating that those genera are not synonymous.

2. *Zuberia* survived into the Rhaetian, probably terminating prior to the end-Triassic, whereas *Dicroidium*, *Johnstonia*, and *Xylopteris* evidently became extinct during Norian time.

3. The lectotype of *Dicroidium superbum* has been widely misunderstood. Re-examination of the lectotype and other material indicates that many Gondwanan specimens representative of *D. superbum* have been misidentified, inter alia, as *D. dubium* and *Xylopteris elongata*.

4. The perceptions of a morpho-continuum and of hybridisation among species of *Dicroidium*, *Xylopteris*, and *Zuberia* lack a credible basis, largely due to misidentification of specimens and greatly expanded circumscriptions of *D. dubium* and *X. elongata*.

5. The fructification *Paraxylopteris queenslandensis* represents a slightly modified vegetative frond resembling *Xylopteris argentina*, but not the structurally complex umkomasiacean male fructification *Pteruchus*. The higher taxonomic affinity of *Paraxylopteris queenslandensis* is uncertain.

6. Strata at Bacchus Marsh and Yandoit Hill, Victoria, previously identified as remnants of a broader Triassic depositional entity, may be post-Triassic based on mega-plant evidence.

7. The Middle Jurassic Walloon Coal Measures, Clarence-Moreton Basin, Queensland, are dominated by ferns (chiefly *Cladophlebis*). More broadly, the Lower and Middle Jurassic of Australasia and Antarctica comprise ferns, lycopods, conifers, cycads and bennettitaleans, but ginkgoaleans are absent.

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