

# Triassic-Jurassic pteridosperms of Australasia: speciation, diversity and decline

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## ABSTRACT

Pteridosperms are preserved abundantly in the Gondwanan Triassic, with many species exhibiting considerable morphological variation that has been attributed to a hybridization model of speciation. This is an improbable explanation given that hybridization is very rare in gymnosperms. Allopatric speciation resulting from geographic and climatic provincialism is a more likely explanation for the morphological diversity which is well represented in Anisian–Norian (Middle and Upper Triassic) floras of Australasia and elsewhere in Gondwana. Most specimens are distributed among three families: Umkomasiaceae, Peltaspermeae and Matatiellaceae. These families, together with other possibly pteridospermous genera, are reviewed herein. Diversity in these families apparently declined by the Rhaetian and they did not persist into the Gondwanan post-Triassic. Australasian post-Triassic strata contain remarkably different floral assemblages to those of the Triassic. No fructifications are clearly pteridospermous and no remains show any obvious relationship with pteridosperms of the Gondwanan Triassic. Caytonian fructifications are not known in Australasian strata; however, associated foliage has been reported from the Eastern Gondwanan Upper Triassic through Middle Jurassic including Australia. Much fern-like foliage, claimed to be pteridospermous from the Lower Jurassic through Eocene of Eastern Gondwana, lacks supporting evidence of such affiliation.

Keywords: pteridosperm, Australasia, Gondwana, Triassic, Jurassic.

## ***Pteridospermas del Triásico-Jurásico de Australia: especiación, diversidad y declive***

### RESUMEN

*Muchas especies de pteridospermas que se encuentran preservadas de forma abundante en rocas triásicas de Gondwana, poseen patrones de variación morfológica notables que han sido atribuidos a modelos de especiación relacionados con la hibridación. Sin embargo, este es un razonamiento improbable, porque la hibridación es un fenómeno que se produce raramente en las gimnospermas. Es más fácil explicar esta diversidad morfológica, que está bien representada en las floras del intervalo Anisiense-Noriense (Triásico Medio y Superior) de Australasia y otras regiones de Gondwana, por un proceso de especiación alopátrica debido a un conjunto de factores relacionados con provincialismos geográficos y climáticos. La mayor parte de los especímenes estudiados en este trabajo pertenecen a tres familias: Umkomasiaceae, Peltaspermeae y Matatiellaceae. Estas, junto con varios géneros posiblemente pteridospérmicos, se revisan en este estudio. La diversidad específica en las familias mencionadas aparentemente declinó a partir del Retiense, y no se restableció en el post-Triásico de Gondwana. Los estratos post-Triásicos de Australasia contienen distintas asociaciones florísticas notablemente distintas. Ninguna de las fructificaciones encontradas hasta el momento son claramente pteridospérmicas. Además, ningún otro tipo de resto hallado presenta alguna relación obvia con las pteridospermas del Triásico de Gondwana. Las fructificaciones de Caytoniales no se conocen en las rocas de Australasia; sin embargo, se han registrado filocenosis relacionables con plantas de este orden en el Este de Gondwana, incluida Australia, desde el Triásico Superior hasta el Jurásico Medio. A partir del Jurásico Inferior hasta el Eoceno, una gran parte de los restos foliares con aspecto de helecho que se han relacionado en Gondwana con las pteridospermas no presentan evidencias reales para atribuirlos a este grupo de gimnospermas.*

*Palabras clave: pteridospermas, Australasia, Gondwana, Triásico, Jurásico.*

## VERSIÓN ABREVIADA EN CASTELLANO

### Introducción y metodología

En Gondwana, el intervalo Anisiense–Noriense (Triásico Medio-Superior) fue un período de máxima abundancia y diversidad de pteridospermas (Retallack, 1977; Anderson and Anderson, 1983, 1989, 2003). Hacia finales de este período, la abundancia y diversidad de las plantas de este grupo se redujo sustancialmente (Retallack, 1977; Anderson et al., 2007; Iglesias et al., 2011). Aparentemente durante el Triásico tardío, algunos de sus representantes se dispersaron más allá de Gondwana (Zan et al., 2008; Kustatscher and van Konijnenburg-van Cittert, 2013) y allí persistieron hasta el Jurásico temprano (Kirchner and Müller, 1992).

Meyen (1984) y Crane (1985) no contemplaron a las pteridospermas como un grupo taxonómicamente unificado. El término pteridosperma que se usa de forma común, encuadra a un grupo de plantas que son desde un punto de vista macroscópico muy diferentes de las gimnospermas actuales. Por esta razón, el término citado se aplicará en este trabajo en un sentido informal (siguiendo a Meyen, 1984) y dentro de él se incluyen plantas que algunos autores consideran que tienen caracteres relacionables con distintos grupos. Sin embargo, en este estudio no se van a definir las posiciones taxonómicas de estos taxones inciertos dentro de los grupos más representativos de pteridospermas. Concretamente, la terminología filogenética utilizada sigue las directrices de Wiley y Lieberman (2011).

De acuerdo con Doyle (2006), distintos autores han propuesto a varios de los linajes de pteridospermas como posibles precursores de las angiospermas. Sin embargo, muchas de sus homologías no están claras por lo que esta hipótesis requiere una profunda comprobación (Doyle, 2006, 2012). Además, estudios genéticos llevados a cabo en un elevado número de gimnospermas actuales (Crisp and Cook, 2011; Davis and Schaefer, 2011; Nagalingum et al., 2011) sugieren que las restricciones impuestas a muchos análisis filogenéticos realizados con anterioridad necesitan una re-evaluación. Doyle (2012) indicó que la radiación de las angiospermas comenzó durante el Cretácico temprano (posiblemente en el Valanginiense), pero no se ha establecido aún una relación clara con una línea precursora (han sido discutidas varias posibilidades por el autor anteriormente mencionado). El dato más antiguo de la cladogénesis de las angiospermas es incierto y Doyle (2012) señaló que la selección de una edad pre-Cretácica indicaba una radiación específica que estuvo notablemente restringida hasta el Cretácico Inferior.

Algunos restos foliares del intervalo Jurásico Inferior-Eoceno de Australia han sido, asimismo, contemplados como pteridospermas. Esta atribución se ha basado únicamente en similitudes morfológicas con fósiles vegetales del intervalo Triásico-Jurásico Inferior. Las fructificaciones, posiblemente de tipo pteridospérmico, del Jurásico de Gondwana son relativamente raras y no se parecen a las que presentan las familias de pteridospermas triásicas. Las cuencas de Australasia, que incluyen estratos del Triásico al Cretácico Inferior y contienen megáfloras de pteridospermas o de plantas similares a estas, se muestran en las Figuras 1 y 2. Este artículo busca clarificar la aparición, el progreso y el declive de las pteridospermas mesozoicas, poniendo especial atención en sus representantes de Australasia.

### Resultados y discusión

Aunque se ha establecido una relación convincente entre *Dicroidium* y las fructificaciones de *Umkomasia* y *Pteruchus*, no hay evidencias suficientes para suponer la fusión de *Xylopteris* y *Johnstonia* con *Dicroidium*. Esta sinonimia se basó originalmente en las semejanzas de la organización de los tallos de estas plantas y ha sido mantenida posteriormente por la teoría de que sus ancestros hibridaron a lo largo de Gondwana (especiación simpátrica). Esto explicaría la diversidad morfológica que tienen las especies de los géneros mencionados. Sin embargo, la hibridación se da raramente en las gimnospermas actuales y es, por esta razón, una explicación improbable para esta diversidad morfológica. Consecuentemente, la especiación en *Umkomasiaceae* (y otros grupos de pteridospermas) fue casi seguro alopátrica, por lo que el provincialismo tuvo una influencia significativa en la evolución de esta familia.

*Umkomasiaceae* se conoce en gran parte del Triásico de Gondwana y, aparentemente, su dispersión se desarrolló más allá de Gondwana durante el Triásico tardío. La diversidad de esta familia declinó hacia finales del Triásico en Australasia, y no se sabe a partir de cuándo en Gondwana. Los intentos de conocer la filogenia de *Umkomasiaceae* a partir de restos foliares han tenido como resultado una significativa divergencia de opiniones y taxonomía (cf. Retallack, 1977; Anderson and Anderson, 1983). La identificación posterior de fructificaciones, restos foliares, tallos y troncos asociados de tipo umkomasiáceo (Axsmith et al., 2000; Cúneo et al., 2003; Taylor et al., 2006) ha mejorado el conocimiento de la morfología de las plantas productoras y su posición en los ecosistemas. Sin embargo, las relaciones filogenéticas entre los miembros de esta familia siguen sin estar bien conocidos porque la mayor parte de sus fructificaciones deben estudiarse con mayor detalle. La disposición de las ramificaciones de los esporófilos de *Pteruchus* ha sido descrita como alternati-

vamente pinnada y helicoidal (cf. Townrow, 1962c; Yao et al., 1995; Anderson and Anderson, 2003; Pattemore and Rigby, 2005). Un conjunto de cúpulas ovuladas y permineralizadas de la Antártida (*Umkomasia resinosa* Klavins et al., 2002) han proporcionado detalles estructurales de los megasporangios. Otras especies del género *Umkomasia* se distinguen en gran medida por la forma y tamaño de sus partes anatómicas (Zan et al., 2008), ya que únicamente llegan a preservarse unos pocos caracteres botánicos. Además, *U. uniramia* Axsmith et al., 2000 con sus óvulos copulados y verticilados, es estructuralmente distinta de otras especies del género. Todo esto parece indicar que *Umkomasiaceae* fue una familia más diversa de lo que se había especulado previamente o, quizás, no es monofilética.

Los datos cuticulares proporcionados por las pteridospermas son generalmente escasos y no están calibrados ambientalmente. El uso de las cutículas para determinar afinidades taxonómicas requiere un enfoque conservador; además, inferir sin error una identidad taxonómica a partir de cutículas requiere la utilización de una base de datos amplia y diversa, y comparaciones con cutículas bien calibradas desde un punto de vista ambiental a partir de una amplia gama de diferentes grupos de plantas (Barclay et al., 2007). Los términos haploquéllico y sindetoquéllico han sido aplicados erróneamente en la descripción de los aparatos estomáticos maduros, suponiendo que la ontogenia de las especies de pteridospermas se puede inferir a partir del conocimiento de estos. Además, estos términos implican afiliación gimnosperma, tendiendo así a sesgar esta caracterización epidérmica.

La familia *Peltaspermaceae* está registrada en gran parte del Triásico de Gondwana, particularmente en estratos inmediatamente posteriores al evento de extinción de finales del Pérmico. Por otra parte, los miembros de la familia *Matatielliaceae* son relativamente raros y están restringidos al Triásico Medio y Superior de Gondwana. Al menos, algunos especímenes identificados como *Stachyopitys* podrían pertenecer a *Matatielliaceae*.

*Pachydermophyllum* del Triásico Medio y Superior de Gondwana, podría distinguirse a partir de especímenes post-Triásicos referidos a este género. Algunos otros restos fósiles del Triásico de Australasia podrían ser posiblemente pteridospermas, pero esto necesita confirmación.

La afiliación de *Rintoulia* es dudosa porque está únicamente basada en cutículas del Cretácico inferior de Victoria. El material tipo de este género indica que podría tratarse de un helecho. Su cutícula no ha sido comparada con un suficiente número de plantas, habiéndose intentado solo unas comparaciones muy particulares. Así mismo, las atribuciones a *Komlopteris* en el post-Jurásico del Este de Gondwana estuvieron basadas en similitudes macroscópicas de ejemplares gondwánicos y europeos del Jurásico más inferior. Además, las evidencias cuticulares no son lo suficientemente convincentes como para garantizar la asignación genérica.

Las fructificaciones de *Caytoniales* se desconocen en Australasia. Sin embargo, podrían aparecer en el Triásico Superior y el Jurásico Inferior de la Antártida. Desafortunadamente, ningún espécimen que pudiera confirmar la existencia de este grupo en la región puede considerarse suficientemente bien conservado. Concretamente, *Sagenopteris* ha sido registrado desde el Triásico Superior hasta el Jurásico Medio del Este de Gondwana.

De forma general, se considera que las coníferas, junto con las pteridospermas, dominaron las floras terrestres jurásicas, particularmente en el Jurásico tardío de Australasia (Turner et al., 2009). En el post-Triásico de Australasia, no hay evidencias de fructificaciones que sugieran, junto con restos foliares, la supervivencia de familias triásicas de pteridospermas. Además, a pesar de los ejemplares que integran las notables colecciones de paleobotánica que se custodian en Australia desde el siglo XIX, y con la posible excepción de *Knezourocarpon*, las fructificaciones pteridospermas parecen estar ausentes de los estratos post-triásicos de Australasia (Tabla 8).

## Conclusiones

1. La hibridación es una explicación improbable de la especiación de las pteridospermas triásicas. La diversidad de las *Umkomasiaceae* y de otros grupos de pteridospermas del Triásico, es el resultado de un proceso alopatrico de especiación. De este modo, el provincialismo geográfico y climático tuvo probablemente una influencia significativa.
2. Un estatus congénico para *Dicroidium*, *Johnstonia* y *Xylopteris* carece de base veraz.
3. A pesar de su aparente similitud morfológica, el género *Pachydermophyllum* del Triásico Medio y Superior de Gondwana podría considerarse como un taxón aparte, ya que es diferente de otros fósiles a él referidos con diferente rango de edad.
4. Los especímenes atribuidos a *Stachyopitys* en el Triásico Medio y Superior de Gondwana, son estructural y estratigráficamente distintos del material extra-gondwánico y también se pueden asignar a *Townrovia* o a un nuevo género.
5. La afiliación a las pteridospermas de *Rintoulia* es dudosa. Particularmente, su afinidad taxonómica usando caracteres cuticulares requiere un estudio más riguroso. Asimismo, la atribución de restos fósiles del

*post-Jurásico del Este de Gondwana a Komlopteris es también dudosa; las evidencias cuticulares son equívocas y requieren una mayor comparación con diferentes tipos de plantas, incluyendo fósiles más recientes.*

6. *Las fructificaciones de Caytoniales no se conocen en Australia, pero posiblemente se encuentran representadas en el Triásico Superior y Jurásico Inferior de la Antártida.*
7. *Las pteridospermas declinaron en Australasia antes del evento de extinción del Triásico más tardío. No hay una evidencia clara de la existencia de fructificaciones que indiquen que las pteridospermas triásicas sobrevivieron a este evento, a pesar de que aparentemente persistieron en el Jurásico Inferior extra-gondwánico.*

## Introduction

The Anisian–Norian was an interval of maximum pteridosperm abundance and diversity in the Gondwanan Triassic (Retallack, 1977; Anderson and Anderson, 1983, 1989, 2003). Toward the close of the Triassic, pteridosperm abundance and diversity had substantially declined (Retallack, 1977; Anderson *et al.*, 2007; Iglesias *et al.*, 2011). Some representatives apparently dispersed beyond Gondwana in the Late Triassic (Zan *et al.*, 2008; Kustatscher and van Konijnenburg-van Cittert, 2013) and persisted there into the Early Jurassic (Kirchner and Müller, 1992).

Meyen (1984) and Crane (1985) did not regard the pteridosperms as taxonomically unified. The widely used term pteridosperm encompasses a group of plants that are megascopically dissimilar from extant gymnosperms. The term is applied herein in an informal collective sense (following Meyen, 1984) and plants that some authors consider to be within a broader concept of the group are also discussed. This paper does not seek to define the higher taxonomic placement of the group's representatives. Phylogenetic terminology applied herein follows Wiley and Lieberman (2011).

Various pteridosperm lineages have been proposed as possible angiosperm precursors by several authors (Doyle, 2006); however, many homologies are obscure and hypotheses require substantiation (Doyle, 2006, 2012). Furthermore, recent genetic studies of a broad range of extant gymnosperms (Crisp and Cook, 2011; Davis and Schaefer, 2011; Nagalingum *et al.*, 2011) suggest that constraints placed on many prior phylogenetic analyses require re-assessment. Doyle (2012) indicated that angiosperm radiation began during the Early Cretaceous (possibly Valanginian) but no clear relationship with a precursor lineage has yet been established (several possibilities were discussed by that author). The earliest date for angiosperm cladogenesis is uncertain and Doyle (2012) noted that selection of a pre-Cretaceous date indicates remarkably restricted species radiation until the Early Cretaceous.

Foliage from the Lower Jurassic–Eocene of Australasia has been regarded as pteridospermous based solely on morphological similarity to Triassic–Early Jurassic pteridosperms globally. Fructifications from the Gondwanan Jurassic that are possibly pteridospermous are relatively rare and do not resemble those attributed to Triassic pteridosperm families. Australasian basins that include Triassic–Lower Cretaceous strata containing pteridosperm or pteridosperm-like megaflores are shown in Figures 1 and 2. This paper seeks to clarify the inception, progression and decline of Mesozoic pteridosperms with a focus on Australasian representatives.

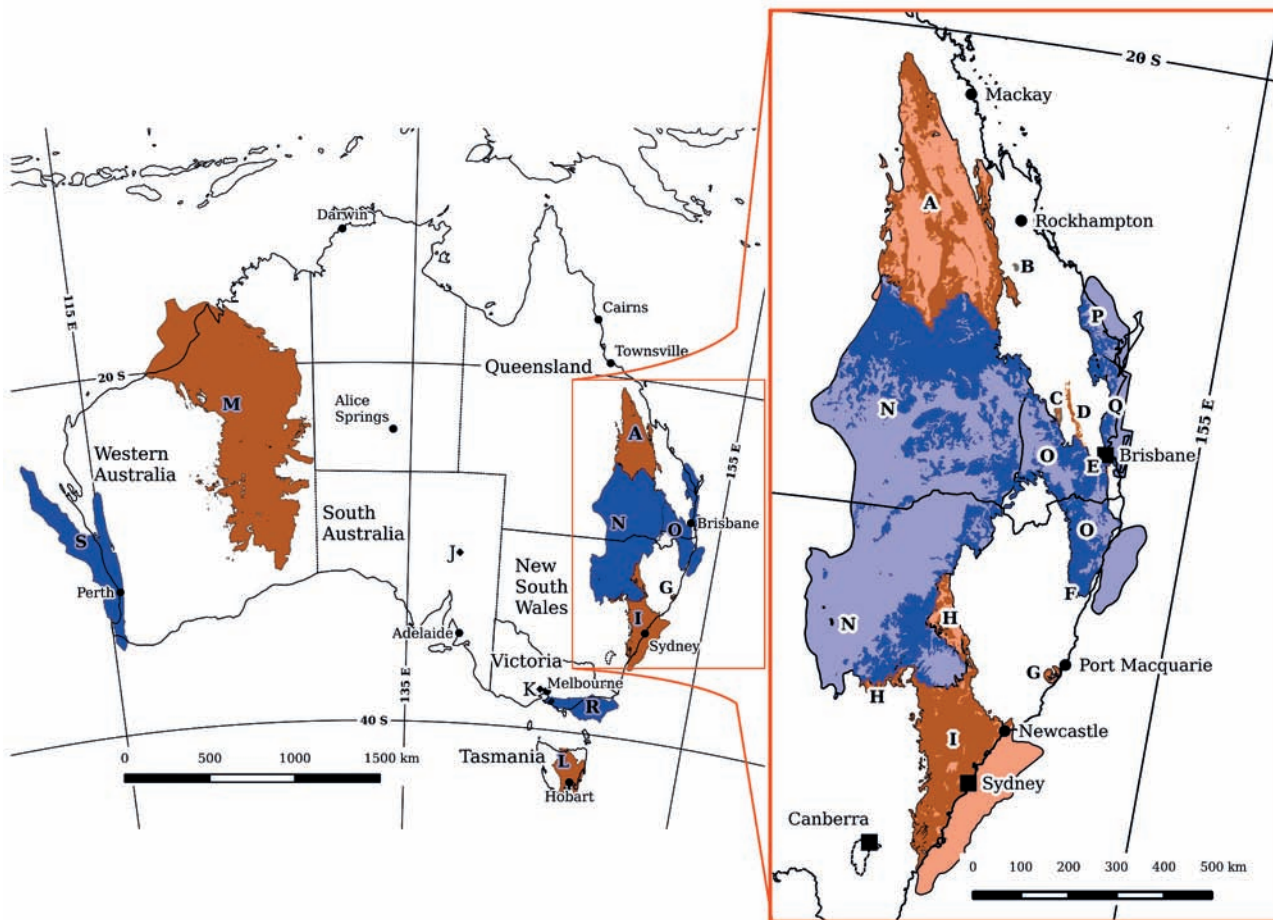
## Triassic pteridosperms

### *Umkomasiaceae Petriella, 1981*

The Umkomasiaceae was proposed to replace the *Corystospermaceae* Thomas, 1933 as a nomenclatural correction (Petriella, 1981; Meyen, 1984). This family includes the fructifications *Umkomasia* Thomas, 1933 emend. Klavins *et al.*, 2002 and *Pteruchus* Thomas, 1933 emend. Townrow, 1962 (Fig. 3). Both fructifications have been widely associated with foliage attributed to *Dicroidium* Gothan, 1912 emend. Townrow, 1957. Other foliar genera have been assigned to the family, but their association with these fructifications remains unconfirmed or speculative (discussed below). Representatives of the Umkomasiaceae are preserved abundantly in the Middle and Upper Triassic of Australasia (Table 1) and elsewhere within Eastern and Western Gondwana (Retallack, 1977; Anderson and Anderson, 1983, 2003).

### *Pollen*

Balme (1995) was unequivocal in his assessment that *Pteruchus* pollen, if found dispersed, is best referred to *Falcisporites* Leschik, 1956 emend. Klaus, 1963. He

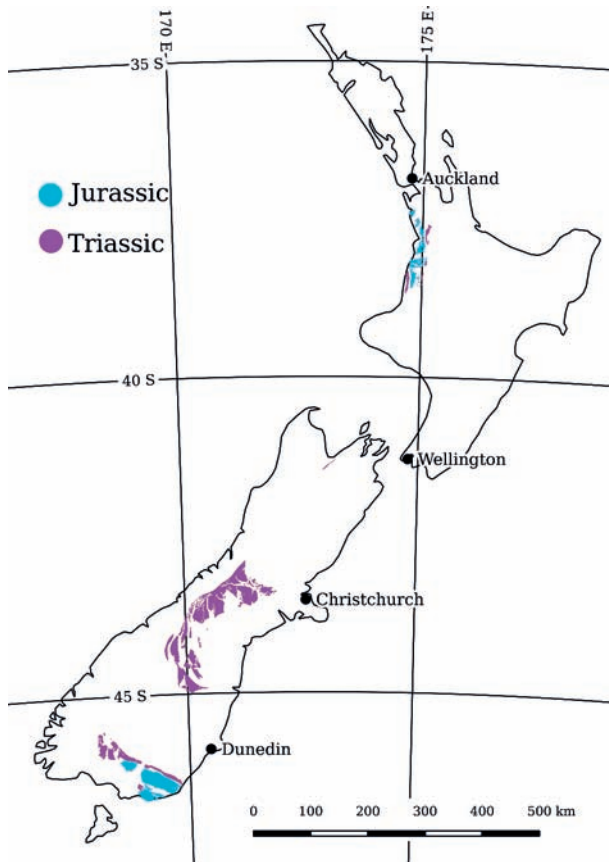


**Figure 1.** Australian sedimentary basins that include outcropping Triassic–Lower Cretaceous strata preserving pteridosperm or pteridosperm-like megafossils; key studies listed in Table 1. Inset: darker shading indicates outcrop. Triassic (brown): A, Bowen Basin; B, Callide Basin; C, Tarong Basin; D, Esk Trough; E, Ipswich Basin; F, Nymboida Sub-Basin; G, Lorne Basin; H, Gunnedah Basin; I, Sydney Basin; J, Leigh Creek Coal Measures comprising five intramontane basins (Kwitko, 1995); K, Victorian Triassic remnants, Yandoit Hill and Bacchus Marsh (Duddy, 2003); L, Tasmania Basin; M, Canning Basin. Jurassic–Lower Cretaceous (blue): N, Surat Basin; O, Clarence–Moreton Basin; P, Maryborough Basin; Q, Nambour Basin; R, Gippsland Basin; S, Perth Basin. Data sources: Geoscience Australia; Queensland Department of Natural Resources and Mines.

**Figura 1.** Cuencas sedimentarias australianas en donde se señalan los afloramientos de edad triásica-cretácica inferior en cuyos estratos se preservan macrofósiles de pteridospermas o plantas similares a estas; estudios clave enumerados en la Tabla 1. Mapa: el sombreado más oscuro indica la existencia de afloramientos. Triásico (marrón): A, Cuenca de Bowen; B, Cuenca de Callide; C, Cuenca de Tarong; D, Depresión de Esk; E, Cuenca de Ipswich; F, Sub-Cuenca de Nymboida; G, Cuenca de Lorne; H, Cuenca de Gunnedah; I, Cuenca de Sydney; J, Depósitos de carbón de Leigh Creek que comprenden cinco cuencas intramontanas (Kwitko, 1995); K, Restos del Triásico de Victoria, Yandoit Hill y Bacchus Marsh (Duddy, 2003); L, Cuenca de Tasmania; M, Cuenca de Canning. Jurásico-Cretácico Inferior (azul): N, Cuenca de Surat; O, Cuenca de Clarence-Moreton; P, Cuenca de Maryborough; Q, Cuenca de Nambour; R, Cuenca de Gippsland; S, Cuenca de Perth. Fuentes: Geoscience Australia; Queensland Department of Natural Resources and Mines.

argued that *Pteruchus* pollen does not resemble the type species of *Alisporites* Daugherty in Daugherty and Stagner, 1941. Further discussion regarding differentiation of these dispersed pollen genera was provided by de Jersey and McKellar (2013) who assigned pollen from the Hettangian of Queensland and New Zealand to *Alisporites*. Both Jansson *et al.* (2008a) and McLoughlin *et al.* (2014) reported that genus as a minor component of their samples from the Toarcian of Queensland. These dispersed pollen

genera are morphologically very similar and may be difficult to distinguish without good preservation. Many authors have associated *Alisporites* with the Umkomasiaceae, but given the work of Balme (1995) it is doubtful that this dispersed pollen genus is necessarily pteridospermous. Contrasting views regarding representatives of these genera in Australasia have been summarized by de Jersey and Raine (1990), Balme (1995) and de Jersey and McKellar (2013). *Pteruchus*-like pollen is known from the Upper



**Figure 2.** Outcropping Rakaia and Murihiku terranes, New Zealand that include Triassic–Jurassic plant fossils; key studies listed in Table 1. Triassic and Jurassic sediments are colour-coded as indicated. For details of fossil sites and terranes see Retallack (1987) and Mortimer (2004, 2005). Data source: GNS Science, New Zealand.

**Figura 2.** Afloramientos de Raika y Murihiku (Nueva Zelanda) que incluyen fósiles vegetales del Triásico-Jurásico; estudios clave enumerados en la Tabla 1. Como se indica, los sedimentos triásico-jurásicos tienen un código de color. Para el conocimiento en detalle de las localidades fosilíferas ver Retallack (1987) y Mortimer (2004, 2005). Fuentes: GNS Science, Nueva Zelanda.

Permian through Lower Jurassic (Balme, 1995) and the fructification had wide geographic extent in the Gondwanan Triassic (chiefly, Anisian–Norian; Anderson and Anderson, 2003). *Alisporites* pollen has been affiliated with conifers and possibly ginkgo-phytes (Balme, 1995; Bomfleur et al., 2013) and has been identified from the Permian through Upper Cretaceous (Mohr and Gee, 1992; Balme, 1995).

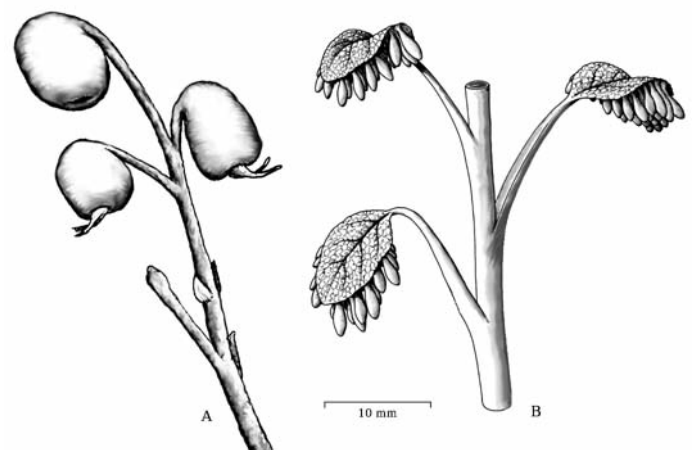
#### Fructifications and foliage

Direct organic connection between *Dicroidium* and the female fructification *Umkomasia* was reported by

Axsmith et al. (2000) from near the Shackleton Glacier in the Ladinian–Carnian of the central Transantarctic Mountains, Antarctica. This association was disputed by Anderson and Anderson (2003), Holmes and Anderson (2005a) and Anderson et al. (2008) on the basis of shoot development (Holmes and Anderson, 2005a, p. 2). However, their arguments were refuted by Axsmith et al. (2007) based on shoot development in a living *Ginkgo* Linnaeus, 1771.

The diagnosis of *Umkomasia uniramia* Axsmith, Taylor, Taylor and Cúneo, 2000 included foliage considered conformable with *Dicroidium odontopteroides* (Morris, 1845) Gothan, 1912. This fructification, that has a terminal whorl of pedicels, each bearing a single ovulate cupule, is structurally unlike other known specimens of the genus (Anderson and Anderson, 2003; Holmes and Anderson, 2005a). Although several likely *Pteruchus* specimens were identified from the same locality, none was found in organic connection with *U. uniramia*. Axsmith et al. (2000) opted not to assign these specimens to *Pteruchus* without identification of an organic attachment to other organs. Poorly preserved pollen grains were located within the pollen sacs and referred to *Alisporites*.

The oldest specimens ascribed to *Umkomasia* were by Chandra et al. (2008) from the Upper Permian of India; no foliage resembling *Dicroidium* was identified in associated strata. They referred their material to *U. polycarpa* Holmes, 1987 (previously described from the Anisian of eastern Australia) and to *U. uniramia*. The fossil-bearing strata had unclear strati-



**Figure 3.** Reconstructed fructifications of the Umkomasiaceae. **A**, *Umkomasia*, modified from Crane (1985); **B**, *Pteruchus*, modified from Yao et al. (1995).

**Figura 3.** Reconstrucción de fructificaciones de Umkomasiaceae. **A**, *Umkomasia*, modificado de Crane (1985); **B**, *Pteruchus*, modificado de Yao et al. (1995).

Location and age range of plant-bearing deposits			Key studies
South Australia	Leigh Creek Coal Measures	Anisian–Norian (coal-bearing strata)	Etheridge (1895); Chapman and Cookson (1926); Amtsberg (1969).
New Zealand	Murihiku and Rakaia terranes	Olenekian–Norian (?Rhaetian)	Arber (1913, 1914, 1917); Bell <i>et al.</i> (1956); Retallack (1980b, 1981, 1983b, 1985, 1987); Pole and Raine (1994).
Tasmania	Tasmania Basin	Carnian–lower Norian (coal-bearing strata)	Feistmantel (1878, 1879, 1890a); Johnston (1885, 1886, 1888, 1893, 1895); Walkom (1924a, 1925b); Townrow (1957, 1962c, 1965, 1966a).
Victoria	Yandoit Hill and Bacchus Marsh	Late Triassic	Chapman (1927); Douglas (1969, 1988).
Western Australia	Fitzroy Trough, Canning Basin	Early–Middle Triassic	Antevs (1913); Townrow (1957); White (1961); Retallack (1995a).
Queensland	Callide Basin	Carnian–Rhaetian	Jack and Etheridge (1892); report in preparation with collections by one of us [GAP].
	Tarong Basin	upper Carnian	None; report in preparation with collections by one of us [GAP].
	Ipswich Basin	Carnian–lowermost Norian	Carruthers (1872); Tenison-Woods (1883); Jack and Etheridge (1892); Shirley (1898); Walkom (1917a); Jones and de Jersey (1947a); Hill <i>et al.</i> (1965); Pattemore and Rigby (2005); Anderson <i>et al.</i> (2008).
	Bowen Basin	upper Anisian–Ladinian	Jensen (1926); White (1964, 1965, 1969, 1971, 1972); Playford <i>et al.</i> (1982).
	Esk Trough	Anisian	Jack and Etheridge (1892); Walkom (1924b, 1928); Hill <i>et al.</i> (1965); Gould (1975); Rigby (1977); Holmes (1987).
New South Wales	Southern Clarence-Moreton Basin: Red Cliff Coal Measures	Anisian	Flint and Gould (1975).
	Gunnedah Basin	Anisian	Tenison-Woods (1883); Dun (1909); Retallack (1977); Holmes (1982).
	Nymboida Sub-Basin	Anisian	Flint and Gould (1975); Retallack (1977); Retallack <i>et al.</i> (1977); Holmes (1987); Holmes and Anderson (2005a, 2013).
	Lorne Basin	Olenekian	Voisey (1939); Retallack (1977); Holmes and Ash (1979).
	Sydney Basin	Induan–Ladinian	Feistmantel (1878, 1879, 1890a); Walkom (1925a, 1932); Retallack (1977, 1980a).

**Table 1.** Australasian Umkomasiaceae: key publications.  
**Tabla 1.** Umkomasiaceae de Australasia: publicaciones principales.

graphic position and were not assigned to a formation.

The diagnosis of *Pteruchus* by Thomas (1933) and the emendation by Townrow (1962c) were based on megascopic morphology, pollen and cuticle. Permineralized specimens from a locality near the Beardmore Glacier in the Middle Triassic of the Queen Alexandra Range, South Victoria Land, Antarctica were assigned to *Pteruchus* by Yao *et al.* (1995) and to *Umkomasia* by Klavins *et al.* (2002). The ultrastructure of in-situ *Pteruchus* pollen from the same location was examined by Osborn and Taylor (1993) and they considered the grains to be most like *Alisporites*. However, Balme (1995) regarded the pollen as strongly degraded and probably attributable to *Falcisporites*. Stem material from this site was

referred to the Umkomasiaceae by Decombeix *et al.* (2014).

The emended diagnosis of *Pteruchus* by Townrow (1962c) specified an alternately pinnate branching arrangement; however, some authors have suggested that their material indicates a likely helical arrangement (Yao *et al.*, 1995; Anderson and Anderson, 2003). Near-complete *Pteruchus* fructifications from the Carnian of Queensland were reported as bilaterally branched, alternate to sub-opposite (Pattemore and Rigby, 2005). A summary of several *Pteruchus* species was provided by Yao *et al.* (1995, Fig. 29). These reports of differing attachment modes may indicate that specimens assigned to *Pteruchus* are more diverse generically than currently accepted.

Holmes and Ash (1979) referred a female fructifi-

cation from the Lorne Basin, New South Wales (Olenekian; Pratt, 2010) to the little-known genus *Karibacarbon* Lacey, 1974 as a new species, *K. feistmantelii* Holmes and Ash, 1979. Holmes (1987) emended the diagnosis of *Umkomasia* to include *Karibacarbon*. However, Retallack (1977) and Anderson and Anderson (2003) considered these two genera to be distinct; indeed, *Karibacarbon* may actually be a peltasperm and therefore unrelated to *Umkomasia* (Taylor *et al.*, 2006; Bomfleur *et al.*, 2011). Holmes and Ash's (1979) specimens assigned to *Dicroidium* and *Pteruchus* from the Lorne Basin pre-date most other specimens attributed to these genera from the Gondwanan Triassic.

*Karibacarbon* was based on material collected from the Luangwa Basin, Zimbabwe; this material included another, even more poorly understood fructification which was ascribed to the genus *Sengewacarbon* Lacey, 1974. The host strata had been regarded as Upper Triassic and approximately coeval with the Molteno Formation of South Africa (Lacey, 1974; Anderson and Anderson, 1983). However, based on information provided by Lacey (1974) and Banks *et al.* (1995), it seems likely that Lacey's (1974) specimens are datable as either Middle Triassic or possibly late Early Triassic. Anderson and Anderson (1989, 2003) regarded these plant-bearing deposits as lowermost Anisian.

Reports of *Pteruchus* and *Dicroidium* from the Nidhpuri area, Madhya Pradesh, India, dated as Early Triassic (Bose and Srivastava, 1971; Pant and Basu, 1973; Srivastava, 1974), were considered more likely to be peltasperms by Retallack (1977). He suspected some of this material to be Late Permian. Retallack (2002) suggested that the *Pteruchus* fructifications described by Srivastava (1974) may belong to *Permotheca* Zalesky, 1929. This area of India is well known for its complex geology and closely associated Permian and Triassic sediments (Pant and Pant, 1987); this is discussed further below vis-à-vis reports of *Glossopteris* Brongniart (1828) 1831 from Triassic sediments at the same locality.

Kerp *et al.* (2006) and Abu Hamad *et al.* (2008) identified *Dicroidium* from the Wadi Himara area, Jordan (Umm Irna Formation; Middle Permian) and noted that associated sediments were palynologically dominated by *Falcisporites*. Their foliar specimens certainly appear *Dicroidium*-like, but no likely associated fructification has been identified from this locality nor elsewhere in the formation. The predominantly sandy Umm Irna Formation is no more than 68 m thick and unconformably overlies Cambrian sandstone (Stephenson and Powell, 2013). The erosional upper contact with Lower Triassic strata has been var-

iously reported as conformable (Makhlouf *et al.*, 1991), unconformable (Kerp *et al.*, 2006; Abu Hamad *et al.*, 2008) and disconformable (Stephenson and Powell, 2013). Systematic palynofloral studies of the formation comprise Stephenson and Powell (2013) and the unpublished work of Abu Hamad (2004). Stephenson and Powell (2013) dated the formation as Wordian–Capitanian (Guadalupian, i.e. Middle Permian). Other than *Dicroidium* material, a single small (2 cm<sup>2</sup>) cycadalean fragment was assigned to *Doratophyllum jordanicus* Mustafa, 2003 by Abu Hamad *et al.* (2008). *Doratophyllum jordanicus* was based on numerous specimens (some with cuticle) from elsewhere in the Umm Irna Formation. Abu Hamad *et al.* (2008) proposed an emendation of the species, modifying diagnostic cuticular characters. No other convincingly Permian flora was identified from the Wadi Himara site and no other typically Triassic flora has been identified from elsewhere in the formation.

Schneebeili-Hermann *et al.* (2015) reported *Dicroidium* from the Upper Permian of Pakistan based on cuticle from minute foliar fragments extracted from the residue of palynological samples. Identification of a genus using only highly fragmented cuticle could be problematic with extant plant material but is considerably more so with fossil specimens (discussed below). Many of the limited available cuticular characters described by Schneebeili-Hermann *et al.* (2015) are affected by environmental conditions (Barclay *et al.*, 2007, Table 1).

### Cuticle

Taxonomic identification using epidermal characters, even for extant plant species, is complex and requires comprehensive comparison of numerous epidermal characters with those of a large and diverse range of plants (Barclay *et al.*, 2007). Although cuticular characters do vary among plant groups, they also vary greatly in response to atmospheric conditions and other environmental factors. Hence, Barclay *et al.* (2007) suggested that reliable determination of taxonomic affinity requires comparison with extant cuticle that is calibrated against a variety of environmental conditions. Recent studies based on the DNA of gymnosperms suggest that extant species are not closely related to Mesozoic and earlier gymnosperms (Crisp and Cook, 2011; Davis and Schaefer, 2011; Nagalingum *et al.*, 2011) and pteridosperms evidently became extinct during the Jurassic (below). Thus, the use of pteridosperm cuticle in establishing taxonomic affinity should be viewed reservedly.



Species	Detail
<i>D. odontopteroides</i> (Morris, 1845) Gothan, 1912  Figure 4A	<b>1-pinnate to 1-pinnatisect</b> Cuticle: Jacob and Jacob (1950); Townrow (1957, 1966a); Lele (1962); Retallack (1977); Anderson and Anderson (1983); Bomfluer and Kerp (2010). Range: Olenekian–Rhaetian (Retallack, 1977; Anderson and Anderson, 1983; Holmes and Anderson, 2005a). Note: Retallack (1977) recognized 6 varieties and other unipinnate species. Anderson and Anderson (1983) accepted 2 unipinnate species with several subspecies and forma (excluding material otherwise regarded as <i>Johnstonia</i> or <i>Xylopteris</i> ).
<i>D. dubium</i> (Feistmantel, 1878) Gothan, 1912  Figure 4B	<b>2-pinnatifid</b> Cuticle: Jacob and Jacob (1950); Retallack (1977); Anderson and Anderson (1983); Bomfluer and Kerp (2010). Range: Olenekian–Norian (Retallack, 1977; Holmes and Ash, 1979; Anderson and Anderson, 1983; Holmes and Anderson, 2005a). Note: Retallack (1977) recognized 3 varieties of this species and other bipinnatifid species. Anderson and Anderson (1983) accepted 4 subspecies but other species recognized by those authors included bipinnatifid fronds.
<i>D. zuberi</i> (Feistmantel, 1878) Gothan, 1912  Figure 4C	<b>2-pinnate</b> Cuticle: Jacob and Jacob (1950); Townrow (1957); Lele (1962); Retallack (1977); Anderson and Anderson (1983); Cantrill <i>et al.</i> (1995). This species has considerable cuticular variation (Retallack, 1977). Townrow (1957) referred specimens with very thick cuticle to <i>Hoegia</i> Townrow, 1957; however, Retallack (1977) regarded this range as natural intra-species variation and chose not to recognize <i>Hoegia</i> . Range: Olenekian–Norian and possibly lower Rhaetian (Retallack, 1977; Holmes and Ash, 1979; Anderson and Anderson, 1983; Holmes and Anderson, 2005a; Pattemore and Rigby, 2005; collection by one of us [GAP] from the Callide Basin with report in preparation). Note: Retallack (1977) recognized 4 varieties and other bipinnate species.
<i>D. superbum</i> (Shirley, 1898) Townrow, 1957  Figure 4D	<b>Tending to 3-pinnatifid</b> 2-pinnate or 2-pinnatifid; pinnules with well-developed lobes; some may be 3-pinnatifid. Cuticle: unknown. Specimens assigned to this species by Townrow (1957), which include cuticle, megascopically resemble <i>D. dubium</i> . Range: Anisian to Norian (Retallack, 1977). Note: Retallack (1977) assigned Townrow's (1957) specimens to <i>D. townrovii</i> Retallack, 1977. Anderson and Anderson (1983) considered these specimens to be a distinct forma within <i>D. superbum</i> .

**Table 2.** Representative species of *Dicroidium*.

**Tabla 2.** *Especies representativas de Dicroidium.*

Although umkomasiaceans are preserved abundantly in the Gondwanan Triassic, cuticular morphology of many species is limited to only a few specimens (Tables 2–4). The stomatal apparatus is one of the most distinctive cuticular features and is often the principal (or only) detail available in cuticular studies of pteridosperms. Barclay *et al.* (2007) suggested that stomatal characters alone are of limited value in determining taxonomic affinity. Likewise, many other characters such as cuticle thickness and stomatal density can be useful indicators of environmental conditions, but absent a large and diverse cuticular dataset these characters are of limited use for taxonomic identification (Barclay *et al.*, 2007).

Stomatal ontogeny is rarely preserved in Mesozoic pteridosperms (notable exception: Barbacka and Bóka, 2000b) and thus is unrecorded for nearly all genera. The terms haplocheilic and syndetocheilic were coined by Florin (1933, p. 14) and were largely developed from his earlier work (Florin, 1931). These terms are applicable as descriptors of stomatal ontogeny in gymnosperms (Baranova, 1987) but have been widely misapplied in the description of mature

stomatal apparatuses based on the assumption that ontogeny can be inferred from the mature apparatus; however, this cannot be assumed (Baranova, 1987; Barclay *et al.*, 2007). Baranova (1987) developed a stomatal classification scheme based on mature stomata. She suggested that integrated mature and ontogenetic stomatal classification schemes have proven to be unserviceable.

Cuticle was considered important for differentiating genera but not species by Retallack (1977) and Retallack *et al.* (1977). Jacob and Jacob (1950) reported similarity of stomatal structures among unipinnate, bipinnatifid and bipinnate species of *Dicroidium*, but marked differences in distribution of stomata and cell size and orientation. Retallack (1977) noted substantial epidermal differences among *D. zuberi* specimens; he suggested that such inconsistency could well result from water stress and other environmental factors. A large Carnian-age collection of pteridosperm cuticle was documented by Anderson and Anderson (1983, 1989). They described umkomasiacean foliar cuticle from a few sites within cycle 2 of the Molteno Formation with nearly all of the

Species	Detail
<i>J. coriacea</i> (Johnston, 1886) Walkom, 1925  Figure 5A.	<b>Entire-Crenate</b> Cuticle: Anderson and Anderson (1983); Bomfluer and Kerp (2010). Range: Anisian–Norian (Retallack, 1977; Holmes, 1982; Holmes and Anderson, 2005a). Note: Retallack (1977) recognized 2 varieties and another species, <i>J. dutoitii</i> (Townrow, 1967) Retallack, 1977, that has a crenate margin. Anderson and Anderson (1983) included all these in <i>Dicroidium coriaceum</i> (Johnston, 1886) Townrow, 1957.
<i>J. stelzneriana</i> (Geinitz, 1876) Frenguelli, 1943  Figure 5B.	<b>1-pinnatifid</b> Cuticle: Anderson and Anderson (1983); Cantrill et al. (1995). Additionally, some cuticular samples examined by Archangelsky (1968) may be from this species (Retallack, 1977). Range: Anisian–Norian (Retallack, 1977; Holmes and Anderson, 2005a). Note: Retallack (1977) recognized 2 varieties. Anderson and Anderson (1983) assigned material with this morphology to <i>Dicroidium crassinervis</i> (Geinitz, 1876) Anderson and Anderson, 1983 and included other unipinnate (and ?bipinnatifid) specimens in several forma of that species.

**Table 3.** Representative species of *Johnstonia*.  
**Tabla 3.** Especies representativas de *Johnstonia*.

best preserved material collected from one site, Little Switzerland, western KwaZulu-Natal, South Africa. Other studies are listed in Tables 2–4.

### Speciation

Species of the foliar genera *Dicroidium* and *Johnstonia* Walkom, 1924 are highly variable in form, as discussed by Townrow (1957), Retallack (1977), Retallack et al. (1977), Anderson and Anderson (1983, 2003) and Holmes and Anderson (2005a). These authors have developed various nomenclatural systems which aimed to express this variability.

Anderson and Anderson (1983) suggested that *Dicroidium* had a reticulate evolutionary history, freely hybridizing across Gondwana (sympatric speciation). They presented anomalous foliar specimens from the Birds River locality, Eastern Cape, South Africa as evidence of hybridization. Anderson and Anderson (1983, pl. 74, Figs. 1–9) illustrated pinnules apparently matching two genera (*Xylopteris* and *Dicroidium*) on the same frond. Holmes and Anderson (2005a) argued that these apparent abnormalities indicated that the species of the two ‘represented’ genera were interspecific and not intergeneric, thus implying a congeneric status for *Dicroidium* with *Xylopteris*.

Hybridization appears not to have been important in gymnosperm evolution and this may explain the lack of evolutionary innovation in the gymnosperms relative to the angiosperms (Oliver et al., 2013). The genetic mechanisms utilized by angiosperms for diversification (Soltis and Soltis, 2009) are almost entirely unused by gymnosperms (Oliver et al., 2013). Thus, hybridization is an unlikely explanation for the anomalous Birds River specimens; they probably

reflect physical damage (Pattemore and Rigby, 2005). Moreover, the primary mode of speciation for representatives of the Umkomasiaceae (and other pteridosperms) was therefore almost certainly allopatric and not sympatric or parapatric (as defined by Wiley and Lieberman, 2011). Consequently, provincialism due to climatic and geographic constraints was probably the dominant influence on speciation (e.g. Retallack, 1977; Artabe et al., 2003).

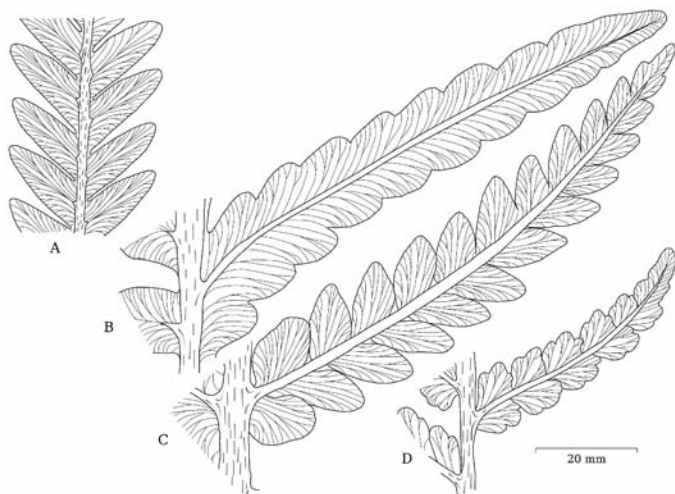
Archangelsky (1968) regarded *Xylopteris* and *Johnstonia* as junior synonyms of *Dicroidium* based on apparent similarity of associated stem material, but he conceded that the evidence was equivocal and his findings somewhat speculative. Subsequently identified stems and trunks from several Gondwanan localities suggest that members of the Umkomasiaceae exhibited a wide range of growth forms akin to that of tree ferns and large conifer-like trees (Axsmith et al., 2000; Cúneo et al., 2003; Taylor et al., 2006). Retallack (1977) retained the genera *Dicroidium*, *Xylopteris* and *Johnstonia* for the three basic leaf forms (Tables 2–4; Figs. 4–6). Other authors follow the approach of Archangelsky (1968), and in part Townrow (1957), by electing not to recognize *Xylopteris* and *Johnstonia*. Townrow (1957) placed *Johnstonia* and *Zuberia* Frenguelli, 1943 in synonymy with *Dicroidium* based on cuticular similarity, but he did not include *Xylopteris*. Retallack (1977) and Retallack et al. (1977) supported many of Townrow’s (1957) and Archangelsky’s (1968) nomenclatural proposals but not the inclusion of *Xylopteris* and *Johnstonia* in *Dicroidium*. Some workers applied an even wider range of genera for Triassic umkomasiacean foliage (e.g. Artabe et al., 2007), essentially following Frenguelli (1943). Retallack (1977) and Retallack et al. (1977) argued that these three genera are easily distinguished and probably represent evo-

Species	Detail
<i>X. argentina</i> (Kurtz, 1921) Frenguelli, 1943 Figure 6A	<b>1-pinnate</b> 1–3 well-spaced pinnae on either side of rachis; pinnules uni-veined (Retallack, 1977). Cuticle: Baldoni (1980); Anderson and Anderson (1983). Range: Carnian–Norian (Retallack, 1977; Anderson and Anderson, 1983; Pattemore and Rigby, 2005).
<i>X. elongatum</i> (Carruthers, 1872) Frenguelli, 1943 Figure 6B	<b>1-pinnate</b> >3 pinnae (usually many more) on either side of rachis; pinules uni-veined. Cuticle: Thomas (1933); Townrow (1962a); Archangelsky (1968); Retallack (1977); Baldoni (1980); Anderson and Anderson (1983); Bomfluer and Kerp (2010). Range: Anisian–Norian (Amtsberg, 1969; Retallack, 1977; Holmes, 1982; Anderson and Anderson, 1983; Holmes et al., 2008).
<i>X. spinifolia</i> (Tenison-Woods, 1883) Frenguelli, 1943 Figure 6C	<b>2-pinnate or 2-pinnatifid</b> Pinnae, pinnules and ultimate segments uni-veined. Cuticle: Jones and de Jersey (1947a); Baldoni (1980); Anderson and Anderson (1983); Bomfluer and Kerp (2010). Range: Anisian–Norian (Amtsberg, 1969; Retallack, 1977; Holmes, 1982; Anderson and Anderson, 1983; Pattemore and Rigby, 2005). Note: Specimens with multi-veined pinnules and ultimate segments were assigned to <i>Dicroidium</i> by Retallack (1977).
<i>X. tripinnata</i> (Jones and de Jersey, 1947) Schopf, 1973 Figure 6D	<b>2-pinnate or 3-pinnatifid</b> Pinnae, pinnules and ultimate segments uni-veined. Cuticle: Retallack (1977). Range: Anisian–lower Norian (Retallack, 1977). Note: Specimens with multi-veined pinnules and ultimate segments were assigned to <i>Dicroidium</i> by Retallack (1977).

**Table 4.** Representative species of *Xylopteris*.  
**Tabla 4.** *Especies representativas de Xylopteris.*

lutionary stages induced by adaptation to a more arid environment. Given that the hybridization model for umkomasiacean speciation is doubtful and that asso-

ciation of *Umkomasia* and *Pteruchus* with *Johnstonia* and *Xylopteris* has not been demonstrated, insufficient evidence exists to support the incorporation of *Johnstonia* and *Xylopteris* in *Dicroidium*. If indeed the leaf morphology of *Johnstonia* and *Xylopteris* resulted from adaptation to a drier environment, then the parent plants' reproductive strategy (and organs) would be expected to have likewise adapted.

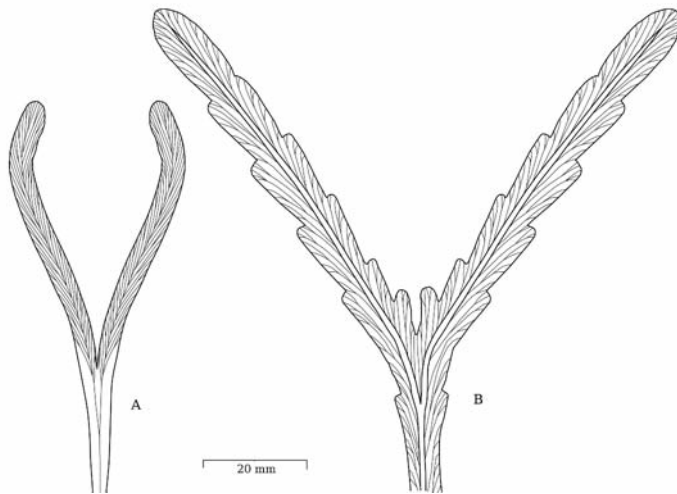


**Figure 4.** Representative species of *Dicroidium*. **A:** *D. odontopteroides*; 1-pinnate to 1-pinnatisect. **B:** *D. dubium*; 2-pinnatifid. **C:** *D. zuberi*; 2-pinnate. **D:** *D. superbum*; tending to 3-pinnatifid. Redrawn from Retallack (1977).

**Figura 4.** *Especies representativas del género Dicroidium.* **A:** *D. odontopteroides*; hojas de 1-pinnadas a 1-pinnatisectas. **B:** *D. dubium*; hojas 2-pinnatífidas. **C:** *D. zuberi*; hojas 2-pinnadas. **D:** *D. superbum*; hojas con tendencias a ser 3-pinnatífidas. Redibujado de Retallack (1977).

#### Extra-Gondwanan reports

*Umkomasia* is predominantly restricted to the Gondwanan Triassic (Anderson and Anderson, 2003), but has also been reported elsewhere, viz., from the: Upper Triassic of northern China and Germany (Kelber and van Konijnenburg-van Cittert, 1997; Zan et al., 2008; Kustatscher and van Konijnenburg-van Cittert, 2013); and the Lower Jurassic (*sensu stricto*, Liassic) of Germany by Kirchner and Müller (1992). Specimens described by the latter authors comprise *Umkomasia* and *Pteruchus*, with foliage ascribed to *Thinnfeldia* Ettingshausen, 1852 and pollen to *Alisporites*. In light of Doludenko's (1971) inclusion of *Thinnfeldia* in *Pachypteris* Brongniart, 1828 emend. Harris, 1964, Barbacka (1994) considered Kirchner and Müller's (1992) use of *Thinnfeldia* as unnecessary. Anderson and Anderson (2003) doubted



**Figure 5.** Representative species of *Johnstonia*. **A:** *J. coriacea*; entire-crenate (redrawn from Frenguelli, 1943). **B:** *J. stelzneriana*; 1-pinnatifid (redrawn from Retallack, 1977).

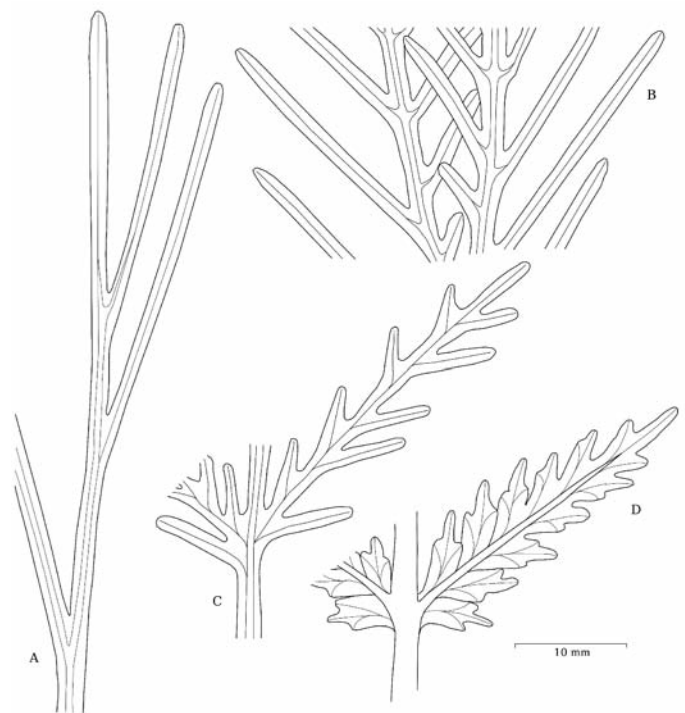
**Figura 5.** Especies representativas del género *Johnstonia*. **A:** *J. coriacea*; hojas con margen entero-crenulado (redibujado de Frenguelli, 1943). **B:** *J. stelzneriana*; hojas 1-pinnatífidas (redibujado de Retallack, 1977).

Kirchner and Müller's (1992) identification of *Umkomasia* and *Pteruchus*. Specimens from the Upper Triassic of northern China, assigned by Zan et al. (2008) to their species *U. asiatica*, apparently resemble the type species structurally and in their unlobed cupules. They suggested that species may have been associated with foliar remains referred to *Thinnfeldia* from the same locality; however, the foliage was described as poor and without cuticle. Possibly, the Upper Triassic and Lower Jurassic of Eurasia may have been a refugium for Triassic pteridosperms from Gondwana. With the possible exception of the German specimens discussed above, there is no evidence from fructifications to suggest that representatives of the Umkomasiaceae existed beyond the Triassic; further, most umkomasiacean foliar species had become extinct prior to the Rhaetian (Retallack, 1977; Tables 2–4). A recent collection by one of us [GAP] from the Callide Basin, Queensland also suggests reduced pteridosperm diversity in the Rhaetian (Table 1).

***Peltaspermaceae* Thomas, 1933**

*Fructifications and foliage*

Peltaspermaceae was established to incorporate the foliar genus *Lepidopteris* (Schimper, 1869) emend. Townrow, 1956. The association of *Lepidopteris* with a female fructification, prior to the designation of a



**Figure 6.** Representative species of *Xylopteris*. **A:** *X. argentina*. **B:** *X. elongatum*. **C:** *X. spinifolia*. **D:** *X. tripinnata*. Redrawn from Retallack (1977).

**Figura 6.** Especies representativas del género *Xylopteris*. **A:** *X. argentina*. **B:** *X. elongatum*. **C:** *X. spinifolia*. **D:** *X. tripinnata*. Redibujado de Retallack (1977).

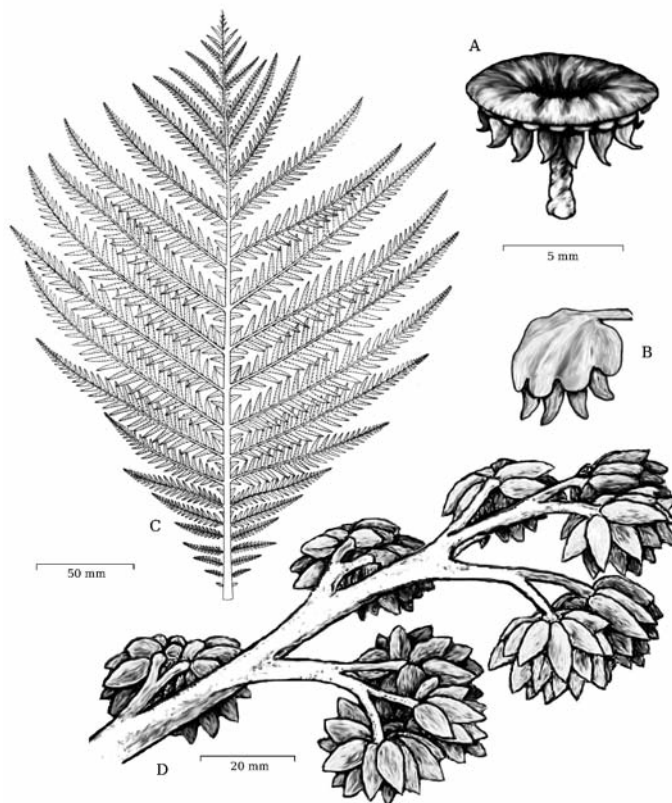
formal name for the fructification, was considered persuasive at the establishment of the family. The diagnosis of *L. natalensis* Thomas, 1933 included not only foliage but a description of the female fructification. Specimens were not in organic connection and were subsequently attributed to separate genera by Harris (1937); the female fructification was referred to *Peltaspermum* Harris, 1937 emend. Townrow, 1960.

Representatives of the Peltaspermaceae have been reported globally from the Triassic, but predominantly from the Middle and Upper Triassic (Zavialova and van Konijnenburg-van Cittert, 2011). They were largely restricted to the northern hemisphere in the Permian and first appeared in easternmost Gondwana following the end-Permian extinction event (Retallack, 2002; Zavialova and van Konijnenburg-van Cittert, 2011). They probably extended into equatorial regions of Permian Gondwana (Taylor et al., 2006) and apparently migrated as far as India in the Early Permian (Srivastava et al., 2011). Rees et al. (2002) considered the Permian peltasperms to be restricted to low-mid latitudes, and regarded attributions to *Lepidopteris* from the Wordian of India as anomalous and possibly erroneous.

Poort and Kerp (1990) proposed the inclusion of new natural genera in the Peltaspermeaceae, along with raising the status of the 'organ genus' *Peltaspermum* to a 'natural genus' (terminology appropriate at that time; Zijlstra, 2014) in a study based on material from the Upper Permian of Europe. Holmes and Anderson (2005b) disagreed with Poort and Kerp's (1990) proposal, maintaining that it was premature to nominate a natural genus without evidence of organic connection. Anderson and Anderson (2003) regarded *Meyenopteris* Poort and Kerp, 1990 as a junior synonym of *Peltaspermum*. Retallack (2002) continued using the traditional 'organ genera', disagreeing in part with Poort and Kerp's (1990) nomenclature. Reconstructions of *Peltaspermum* and associated organs based on material from the Upper Triassic of South Africa were provided by Retallack and Dilcher (1988) and Anderson and Anderson (2003) and from the lowermost Triassic of Australia by Retallack (2002).

Although relatively rare, *Peltaspermum* is widely distributed in the Middle and Upper Triassic of Gondwana (Fig. 7A; Table 5). The largest collection of Gondwanan specimens was figured from the Carnian of South Africa by Anderson and Anderson (2003). The stomata of *Peltaspermum* were reported to resemble those of *Lepidopteris* (Townrow, 1960). The male fructification, *Antevsia* Harris, 1937 emend. Townrow, 1960, has been associated with *Lepidopteris* in the Middle and Upper Triassic of Gondwana (Fig. 7D; Table 5) and of the northern hemisphere (Harris, 1937; Townrow, 1960; Dobruskina, 1994; Zavialova and van Konijnenburg-van Cittert, 2011). In-situ pollen of *Antevsia* from the German Rhaetian was analyzed by Townrow (1960) and Zavialova and van Konijnenburg-van Cittert (2011); the grains conform with the dispersed pollen genus *Cycadopites* Wodehouse, 1933 ex Wilson and Webster, 1946.

*Lepidopteris* has both northern and southern hemisphere distribution, spanning the Late Permian through Rhaetian (Harris, 1937; Townrow, 1960;



**Figure 7.** Middle–Upper Triassic representatives of the Peltaspermeaceae. **A**, *Peltaspermum rotula* Harris, 1937, redrawn from Crane (1985); **B**, *P. thomasii* Harris, 1937 emend. Townrow, 1960, redrawn from Retallack and Dilcher (1988); **C**, *Lepidopteris stormbergensis* (Seward, 1903) Townrow, 1956, from Anderson and Anderson (1989); **D**, *Antevsia zeilleri* (Nathorst, 1910) Harris, 1937, redrawn from Crane (1985). Common scale for A and B as indicated. **Figura 7.** Representantes de Peltaspermeaceae del Triásico Medio-Superior. **A**, *Peltaspermum rotula* Harris, 1937, redibujado de Crane (1985); **B**, *P. thomasii* Harris, 1937 emend. Townrow, 1960, redibujado de Retallack and Dilcher (1988); **C**, *Lepidopteris stormbergensis* (Seward, 1903) Townrow, 1956, de Anderson and Anderson (1989); **D**, *Antevsia zeilleri* (Nathorst, 1910) Harris, 1937, redibujado de Crane (1985). Como se indica, A y B presentan la escala en común.

Baldoni, 1972; Poort and Kerp, 1990; Retallack, 2002; Anderson and Anderson, 2003; Pacyna, 2014).

Genus	Key references
<i>Lepidopteris</i>	Frenguelli (1943); Townrow (1956, 1966b); Hill et al. (1965); Baldoni (1972); Rigby (1977); Holmes and Ash (1979); Holmes (1982); Retallack (1977, 1983a, 1987, 1995a, 2002); Retallack and Dilcher (1988); Anderson and Anderson (1989); Gnaedinger and Herbst (1998a); Anderson and Anderson (2003); Holmes and Anderson (2005b, 2013).
<i>Peltaspermum</i> (female)	Townrow (1956, 1960); Retallack (1981, 1983b, 1987, 2002); Anderson and Anderson (2003); Holmes and Anderson (2005b, 2013); Arce and Lutz (2010).
<i>Antevsia</i> (male)	Townrow (1960); Pole and Raine (1994); Anderson and Anderson (2003); Holmes and Anderson (2005b, 2013); Pattemore and Rigby (2005).

**Table 5.** *Lepidopteris* and associated fructifications from the Middle and Upper Triassic of Gondwana. **Tabla 5.** *Lepidopteris* y fructificaciones asociadas del Triásico Medio y Superior de Gondwana.

Gondwanan specimens assigned to this genus have been discussed widely (Fig. 7C; Table 5). The peltasperms are a dominant floral component across a large part of the Eurasian Middle and Upper Triassic and include a wider range of foliar genera than is evident from Gondwanan Triassic assemblages (Holmes, 1982; Dobruskina, 1994). However, the peltasperm foliage *Scytophyllum* Bornemann, 1856, which is predominantly a genus of the northern hemisphere, has been reported from Western Gondwana (Zamuner *et al.*, 1999; Anderson and Anderson, 2003).

Most Australasian peltasperms have been recorded from the Triassic of New South Wales (Table 5) but also have been reported from elsewhere in the Australian Triassic (Hill *et al.*, 1965; Rigby, 1977; Pattemore and Rigby, 2005) and the Middle and Upper Triassic of New Zealand (Retallack, 1981, 1983a, b; Pole and Raine, 1994). Triassic megafloras (including peltasperms) of New Zealand are from the Rakaia and Murihiku terranes (Retallack, 1987; Mortimer, 2004, 2005; Fig. 2). Specimens from the Rakaia Terrane, Torlesse Supergroup are Ladinian in age (perhaps also late Anisian). Triassic remains from the Murihiku Terrane are generally poor and may be no younger than late Norian (Retallack, 1987), although subsequently, some have been dated as Rhaetian (Pole and Raine, 1994). The Murihiku Terrane also includes Jurassic flora. Most reported peltasperm-like foliage from the New Zealand Triassic has been attributed to *Pachydermophyllum* (Retallack, 1981, 1983a,b; Pole and Raine, 1994). Given the work of Bomfleur *et al.* (2011), Triassic Gondwanan specimens attributed to this genus may be more appropriately assigned to the Matatiellaceae Anderson and Anderson, 2003 (below).

Taylor and Taylor (1993, Fig. 15.31), Taylor *et al.* (2006, Fig. 43) and Taylor *et al.* (2009, Fig. 15.81) depicted *Lepidopteris* with *Antevsia* attached to the distal end of the rachis. Anderson and Anderson (2003, p. 154) noted this as a curious reconstruction, apparently based on specimens collected from the South African Molteno Formation. Attachment of these two organs was unknown to those authors and it appears that the original material upon which this reconstruction was based has never been published (Anderson and Anderson, 2003; Taylor *et al.*, 2009). No organic connection has yet been identified among *Lepidopteris*, *Peltaspermum* and *Antevsia*.

*Peltaspermum thomasi* Harris, 1937 emend. Townrow, 1960 from the Carnian of South Africa (Fig. 7B) was originally recorded by Thomas (1933) prior to the establishment of this genus; it had been included with co-preserved foliage assigned to *Lepidopteris*. This species differs from other Triassic *Peltaspermum*

species in that pedicels are attached laterally rather than peltately (Townrow, 1960; Anderson and Anderson, 2003); cf. Figures 7A and 7B. Townrow (1960) noted this difference but considered the fructification to be otherwise consistent with the type species, *P. rotula* Harris, 1937. *Peltaspermum thomasi* has been allied with Permian peltasperms from the northern hemisphere but this is no longer supported (Kerp and Haubold, 1988). Anderson and Anderson (2003) identified no further specimens attributable to this species, despite much additional collecting from Thomas's (1933) original site. By contrast, Taylor *et al.* (2009) figured *P. thomasi* as peltately attached but with the pedicel forming a very acute angle with the fructification disc; probably caused by lithostatic compression.

#### *Survivors of the end-Permian extinction event*

*Peltaspermum* was reported from the Coal Cliff Sandstone, Sydney Basin (Retallack, 2002), post-dating the end-Permian extinction event (Metcalf *et al.*, 2015). Although the age of the Coal Cliff Sandstone was not confirmed as lowermost Triassic, the underlying unit was dated at 252.6 Ma (Metcalf *et al.*, 2015), only 0.4 Myr prior to the Permo-Triassic boundary. This is the only known occurrence globally of *Peltaspermum* immediately post-dating that extinction event; moreover, this is the earliest record of *Peltaspermum* and *Lepidopteris* in easternmost Gondwana (Retallack, 2002; Table 5). Peltasperms have been recorded from the Lower Triassic of the northern hemisphere (Naugolnykh, 2012).

The male fructification *Permotheca* Zalessky, 1929 is largely confined to the Permian of Russia (Gomankov and Meyen, 1986; Krassilov *et al.*, 1999; Naugolnykh, 2013) but has been identified from the Coal Cliff Sandstone in association with *Peltaspermum* and *Lepidopteris* (above); this is the youngest known occurrence of *Permotheca* (Retallack, 2002). The Lower Triassic of the Sydney Basin has low plant diversity which was not restored to levels equivalent to that of the Permian until the Middle Triassic (Retallack, 1995b).

Retallack's (2002) circumscription of his species *Permotheca helbyi* is based on a single specimen having synangia mounted individually on short stalks; each synangium has 15–20 basally fused pollen sacs. That basal fusion extends for a quarter the length of each sac. An attempt by Retallack (2002) to recover in-situ pollen revealed small clusters of *Falcisporites* pollen but included other dispersed pollen genera; he regarded the clustered pollen as

most likely associated with the *Permotheca* fructification.

### ***Matatiellaceae Anderson and Anderson, 2003***

#### *Fructifications and foliage*

Representatives of the Matatiellaceae were reassessed by Bomfleur et al. (2011), including the male fructification *Townrovia* Retallack, 1981 and the foliage *Dejerseya* Herbst, 1977 emend. Bomfleur et al. 2011. The family name derives from the female fructification, *Matatiella* Anderson and Anderson, 2003 emend. Bomfleur et al. 2011. These plant organs were described in considerable detail by Bomfleur et al. (2011) including seed, pollen sac and foliar cuticle. They broadly affiliated the family with the peltasperms but the phylogeny remains speculative.

*Matatiella* is rare and restricted to the Upper Triassic of New Zealand, South America, South Africa and Antarctica (Anderson and Anderson, 2003; Arce and Lutz, 2010; Bomfleur et al., 2011). Both *Townrovia* and *Matatiella* apparently have opposite to alternate, bilaterally branched petiolate sporophylls. However, the original circumscription of *Matatiella* by Anderson and Anderson (2003) suggested that branching is helical.

*Townrovia* was based on material from the Ladinian of New Zealand and on Tasmanian specimens previously known as *Pteruchus petasatus* Townrow, 1965. The latter were regarded as Rhaetian–earliest Jurassic by Townrow (1965) but, being collected from coal measures, are more likely Carnian–Norian in age (Reid, 2014). Retallack (1981) suggested that *Townrovia* is most like the peltasperm male fructification *Antevsia*. Megascopic structure and pollen distinguish *Townrovia* from *Pteroma* Harris, 1964 and *Antevsia* (Retallack, 1981); pollen grains from the latter resemble *Cycadopites* (see above), while those of *Townrovia* and *Pteroma* are akin to *Falcisporites* (see below). *Pteroma* is unknown from Gondwana and is apparently restricted to the Jurassic (Yao et al., 1995).

*Townrovia* is rare and has only been identified from the Middle and Upper Triassic of Tasmania, New Zealand and Antarctica (Bomfleur et al., 2011; Chatterjee et al., 2013). Based on the occurrence of specimens at the same Antarctic Upper Triassic locality, Bomfleur et al. (2011) associated *Townrovia* with *Matatiella* and *Dejerseya*; they ranked these with the Peltaspermales based on structural similarity. The fructification's stem apparently arises from a short shoot (Bomfleur et al., 2011). *Dejerseya* was estab-

lished by Herbst (1977) for sterile fronds previously referred to *Rienitsia* Walkom, 1932. The genus has since been identified from several Gondwanan Middle and Upper Triassic localities (Anderson and Anderson, 1989, 2003; Bomfleur et al., 2011).

The pollen sacs of *Townrovia* are attached to a central receptacle in two or three irregular rows. In-situ pollen resembling *Falcisporites* were recovered by Bomfleur et al. (2011). *Falcisporites*-like pollen grains were also identified by Bomfleur et al. (2011) within the micropylar canal of *Matatiella* ovules. These authors considered it likely that pollen analysis of specimens assigned to *Stachyopitys lacrisporangia* Anderson and Anderson, 2003 from the Carnian of South Africa would indicate that this species belongs to *Townrovia*. Similarly, specimens regarded by Holmes and Anderson (2007) as probably assignable to *Stachyopitys* may represent the oldest occurrence of *Townrovia*.

#### *Stachyopitys Schenk, 1867 in the Gondwanan Triassic*

*Stachyopitys*, from the Gondwanan Middle and Upper Triassic (mostly Carnian–lowermost Norian), broadly resembles *Antevsia* (above) and *Townrovia* (Bomfleur et al., 2011, table 2). *Stachyopitys* was based on Lower Jurassic specimens from Germany and is widely regarded as ginkgoalean (van Konijnenburg-van Cittert, 2010). It is known from the Lower and Middle Jurassic of the northern hemisphere (Wang et al., 2007) and the Triassic of the southern hemisphere (Anderson and Anderson, 2003). It is rare globally with most specimens reported from the Carnian of South Africa (Anderson and Anderson, 2003). Those authors figured several specimens of *Stachyopitys* attached to bulbous bases, and one specimen apparently shows the ginkgoalean foliage, *Sphenobaiera* Florin, 1936, attached to the protuberant base of a *Stachyopitys* fructification. They associated this genus with the female fructification *Hamshawvia* Anderson and Anderson, 2003, which they also considered to be in organic attachment to *Sphenobaiera* in another specimen.

The above Gondwanan report can be contrasted with *Stachyopitys* and its allied organs from the northern hemisphere. The female fructification *Schmeissneria* Kirchner and van Konijnenburg-van Cittert, 1994 from the Lower Jurassic of Germany was associated with *Stachyopitys* by Kirchner and van Konijnenburg-van Cittert (1994). *Schmeissneria* was also associated with ginkgoalean foliage based on organic connection; but *Schmeissneria* does not resemble *Hamshawvia*. The latter genus has eight or

more ovules mounted below (and apparently partially embedded within) laminae. *Schmeissneria* has a winged ovule partially enclosed within a cupule that is attached, together with numerous other cupules, along an axis (Kirchner and van Konijnenburg-van Cittert, 1994; van Konijnenburg-van Cittert, 2010); it was considered to be a possible basal angiosperm by Wang et al. (2007).

Bomfleur et al. (2011) suggested that Gondwanan material attributed to *Stachyopitys* shows significant differences to established northern hemisphere species in size, shape, number and attachment of pollen sacs and in branching complexity. They compared *Stachyopitys* with *Antevsia*, *Permotheca*, *Townrovia* and *Pteruchus*. The significant differences between northern and southern hemisphere specimens referred to *Stachyopitys*, vis-à-vis morphology and associated organs, is suggestive that some, if not all, material assigned to *Stachyopitys* from Gondwana is attributable to *Pteruchus Townrovia* or a new genus and that genuine *Stachyopitys* material may be restricted to the extra-Gondwanan Jurassic.

### ***Incertae sedis***

#### *Pachydermophyllum* Thomas and Bose, 1955

The foliar genus *Pachydermophyllum* was based on Jurassic specimens from Yorkshire (Thomas and Bose, 1955; Retallack, 1981). Retallack (1977) considered the cuticle of *Pachydermophyllum* as closely resembling, but still distinct from, *Lepidopteris*. The type species of *Pachydermophyllum* was re-combined with *Pachypteris* by Harris (1964), but Retallack (1977) viewed cuticular and megascopic differences sufficient to maintain their generic separation. Thomas and Bose (1955) had noted cuticular differences between these genera. Numerous specimens from the Middle and Upper Triassic of Gondwana were assigned to *Pachydermophyllum* by Retallack (1981), including material from near Fingal, Tasmania (presumably from coal measures of Carnian-lower Norian age; Reid, 2014) which was previously identified as *Pachypteris* by Townrow and Jones (1969).

Retallack (1981, 1983b, 1987) and Pole and Raine (1994) reported *Pachydermophyllum*, *Peltaspermum* and *Antevsia* from the Middle and Upper Triassic of New Zealand. Anderson and Anderson (2003) considered those specimens assigned to the latter genera (fructifications) attributable to *Matatiella* and they regarded the foliage as likely to be *Kurtziana* Frenguelli, 1942 – not *Pachydermophyllum* – and associated with *Matatiella*. They suggested restriction

of *Pachydermophyllum* to the northern hemisphere and that Gondwanan material previously assigned to this genus was probably referable to *Kurtziana*. In contrast, Bomfleur et al. (2011) preferred attribution of *Pachydermophyllum* to the Matatiellaceae, and they disagreed with Anderson and Anderson's (2003) generic circumscription of *Kurtziana* (below). McLoughlin et al. (2002) assigned Lower Cretaceous Victorian specimens to *Pachydermophyllum*.

The taxonomic relationship of *Lepidopteris*, *Pachydermophyllum* and *Pachypteris* has yet to be resolved (Thomas and Bose, 1955; Harris, 1964; Retallack, 1977; Anderson and Anderson, 1989, 2003). Bomfleur et al. (2011) postulated that *Pachydermophyllum*, *Linguifolium* and *Dejerseya* are intergradational apropos of megascopic and microscopic characters. Given this association, and their apparent autochthonous preservation with *Matatiella*, Bomfleur et al. (2011) suggested that these genera may belong to the Matatiellaceae (above). *Linguifolium* and *Dejerseya*, together with the fructifications *Matatiella* and *Townrovia*, are evidently restricted to the Middle and Upper Triassic of Gondwana, while *Pachydermophyllum* has been reported globally, through much of the Mesozoic. If this intergradational foliar series were confirmed it may indicate that specimens assigned to *Pachydermophyllum* from the Gondwanan Middle and Upper Triassic are generically distinct from other material referred to this genus, despite their apparent similarity.

#### *Linguifolium* Arber, 1917 emend. Pattemore and Rigby in Pattemore et al., in press

*Linguifolium* has been widely reported from the Middle and Upper Triassic of Gondwana with the exception of India (Table 6). The genus includes several species but its taxonomic affinity has proven debatable (Retallack, 1980b; Webb, 1980; Anderson and Anderson, 1989; Pattemore and Rigby, 2005). Bomfleur et al. (2011) indicated that the genus may belong to the Matatiellaceae (above). No fructifications have been allied with the genus. Retallack (1980b) suggested association with a seed from the Ladinian of New Zealand but this has not been confirmed from elsewhere in Gondwana.

Few specimens have been attributed to the genus from the northern hemisphere. These comprise Lower Jurassic specimens from eastern Russia (east of Vladivostok: Krassilov and Shorokhova, 1973) and from the Upper Triassic of Germany (Kelber, 1998). Foliar remains from the Indian Jurassic were referred



Location	Age	References
Australia	Middle-Late Triassic	Hill <i>et al.</i> (1965); Flint and Gould (1975); Webb (1980); Retallack (1980b); Playford <i>et al.</i> (1982); Pattemore and Rigby (2005); Holmes <i>et al.</i> (2010); Holmes and Anderson (2013).
New Zealand	Middle-Late Triassic	Arber (1913, 1917); Bell <i>et al.</i> (1956); Retallack (1980b, 1981, 1983b, 1985, 1987).
Antarctica	Middle-Late Triassic	Escapa <i>et al.</i> (2011); Cantrill and Poole (2012) and references therein.
South America	Late Triassic	Frenguelli (1941); Retallack (1980b); Gnaedinger and Herbst (1998b, 2004); Morel <i>et al.</i> (1999, 2003, 2011); Herbst <i>et al.</i> (2005); Moisan <i>et al.</i> (2010).
South Africa	Late Triassic	Anderson and Anderson (1989, 2003).

**Table 6.** *Linguifolium* from the Gondwanan Triassic: key references. The genus has been reviewed by Pattemore et al. (in press).

**Tabla 6.** *Linguifolium del Triásico de Gondwana: referencias principales.*

to *Linguifolium curvatum* Bose and Banerji, 1984; this is the first report of the genus from India (Bose and Banerji, 1984).

#### *Kurtziana Frenguelli, 1942*

*Kurtziana* was erected to accommodate foliar specimens from the Upper Triassic of western Argentina (Cuyo Basin). It has since been identified from the Lower Jurassic of South America and from the Middle and Upper Triassic of Australia and South Africa (Table 7). Artabe *et al.* (1991) examined cuticle of *Kurtziana* from the Lower Jurassic and considered the genus to be cycadalean. Herbst and Gnaedinger (2002) accepted Frenguelli's (1942) diagnosis of *Kurtziana*, discounting subsequent emendations; they referred Jurassic foliage with preserved cuticle to their new genus *Alicurana*. Thus, *Kurtziana* was retained for Triassic specimens. They tentatively suggested that *Kurtziana* is a pteridosperm, but considered *Alicurana* to be cycadalean as did Morel *et al.* (2003).

Numerous non-cuticular specimens referred to *Kurtziana* by Holmes and Anderson (2005b) from the Nymboida Coal Measures, eastern Australia (Anisian) show considerable variation in leaf size, shape and pinnule separation. These authors suggested that the foliage was probably leathery and consequently rarely preserved clear venation detail. Specimens

previously described as *Dicroidium eskensis* (Walkom, 1928) Jacob and Jacob, 1950 from the Esk Trough (Anisian) and Nymboida Coal Measures were assigned to *Kurtziana* by Herbst and Gnaedinger (2002).

Anderson and Anderson (2003) considered *Kurtziana* to be associated with the female fructification *Matatiella*; they suggested that Gondwanan material previously referred to *Pachydermophyllum* probably belongs to *Kurtziana* and that *Pachydermophyllum* is restricted to the northern hemisphere. However, Bomfleur *et al.* (2011) considered the generic circumscription of *Kurtziana* by Anderson and Anderson (2003) to be too broad, accommodating material attributable to *Pachydermophyllum*. A comparison of various Mesozoic peltasperm and other foliar genera, including *Kurtziana*, was provided by Bomfleur *et al.* (2011, Table 1). *Kurtziana* and *Alicurana* have not been confidently associated with any fructification.

#### *Dordrechtites Anderson, 1978 emend. Bergene et al. 2013*

*Dordrechtites* is a poorly understood genus reported from the Anisian-Carnian of Antarctica, South Africa, South America and Australia (Anderson and Anderson, 2003; Bergene *et al.*, 2013). Bergene *et al.* (2013) described anatomically preserved

Location	Key references
South America	Frenguelli (1942, 1944); Arrondo and Petriella (1980); Petriella and Arrondo (1982); Artabe <i>et al.</i> (1991, 2007); Artabe and Stevenson (1999); Herbst and Gnaedinger (2002); Anderson and Anderson (2003); Holmes and Anderson (2005b); Spalletti <i>et al.</i> (2007); Morel <i>et al.</i> (2011).
Australia	Herbst and Gnaedinger (2002); Holmes and Anderson (2005b, 2013).
South Africa	Anderson and Anderson (2003).

**Table 7.** *Kurtziana* and *Alicurana*: key references.

**Tabla 7.** *Kurtziana y Alicurana: referencias principales.*

*Dordrechtites* from the Anisian of South Victoria Land, Antarctica. Although generally rare, the fructification's dehisced scales are reportedly common in the Carnian Molteno Formation, South Africa (Anderson and Anderson, 2003). Playford et al. (1982) and Bergene et al. (2013) suggested that the genus is allied with the pteridosperms. Anderson and Anderson (2003) placed *Dordrechtites* within Pinopsida. No associated organs are known.

*Dordrechtites dikeressa* Rigby in Playford et al. 1982, from the Moolayember Formation of the Bowen Basin (upper Anisian–Ladinian; Draper, 2013), has a general form somewhat like *Umkomasia*. It has an open-branching habit and paired cupulate seeds, but differs from *Umkomasia* in possessing strongly ornamented cupules and ovules (Playford et al., 1982).

#### *Petriellales* Taylor, Del Fueyo and Taylor, 1994

Representatives of the Petriellales have been reported from the Middle and Upper Triassic of Gondwana (Taylor et al., 1994; Anderson and Anderson, 2003; Holmes and Anderson, 2005b; Taylor et al., 2009; Morel et al., 2011) except India (Bomfleur et al., 2014). The order is regarded by some as pteridospermous (e.g. Taylor et al., 2009; Decombeix et al., 2010); other authors consider it to be unlike any other seed plant group (e.g. Bomfleur et al., 2014). It comprises two families: Petriellaceae Taylor, Del Fueyo and Taylor, 1994 and Kannaskoppiaceae Anderson and Anderson, 2003. Bomfleur et al. (2014, p. 1064) regarded the differences between these as insufficient to maintain their separation. While no fructifications allied with these families are known from Australasia, the foliage *Rochipteris* Herbst, Troncoso and Gnaedinger, 2001 has been recorded from the Anisian–Carnian of Australasia (Herbst et al., 2001; Barone-Nugent et al., 2003; Holmes and Anderson, 2005b).

#### *Glossopteris*-like foliage

*Glossopteris* Brongniart (1828) 1831 is well known from and regarded as confined to the Gondwanan Permian, but foliage has been ascribed to this genus from Triassic strata (Johnston, 1886, 1888; du Toit, 1927; Thomas, 1952; Anderson and Anderson, 1985; Pant and Pant, 1987; Holmes, 1992; Srivastava and Agnihotri, 2010). However, no associated fructifications have yet been identified from the post-Permian (Pant and Pant, 1987). The foliage *Gontriglossa* Anderson and Anderson, 1989, from the Gondwanan

Triassic, megascopically resembles *Glossopteris* but differs in mode of attachment and cuticle. Moreover, *Gontriglossa* has groups of petiolate leaves arranged in whorls (Anderson and Anderson, 1989, 2003). Material from the Triassic of southern Africa, previously assigned to *Glossopteris*, has been referred to *Gontriglossa* by Anderson and Anderson (1989, 2003).

Numerous reports of *Glossopteris* from the Indian Triassic were summarized by Pant and Pant (1987), Srivastava and Agnihotri (2010) and Bhowmik and Parveen (2012). Pant and Pant (1987) cautioned that many specimens have been insufficiently described and the majority were from Nidhpuri, Sidhi district, Madhya Pradesh. This area is structurally complex and differentiation between Permian and Triassic sediments is not always clear (Pant and Pant, 1987). The three specimens described by those authors, from Nidhpuri, were reportedly preserved in close association with *Dicroidium*. Although almost-complete, the specimens do not show the critical feature of petiole attachment. The putatively Triassic specimens discussed by Srivastava and Agnihotri (2010) and Bhowmik and Parveen (2012) are also from Nidhpuri.

*Glossopteris* leaves were identified by Holmes (1992) from several localities in the Triassic of eastern Australia. Although he assigned specimens to established and new glossopterid species, he concluded that there was nothing other than megascopic foliar form to suggest a relationship between Triassic and Permian specimens referred to *Glossopteris*. Subsequently, Holmes et al. (2010) re-assigned the specimens to *Gontriglossa*.

*Glossopteris*-like foliage from the Middle Triassic of the Sydney Basin was likened to *G. moribunda* Johnston, 1886 from the Tasmanian Triassic by Retallack (1980a) based on megascopic resemblance. Anderson and Anderson (1989) referred this and other material, from the Middle Triassic of Queensland and New South Wales, to *Gontriglossa*.

Rigby and Schopf (1969) reported a mixed Permian and Triassic Gondwanan flora from the Allan Hills (then known as Allan Nunatak), South Victoria Land, Antarctica, based on specimens they collected in January 1966. One of those authors (Rigby; also co-authoring the present paper), takes responsibility for this and the next paragraph, which were written from memory, lacking his field notes.

The collection site was a gently sloping scree field seated in a small, shallow, water drainage feature in the more or less horizontally stratified Permian outcrop. This feature probably pre-dated the onset of the Pleistocene glaciation in the area. Locally the Permian is known to be overlain by Triassic strata. Each sequence was dated by the presence of typical non-

marine Gondwanan floral assemblages. The scree comprises angular to subangular slabs of black to dark brown mudstone bearing incomplete leaves of *Glossopteris* spp. lying parallel to the bedding plane. This mudstone showed no megascopic mineral fragments. A single largish slab (about 20–30 kg) bore fragments of Triassic plants. This slab petrographically resembled the other slabs, apart from being impregnated with sparse mica flakes, apparently muscovite, about 1 mm or less in diameter. At the time of collection Rigby (*contrario sensu*) regarded this slab as an erratic, and still does, but his co-worker (J.M. Schopf) disagreed as he did not accept the presence or absence of the mica flakes had any significance (possibly because it conflicted with his concept that the locality, the shards and the erratic demonstrated the presence of a mixed Permian and Triassic flora). Rigby had left the employ of the U. S. Geological Survey when the final draft of Rigby and Schopf (1969) was submitted for publication, and thus had no opportunity to express a dissenting opinion; i.e. that the plant remains from the scree field suggested that the rock slabs were derived from both Permian and Triassic strata but not that all the slabs were derived by glacial erosion of a single stratigraphic unit. The only way that it could be demonstrated the two floras were mixed would be the occurrence of species typifying both floras occurring on the same slab. That did not happen. (Rigby, *contrario sensu*).

The Triassic of the Allan Hills, South Victoria Land, now known as the Lashly Formation (Ballance, 1977; McManus *et al.*, 2002), is considered to be regionally extensive (Ballance, 1977); the fossiliferous upper section is Middle and Late Triassic in age (McManus *et al.*, 2002; Escapa *et al.*, 2011; Awatar *et al.*, 2014). *Dicroidium* species identified from this formation by Townrow (1967) and Rigby and Schopf (1969) support this age range. *Glossopteris* has not subsequently been recorded from this formation (McManus *et al.*, 2002). Townrow (1967) examined material from both the Permian and Triassic of the Allan Hills; he reported *Glossopteris* exclusively from Permian strata.

## Summary

Although a convincing association has been established between *Dicroidium* and the fructifications *Umkomasia* and *Pteruchus*, insufficient evidence exists to support the merging of *Xylopteris* and *Johnstonia* into *Dicroidium*. That synonymy was originally based on resemblance of stem material and has subsequently been supported by the notion that their host plants hybridized across Gondwana (sympatric

speciation), thus resulting in substantial morphological diversity among species of these genera. However, hybridization is rare in modern gymnosperms, and is therefore an improbable explanation for this morphological diversity. Consequently, speciation in the Umkomasiaceae (and other pteridosperm groups) was almost certainly allopatric; thus, provincialism probably had a significant influence on speciation.

The Umkomasiaceae is known through much of the Gondwanan Triassic and its dispersal apparently extended beyond Gondwana by the Late Triassic. The family's diversity declined toward the close of the Triassic and it is unknown thereafter in Gondwana. Attempts to understand the family's phylogeny based on foliage resulted in significantly differing opinions and taxonomy (cf. Retallack, 1977; Anderson and Anderson, 1983). Subsequent identification of associated umkomasiacean fructifications, foliage, stems and trunks (Axsmith *et al.*, 2000; Cúneo *et al.*, 2003; Taylor *et al.*, 2006) has improved understanding of their parent plants' morphology and position in the ecosystem. However, phylogenetic relationships among members of the family and more widely remain obscure because most of the fructifications are poorly understood. The branching arrangement of *Pteruchus* sporophylls has been variously described as alternately pinnate and helical (cf. Townrow, 1962c; Yao *et al.*, 1995; Anderson and Anderson, 2003; Pattemore and Rigby, 2005). Permineralized ovulate cupules from Antarctica (*Umkomasia resinosa* Klavins *et al.*, 2002) have provided megasporangial structural detail but other species are largely distinguished by shape and size of parts (Zan *et al.*, 2008) as little other botanical detail is available. Furthermore, *U. uniramia* Axsmith *et al.* 2000, with its whorled cupulate ovules, is structurally unlike other species of the genus. Thus, it seems that the Umkomasiaceae is either more diverse than previously recognised or perhaps is not monophyletic.

Cuticular data for pteridosperms are generally limited and are not calibrated environmentally. Using cuticle to determine taxonomic affinity requires a conservative approach; confident identity requires a large and diverse cuticular dataset and comparison with environmentally-calibrated cuticle from a wide range of plant groups (Barclay *et al.*, 2007). The terms haplocheilic and syndetocheilic have been widely misapplied to the description of mature stomatal apparatuses on the assumption that ontogeny can be inferred from the mature apparatus. Further, these terms imply gymnospermous affiliation, thus tending to bias the epidermal characterization.

The Peltaspermaceae is known through much of

the Gondwanan Triassic, notably from strata immediately post-dating the end-Permian extinction event. Representatives of the Matatielliaceae are relatively rare and restricted to the Gondwanan Middle and Upper Triassic. At least some Triassic specimens identified as *Stachyopitys* may belong to the Matatielliaceae or Umkomasiaceae. *Pachydermophyllum*, from the Gondwanan Middle and Upper Triassic, may be distinct from post-Triassic specimens referred to this genus. Several other organs from the Australasian Triassic are possibly pteridospermous but these await confirmation.

### Post-Triassic pteridosperms

#### Evidence from pollen

Fructifications from the Jurassic of Australasia that were possibly allied to the pteridosperms are limited (discussed below; Table 8). The Triassic–Jurassic boundary marks the upper stratigraphic limit of *Falcisporites* and *Alisporites* palynofloral dominance in Australasia (de Jersey and McKellar, 2013) supporting the view that the Umkomasiaceae and Matatielliaceae substantially declined at or near this boundary. *Alisporites* has been recorded from the

Hettangian (de Jersey and McKellar, 2013) and the Pliensbachian–Toarcian (Jansson *et al.*, 2008a; McLoughlin *et al.*, 2014) of the Clarence-Moreton Basin. Significantly, those reports did not identify *Falcisporites* from the Lower Jurassic of the Clarence-Moreton Basin. Balme (1995) confidently allied *Falcisporites* pollen with the fructification *Pteruchus* (above) while *Alisporites* has been attributed to a wider range of gymnosperms (conifers and possibly ginkgophytes) and has been identified through to the Upper Cretaceous (discussed above). Thus, the decline in *Alisporites* dominance near the Triassic–Jurassic boundary may have been unrelated to the decline in pteridosperms at that time. As indicated earlier, the widely espoused association of *Alisporites* with Triassic pteridosperms is doubtful (Balme, 1995).

The dispersed pollen genus *Cycadopites* has been allied with a range of Mesozoic gymnosperms (Balme, 1995; Zavialova and van Konijnenburg-van Cittert, 2011) and its spatiotemporal distribution cannot therefore be regarded as corresponding to that of the Peltaspermeae. However, as for the Umkomasiaceae and Matatielliaceae, there is no evidence from fructifications suggesting that the Peltaspermeae existed above the Triassic–Jurassic boundary in Australasia. *Cycadopites* has been iden-

Basin/Locality	Epoch	Key references
Clarence-Moreton and Surat Basins (Queensland)	Early–Late	Carruthers (1872); Tenison-Woods (1883); Etheridge (1888, 1889); Jack and Etheridge (1892); Walkom (1917a, 1917b, 1921b); Hill <i>et al.</i> (1966); Gould (1974a, 1974b, 1975, 1980); Rigby (1978); McLoughlin and Drinnan (1995); Jansson <i>et al.</i> (2008b); Turner <i>et al.</i> (2009); Tidwell <i>et al.</i> (2013); McLoughlin <i>et al.</i> (2014); Pattemore <i>et al.</i> (2014) and references therein.
Nambour Basin (Queensland)	Early	Jones and de Jersey (1947b); Woods (1953); Pattemore (2000); Pattemore and Rigby (2005); Pattemore <i>et al.</i> (2014).
Surat Basin (New South Wales)	Early	Tenison-Woods (1883); Pattemore <i>et al.</i> (2014).
Talbragar Fish Beds (New South Wales)	Late	Walkom (1921a); Retallack (1981); White (1981, 1986); McLoughlin <i>et al.</i> (2002).
Canning, Carnarvon and Perth basins (Western Australia)	Early–Late	Walkom (1921b); McLoughlin and Pott (2009).
New Zealand	Early–Late	Arber (1914, 1917); Edwards (1934); Blaschke and Grant-Mackie (1976); Pole (2001, 2004, 2009); Thorn (2001, 2005); Tidwell <i>et al.</i> (2013); Pattemore <i>et al.</i> (2014) and references therein.
Other and general discussion	Early–Late	Grant-Mackie <i>et al.</i> (2000); Turner <i>et al.</i> (2009); Pole (2009).

**Table 8.** Principal plant megafossil localities in the Jurassic of Australasia.

**Tabla 8.** Principales localidades del Jurásico de Australasia con megaflores.

tified as a minor component of the Clarence-Moreton Basin's Pliensbachian–Toarcian palynoflora (McLoughlin et al., 2014).

### **Putative pteridospermous Gondwanan lineages**

*Rintoulia* McLoughlin and Nagalingum in McLoughlin et al., 2002

*Rintoulia* was based chiefly on material from the Lower Cretaceous of Victoria, with its designated type species, *R. variabilis* (Douglas, 1969) McLoughlin and Nagalingum in McLoughlin et al., 2002. The basionym of the type species is *Rienitsia variabilis* Douglas, 1969 and thus, *ipso facto*, the specimens listed by Douglas (1969, p. 27) collectively typify *Rintoulia variabilis*. Douglas's (1969) specimens include small circular–oval features on pinnules (presumably sori) that he described as undoubtedly fertile; these features were included in his species diagnosis (adopted without emendation or comment by McLoughlin et al., 2002).

Douglas's (1969) specimens are the only ones assigned to the genus having preserved epidermal cell structure. The additional specimens of McLoughlin et al. (2002) and Jansson et al. (2008b) include, at best, very poor epidermal detail. McLoughlin et al. (2002) regarded Douglas's (1969) described cuticle as similar to *Lepidopteris* from the Gondwanan Triassic; Jansson et al. (2008b) likewise suggested pteridospermous affinity. However, the cuticular characters noted by McLoughlin et al. (2002) are insufficient for reliable determination of such affiliation. Douglas's (1969) figured stomata are best categorized as stephanocytic (as defined by Baranova, 1987; Carpenter, 2005; Barclay et al., 2007). Although *Lepidopteris* is compatible with this categorization (Townrow, 1960, text-Figs. 2E-L, 3A-C, 3G-H; Anderson and Anderson, 1989, pls. 17-24), many other groups are likewise, such as fossil and extant conifers, angiosperms and others (Carpenter, 2005). No fructifications have been associated with the genus and Douglas's (1969) cuticular specimens have never been comprehensively compared with other plant cuticle, thus leaving open the question of taxonomic affinity (discussed above; Barclay et al., 2007).

*Komlopteris* Barbacka, 1994 and similar foliage

Walkom (1921a) attributed specimens to *Thinnfeldia* from the Talbragar Fish Beds, east of Dubbo, New South Wales. These beds have been regarded as

approximately coeval with nearby outcropping Lower Jurassic Purlawaugh Formation of the Surat Basin, but recent evidence suggests they are of Late Jurassic age (Beattie and Avery, 2012). Walkom's (1921a) material has since been variously included in *Pachypteris*, *Pachydermophyllum* (Townrow, 1965; Retallack, 1981) and *Rintoulia* (above). *Pachypteris* has also been reported from the Middle Jurassic of Queensland (Hill et al., 1966; Gould, 1980).

Jones and de Jersey (1947b) and Woods (1953) identified *Thinnfeldia* and *Pteruchus* from the Lower Jurassic of the Nambour Basin but the specimens were neither figured nor retained institutionally. Jack and Etheridge (1892) ascribed specimens to *T. media* Tenison-Woods, 1883 from the Jurassic of the Clarence-Moreton Basin and Walkom (1919) tentatively recorded this species from the Burrum Coal Measures (Lower Cretaceous: Albian) of the Maryborough Basin. The description of *T. media* by Tenison-Woods (1883) was based on apparently bipinnate specimens from New South Wales, but their exact collection location is unclear.

Given the recognition of *Thinnfeldia* as a junior synonym of *Pachypteris*, based on material from the northern hemisphere (Doludenko, 1971; Doludenko et al., 1998), the taxonomic position of Australasian specimens ascribed to these genera requires re-assessment. Retallack (1981) endorsed Doludenko's (1971) inclusion of *Thinnfeldia* in *Pachypteris* but suggested that many specimens, previously referred to *Thinnfeldia*, probably belong to a new genus. *Komlopteris* Barbacka, 1994 included a range of Lower Jurassic–Lower Cretaceous specimens from Sweden, Hungary, India and possibly China (Barbacka, 1994). These had previously been referred to *Thinnfeldia* but were not considered attributable to *Pachypteris*.

Barbacka and Bóka (2014) associated *Komlopteris* with the female fructification *Sacculotheca*, newly erected by those authors based on specimens from the lowermost Jurassic (Hettangian) of Hungary. These organs were not in organic connection; their association was proposed based on cuticular resemblance and occurrence at the same locality (Barbacka and Bóka, 2014). Barbacka (1994) tentatively suggested that *Komlopteris* belonged to the Umkomasiaceae. However, *Sacculotheca* differs structurally from other Mesozoic pteridosperm fructifications (Barbacka and Bóka, 2014); hence its higher taxonomic placement is uncertain. The genus is known only from the lowermost Jurassic of Hungary.

Barbacka (1994) proposed the combination *Komlopteris indica* (Feistmantel, 1877) Barbacka, 1994 with specimens from the Indian Lower Cretaceous

including cuticular specimens described by Maheshwari (1986). Stomata are stephanocytic and show considerable variability in size and arrangement of subsidiary cells (Maheshwari, 1986, pl. 2). McLoughlin *et al.* (2002) ascribed non-cuticular specimens to *K. indica* from the Lower Cretaceous of the Gippsland Basin, Australia. An ultrastructural study of cuticle from specimens assigned to both *Pachypteris* and *Komlopteris* from the Indian Lower Cretaceous (Bajpai and Maheshwari, 2000) revealed differences but did not conclusively separate the genera based on microscopic characters. Guignard *et al.* (2001) observed considerable ultrastructural variation among specimens from the European Lower Jurassic assigned to the type species of *Komlopteris*. This variation was attributed to the degree of foliar sun exposure. The limited available cuticle from Eastern Gondwana does not clearly support assignment to this genus; moreover, specimens have been degraded by fungal growth (Bajpai, 1997; Guignard *et al.*, 2001). An extended cuticular comparison would almost certainly identify other possible affinities. Maheshwari (1986) suggested the Indian material with preserved cuticle was probably cycadalean.

McLoughlin *et al.* (2008) assigned foliar fragments to *Komlopteris* (placed within the *Corystospermales* by those authors) from the lower Eocene of Tasmania. They described cuticle but no associated fructification was reported and no pollen was identified as *Falcisporites* or *Alisporites* (the palynofloral assemblage having been assessed, albeit unpublished). McLoughlin *et al.* (2008) noted some cuticular distinction from Barbacka's (1994) *Komlopteris*. Described stomata are mature, yet haplocheilic development was suggested; this cannot be assumed (Baranova, 1987, p. 56). Furthermore, the term 'haplocheilic' implies gymnospermous affiliation (above). The application of a mature stomatal classification scheme (e.g. Barclay *et al.*, 2007) without biased descriptive terms suggests a broader range of possibilities and a comprehensive cuticular comparison with younger cuticle may better define taxonomic affinity. Attribution of these specimens to the *Corystospermales* is dubious because, as discussed above, there is no persuasive evidence from fructifications that the *Umkomasiaceans* post-dated the Triassic in Eastern Gondwana and the Early Jurassic globally.

McLoughlin *et al.* (2015) tentatively suggested placement of Jurassic specimens attributed to *Rintoulia* and *Komlopteris* in the *Umkomasiaceae*. Those authors also identified specimens from the uppermost Jurassic (or lowermost Cretaceous) of the Laura Basin, northern Queensland as '*Pachypteris* sp.

or *Lepidopteris* sp.' together with a '*Peltaspermum*-like organ'. This indifferently preserved material has barely perceptible venation and the suggested fructification (uncatalogued but on same slab as QMF15346; re-examined by GAP) is undoubtedly a fern crozier; no ovules were identified and the purported fructification is structurally unlike *Peltaspermum*. The foliage was originally referred to *Pachypteris* by Rozefelds (1988). There is no evidence to suggest that these specimens are anything other than fern fronds.

#### *Knezourocarponaceae* Pattemore in Pattemore *et al.*, 2014

The family *Knezourocarponaceae*, as currently known, is restricted to the Toarcian of eastern Australia. It includes one genus, *Knezourocarpon* Pattemore, 2000 and comprises a collection of male and female fructifications which have not yet been associated with foliage or pollen (Pattemore, 2000; Pattemore *et al.*, 2014). They were considered catkin-like, but their higher taxonomic affinity is conjectural. Pattemore *et al.* (2014) tentatively suggested ginkgoalean or pteridosperm affiliation based on megascopic form. *Knezourocarpon* includes material that was previously regarded as belonging to *Caytonia* Thomas, 1925 emend. Harris, 1940 (see below) and *Palissya* Endlicher, 1847 emend. Florin, 1958. *Palissya* of the northern hemisphere is widely regarded as a conifer and the genus is designated on both fructifications and foliage (Pattemore *et al.*, 2014).

#### *Pentoxylales* Pilger and Melchior, 1954

The *pentoxylaleans* comprise a distinct order of foliage and fructifications from the Upper Jurassic and Lower Cretaceous of Gondwana (Howe and Cantrill, 2001). However, assignable foliage may extend back to the Early Jurassic (Drinnan and Chambers, 1985). Australasian attributions to this order have been summarized by Harris (1962), Drinnan and Chambers (1985, 1986), Howe and Cantrill (2001) and McLoughlin *et al.* (2002). The male fructification *Sahnia laxiphora* Drinnan and Chambers, 1985 from the Lower Cretaceous of Victoria possesses microsporangiate structures attached to a central conical receptacle. Dispersed pollen resembles *Cycadopites* (Osborn *et al.*, 1991). In-situ pollen retrieved from Drinnan and Chambers's (1985; 1986) specimen was likened to bennettitalean pollen (Osborn *et al.*, 1991). The pollen and organ

morphologies indicate that this group is taxonomically distinct (Meyen, 1984) from plant groups generally regarded as pteridospermous; moreover, these organs are structurally unlikely to be allied with any pteridosperms of the Gondwanan Triassic.

*Caytoniaceae* Thomas, 1925

Caytoniaceae includes female and male fructifications together with foliage which, although not confirmed through organic attachment, have been widely regarded as associated. The female fructification, *Caytonia* Thomas, 1925 emend. Harris, 1940, was defined from Bajocian floras of Yorkshire, England (Thomas, 1925; Harris, 1932b, 1940) and Greenland (Harris, 1933, 1940). Harris's (1940) emendation of the genus included sub-opposite bilateral attachment of branches together with a short cupule stalk with longitudinally and laterally recurved lamina forming a cupule containing ovules. Ovules are small and mounted in a curved row on the cupule wall. Later contributions by Reymanówna (1973, 1974) and Krassilov (1977) added considerable morphological detail. Subsequently collected material has revealed greater diversity among caytonialean female fructifications (Barbacka and Bóka, 2000a).

The male fructification, *Caytonanthus* Harris, 1937, has been identified from several Jurassic localities in the northern hemisphere (Harris, 1937, 1941; Brik, 1941; Reymanówna, 1973; Krassilov, 1977; Osborn, 1994; Taylor et al., 2006). Harris (1941) characterized the genus as including pinnately branched microsporophylls with bilateral branches divided into ultimate branchlets (or lobes) and terminating as a group of sporangial sacs. Harris's (1941) speciation of *Caytonanthus* was entirely based upon statistical analysis of pollen sizes as he had only fragmentary megascopic material. Speciation and associated female organs and foliage were summarized by Couper (1958). *Caytonanthus* pollen has been discussed by several authors (Harris, 1941; Couper, 1958; Townrow, 1962b; Pederson and Friis, 1986; Zavada and Crepet, 1986; Osborn, 1994; Balme, 1995; Taylor et al., 2006, 2009). Pollen are referred to the bisaccate

pollen genus *Vitreisporites* Leschik, 1955 if found dispersed (Taylor et al., 2006).

Foliage assigned to *Sagenopteris* Presl in Sternberg, 1838 emend. Harris, 1964 has been reported globally from sediments spanning much of the Mesozoic (Harris, 1932a, 1932b; Banerji and Lemoigne, 1987; Dobruskina, 1994; Sender, 2005; Kustatscher et al., 2007; Escapa et al., 2008). Rees (1993) emended the diagnosis to include undulating and sometimes lobed leaf margins, but given the work of Schweitzer and Kirchner (1998) regarding the distinction between *Sagenopteris* and *Scoresbya* Harris, 1932, many of Rees's (1993) specimens referred to *Sagenopteris* may be better attributed to *Scoresbya* (below). *Sagenopteris* is compound and palmate. Leaflets are lanceolate with the main vein not centred; venation is reticulate. Petioles bear two pairs of leaflets apically. Specimens from the Lower Jurassic (Hettangian) of Hungary show stages in leaf maturity and include preserved cuticle (Barbacka and Bóka, 2000b); these provide a rare example of preserved stomatal ontogeny (Barclay et al., 2007).

*Sagenopteris* has been reported from several Triassic and Jurassic localities in Australia (Table 9). Triassic specimens from Gondwana are rare. All Australian Triassic specimens are incomplete and none shows leaflet attachment; some may be assignable to *Rochipteris* or to other genera with reticulate venation.

Few specimens have been referred to *Caytonia* from Australia (Clifford, 1998; Jansson et al., 2008b). Those identified by Jansson et al. (2008b) from the Toarcian of Queensland are unlike this genus and were referred to *Knezourocarpon* by Pattemore et al. (2014). Clifford's (1998) fructifications from the Lower Jurassic of Queensland are incomplete, small and poorly preserved, and differ considerably from those of Jansson et al. (2008b). His specimens, assigned to *C. tierneyi* Clifford, 1998, are very unlikely to belong to the genus; Jansson et al. (2008b) interpreted them as detached fertile fern pinnae. Their very poor preservation militates against precise generic identity.

Indifferently preserved specimens from the Upper Triassic of Antarctica was described as *Caytonia* sp. by Banerji and Lemoigne (1987) and figured as

Period	Key references
Jurassic	Feistmantel (1879, 1890a); Tenison-Woods (1883); Walkom (1917a); Jones and de Jersey (1947b); Hill et al. (1966); Gould (1974a, 1974b); Jansson et al. (2008b); Turner et al. (2009).
Triassic	Feistmantel (1878, 1890a, 1890b); Johnston (1886, 1888); Shirley (1898); Walkom (1925b).

**Table 9.** Reports of *Sagenopteris* in the Triassic and Jurassic of Australia.  
**Tabla 9.** Registros de *Stagenopteris* en el Triásico y Jurásico de Australia.

'female utricles' (with suggested caytonialean affinity) by Lemoigne (1987). It is improbable they belong in *Caytonia*, as there is no evidence of a cupule and pedicel formed from a modified lamina, nor any indication of axial attachment. They were preserved with foliar remains identified as *Sagenopteris*, *Scoresbya*, *Dicroidium* and other typically Triassic genera.

Two poorly preserved specimens were referred to *Caytonanthus* sp. by Rees (1993) from the Lower Jurassic of Antarctica, together with leaves referred to *Sagenopteris* (re-figured by Rees and Cleal, 2004). Birkenmajer and Ociepa (2008) identified *Sagenopteris* from the Lower and Middle Jurassic of Antarctica. Many specimens reported as *Sagenopteris* by Rees (1993) and Birkenmajer and Ociepa (2008) probably belong to *Scoresbya* as the larger specimens are deeply lobed. *Caytonanthus* has not been reported from Australasia. Bose and Banerji (1984) ascribed detached cupules from the Indian Jurassic to their species *Caytonia indica*; these were mostly immature and few contained ovules. Although the figured mature cupule shows some similarity to *Caytonia*, its extremely fragmentary condition, without indication of axial attachment, hinders precise identification.

*Scoresbya* is very similar to *Sagenopteris*. Harris (1932a) noted the similarity and a possible relationship with *Sagenopteris*. Schweitzer and Kirchner (1998) considered that *Sagenopteris* should be reserved for specimens with four undivided lobes and that *Scoresbya* should be retained for material in which lobes bifurcate at least once. *Scoresbya* has been reported from the Jurassic of Germany, Greenland, China and Iran, and the Triassic of Mexico and Australia (Harris, 1932a; Herbst, 1974; Weber, 1995; Schweitzer and Kirchner, 1998; Taylor et al., 2009; Holmes et al., 2010). Emendations of the genus were proposed by Kräusel and Schaarschmidt (1968) based on Lower Jurassic specimens from Germany and by Weber (1995) using material from the Upper Triassic of Sonora, Mexico. Despite its resemblance to *Sagenopteris*, this foliage has no clearly associated fructification; hence its familial placement is uncertain.

#### *Ktalenia* Archangelsky, 1963

The female fructification *Ktalenia* and its associated foliage *Rufloflinia* Archangelsky, 1963 have been described from the Lower Cretaceous of Argentina (Archangelsky, 1963; Taylor and Archangelsky, 1985; Taylor et al., 2006; Carrizo et al., 2014). One specimen reportedly has organic connection between foliar and fertile organs (Taylor and Archangelsky, 1985, Figs. 1,

4); a fructification stem was identified arising from a bifurcation along the basal section of a vegetative primary rachis (Taylor and Archangelsky, 1985, Fig. 25). These organs were considered to be pteridospermous; it was suggested that *Ktalenia* cupules structurally resemble those of *Caytonia* (Taylor and Archangelsky, 1985; Carrizo et al., 2014). Carrizo et al. (2014) referred *Rufloflinia* to the Caytoniales. *Ktalenia* differs from *Caytonia* by containing fewer (probably one or two) ovules; however, the eight or many more ovules within a *Caytonia* cupule are mounted distinctively in a curved row on the cupule wall (Harris, 1940) and there is no evidence of this structure in *Ktalenia* cupules. The only distinctly caytonialean feature to be described is a beak-like extension observed in one specimen likened by Taylor and Archangelsky (1985) to the cupular mouth of *Caytonia*. If the fructification stem does indeed arise from the rachis of a vegetative frond then this structural arrangement is unusual, being unknown from either *Caytonia* or any other Mesozoic pteridosperm. Fructifications of Triassic pteridosperms appear to have emerged ginkgoalean-like from short shoots (Axsmith et al., 2000; Bomfleur et al., 2011). *Ktalenia* and *Rufloflinia* are not known from Eastern Gondwana.

#### Summary

Pteridospermous affiliation of *Rintoulia* is doubtful, the notion being based entirely on foliar cuticle from the Lower Cretaceous of Victoria. The type material indicates that it may be a fern and its cuticle has not been compared with a sufficiently wide range of plants, only very selective comparisons having been attempted. Likewise, attributions to *Komlopteris* from the post-Jurassic of Eastern Gondwana were based on megascopic similarity to material from the European lowermost Jurassic; moreover, cuticular evidence does not convincingly support the generic assignment.

Caytonialean fructifications are unknown from Australasia; however, they may occur in the Upper Triassic and Lower Jurassic of Antarctica but none can be regarded as sufficiently well preserved for confident identification. *Sagenopteris* has been reported from the Upper Triassic through Middle Jurassic of Eastern Gondwana.

It has been widely regarded that conifers and pteridosperms dominated Jurassic terrestrial floras, particularly in the later Jurassic in Australasia (Turner et al., 2009). In the Australasian post-Triassic, there is no evidence from fructifications suggesting foliage can be attributed to any pteridosperm family known



from the Triassic. Furthermore, with the possible exception of *Knezouocarpon*, convincingly pteridospermous fructifications are seemingly absent in Australasian post-Triassic strata; this is despite considerable collections having accrued since the late 19th century (Table 8).

## Conclusions

1. Hybridization is a doubtful explanation for Triassic pteridosperm speciation. Diversity in the Umkomasiaceae and other pteridosperm groups of the Triassic almost certainly resulted from allopatric speciation; thus, geographic and climatic provincialism probably exerted a significant influence.
2. Congeneric status for *Dicroidium*, *Johnstonia* and *Xylopteris* lacks a reliable basis.
3. *Pachydermophyllum* of the Gondwanan Middle and Upper Triassic may be better regarded as generically distinct from other material referred to it, despite apparent similarity with representatives of this genus from outside this age range.
4. Gondwanan Middle and Upper Triassic specimens referred to *Stachyopitys* are structurally and stratigraphically distinct from extra-Gondwanan material and may be attributable to *Pteruchus Townrovia* or a new genus.
5. Pteridospermous affiliation for *Rintoulia* is dubious; in particular, determining taxonomic affinity using cuticular characters requires a more rigorous approach. Likewise, attributions to *Komlopteris* from the Eastern Gondwanan post-Jurassic are doubtful; cuticular evidence is equivocal and requires comprehensive comparison with a wide range of plants, including younger material.
6. Caytonialean fructifications are unknown from Australasia but are possibly represented in the Upper Triassic and Lower Jurassic of Antarctica.
7. Pteridosperms declined in Australasia before the latest Triassic extinction event. There is no clear evidence from fructifications that Triassic pteridosperm families of Australasia survived this event, despite apparently persisting in the extra-Gondwanan Early Jurassic.

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