An early Triassic fossil flora from Culvida Soak, Canning Basin, Western Australia

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Abstract

New collections of fossil plants and reinterpretation of previous paleobotanical work indicate that the Culvida Sandstone is late Early to early Middle Triassic (late Scythian-Anisian), or some 244-248 Ma in age. Most of the fossils have been identified with well known species, with the exception of *Chiropteris whitei* sp nov and *Pleuromeia dubia* (Seward) comb nov. This fossil flora is most similar to that of the Newport and Camden Haven Formations of New South Wales. There are also strong similarities with the fossil flora of the Parsora Beds of the South Rewa Basin, India, and the Burgersdorp Formation of South Africa. The Culvida flora is dominated by *Dicroidium zuberi* like southeastern Australian floras of humid cool temperate paleolatitudes, but it also contains *D. hughesii* which dominated monsoonal subtropical floras of India and South Africa. The Culvida flora was thus transitional between these two floristic regions. Despite these regional differences in dominance, early Triassic floras were surprisingly cosmopolitan and low in diversity following the Permian-Triassic life crisis.

Introduction

The early Triassic was peculiar for world vegetation because of low diversity cosmopolitan floras (Retallack 1995). The homogeneity of early Triassic floras across the great Pangean landmass presents a challenge to modern concepts of uniformitarianism, and is in stark contrast to diverse and provincialized floras of the late Permian and Middle Triassic. Low diversity early Triassic fossil floras have been found in Argentina, New South Wales, central Queensland and Tasmania, all high latitude humid parts of the Gondwana supercontinent (Retallack 1977). The Canning Basin of Western Australia is one of the few regions with Early Triassic fossil floras from the low latitude northern edge of the supercontinent. This paper describes one of these fossil floras that have remained until now poorly known.

A newly described collection

A collection of fossil plants was made in 1973 by G R Evans and L N Brown of Mines Administration Pty Ltd of Brisbane, and forwarded to me for study by R J Paten. The specimens are now housed under numbers F9143 to 9160 in collections of the Geological Survey of Western Australia.

The fossils are impressions in white shale, with irregular areas of red and purple stain. This colour is typical for the mottled zone of a deep lateritic paleosol, and is presumed to be a Cenozoic alteration of a pre-existing Triassic plant-bearing shale that may have been grey to brown in color. The fossils were collected from the Culvida Sandstone at Culvida Soak (Fig 1: grid reference 506468 on Cornish 1:250,000 sheet). The matrix of the fossils is most similar to the interval 140-170 m

above the base of the Culvida Sandstone in BMR Cornish number 2 borehole (Yeates et al. 1975).

The following fossil species were identified from this collection and are discussed in more detail at the end of this paper.

Pleuromeia dubia (Seward) comb nov Cladophlebis carnei Holmes & Ash 1979 Chiropteris whitei sp nov Dicroidium hughesi (Feistmantel) Lele 1962a Dicroidium narrabeenense Jacob & Jacob 1950 Dicroidium zuberi (Szajnocha) Archanglesky 1968 Umkomasia sp indet Lepidopteris madagascariensis Carpentier 1935

Reinterpretation of previous collections

Earlier paleobotanical work by White (1961) and White & Yeates (1976) can now be revised. Updated lists for localities (Fig 1) currently recognized within the Culvida Sandstone (by Yeates *et al.* 1975) are given below, with commentary following.

CO8 Equisetales gen et sp indet (White 1961 Pl 2, Figs 5,6, Pl 3, Fig 1)

Dicroidium zuberi (Szajnocha) Archangelsky 1968 (White 1961)

Taeniopteris sp indet (White 1961)

CO62 Dicroidium hughesii (Feistmantel) Lele 1962a (White 1961, Pl 3, Fig 6)

Dicroidium narrabeenense (Walkom) Jacob & Jacob 1950 (White 1961, Pl 3, Figs 3,4B)

Pteruchus barrealensis (Frenguelli) Holmes & Ash 1979 (White 1961, Pl 3, Fig 4A)

Chiropteris whitei sp nov (White 1961, Pl 3, Fig 5)

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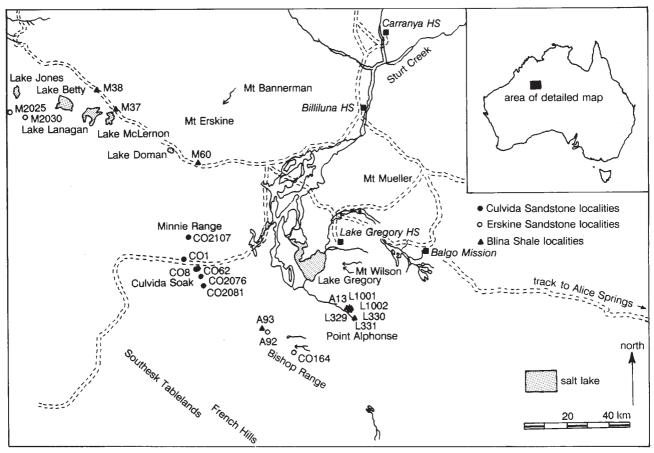


Figure 1. Triassic fossil localities in the eastern Canning Basin, Western Australia.

CO2076 Dicroidium hughesii (Feistmantel) Lele 1962a (White & Yeates 1976)

CO2107 Tomiostrobus sp indet (White & Yeates 1976)

Pleuromeia dubia (Seward) comb nov (White & Yeates 1976, Pl 13, Figs 47,48)

Sphenopteris sp indet (White & Yeates 1976)

Umkomasia sp indet (White & Yeates 1976,
Pl 13, Figs 48,49)

CO2108 Equisetales gen et sp indet (White & Yeates 1976)

Culvida Dicroidium narrabeenense (Walkom) Jacob & Soak Jacob 1950 (White & Yeates Pl 13, Fig 46)

Taeniopteris sp indet (White & Yeates 1976)

White's identification of *Dicroidium odontopteroides* from these localities is unproven, because it was based on fragments without a fork. These are more likely to belong to *Dicroidium zuberi*, a leaf taxon thought to have had ovuliferous organs of *Umkomasia* and pollen organs of *Pteruchus barrealensis* [the latter listed by White (1961) as "*Lycopodites* sp"). Several relatively complete specimens of *Dicroidium hughesii* and *Chiropteris whitei* in the newly described collection are identical to fragments identified by White (1961), as "*Linguifolium*" and "*Ginkgoites antarctica*" respectively. Small wedge shaped sporophylls widely referred to *Araucarites* have been referred to *Tomiostrobus* by Sadovnikov (1982). The

rounded tips of sporophylls in the cone figured by White & Yeates (1976, Pl 13, Fig 47) are similar to those of *Pleuromeia dubia* (Seward) comb nov.

Geological age of the fossil flora

The flora of the Culvida Sandstone can be identified confidently as part of the Dicroidium zuberi oppelzone, of late Early to early Middle Triassic age (Scythian-Anisian: Retallack 1977). Seven of its 13 species are known also from the Newport Formation of the Sydney Basin, NSW (Retallack 1980a), five from the Parsora Beds of the South Rewa Basin, India (Lele 1962a,b; Rao & Lele 1963; Bose 1974), three from the Camden Haven Formation near Laurieton, NSW (Holmes & Ash 1979) and three from the Burgersdorp Formation of South Africa (Anderson & Anderson 1985). Dicroidium zuberi is especially common in low diversity assemblages in the lowest Triassic fossil plant horizons of the Barreal and Cacheuta Basins of Argentina (Frenguelli 1944a,b, 1948; Anderson & Anderson, 1983), and is also known from early Triassic (Malakhovian or Scythian) marine rocks in New Zealand (Retallack 1985). There is no evidence of Dicroidium odontopteroides or any other Middle Triassic forms. Considering recent radiometric dating of Middle Triassic rocks with D. odontopteroides in New South Wales and New Zealand (Retallack et al. 1993), the Culvida Soak flora is some 248-244 million years old.

Thus, the Culvida Sandstone is about the same age as the Erskine Sandstone and Blina Shale, which successively underlie the Culvida Sandstone in the Canning Basin. The Blina Shale has also yielded the lycopsid Pleuromeia indica (Lele) Dobruskina (1985: see White & Yeates 1976, Pl 6, Figs 18-21, Pl 12, Figs 42-44) as well as a sparse marine fauna (Gorter 1978). Plant fossils from the Erskine Sandstone include the characteristic rounded sporophylls, as well as other remains of Pleuromeia sternbergi (Münster) Corda in Germar (1852: see Foord 1890; Brunnschweiler 1954; White & Yeates, 1976, Pl 6, Fig 17b, Pl 8, Fig 29) as well as abundant Dicroidium zuberi (Szajnocha) Archangelsky (1968: see Antevs 1913; Townrow 1957). These rock units probably represent beach ridges and coastal lagoons respectively, outboard of the fluvial Culvida Sandstone. Marine regression that created the general sequence Blina-Erskine-Culvida Formations in the Canning Basin (Gorter, 1978) also created the correlative sequence of Garie-Newport Formations in the Sydney Basin (Retallack 1975, 1980a).

Paleoecology and paleoclimatology of Culvida Soak

The Culvida Soak fossil flora has most plants of the Dicroidietum zuberi fossil plant association of eastern Australia (Retallack 1977). This was a broadleaf flora dominated by the extinct seed fern *Dicroidium zuberi*, whose presence is confirmed for the Culvida flora by its characteristic pollen-bearing and ovuliferous organs. This widespread early Triassic assemblage was probably a heath or forest assemblage of nutrient poor soils. These indications of oligotrophy include low species diversity and thick leathery leaves. The Culvida Soak flora shows rather smaller leaf size in *Dicroidium zuberi* and *D. narrabeenensis*, and fewer pteridophytes than comparable floras of eastern Australia, and this may be an indication of a drier climate.

The Culvida flora also contains a few specimens of Dicroidium hughesii, which is the dominant taxon of a fossil plant association that can be termed the Dicroidietum hughesii. Based on the fossil flora of the Burgersdorp Formation near Aliwal North, South Africa, this association contains a variety of pinnate cycadophyte and ginkgolike leaves not found in early Triassic floras of southeastern Australia (Anderson & Anderson 1985). Cycadophytes and ginkgolike remains also are found in the flora of the Parsora Beds of India (Lele 1962a,b; Rao & Lele 1963; Bose 1974), which is another example of the Dicroidietum hughesii. This fossil plant assemblage of India and South Africa lies within the dry to monsoonal subtropical paleoclimatic belt of the Gondwana supercontinent (Parrish 1990), whereas the Dicroidietum zuberi of southeastern Australia is within the humid cool temperate paleoclimatic region within the Antarctic circle (Anderson & Anderson 1985). The Culvida flora was probably near the ecotone between these two floristic regions. Its mix of species from north and south may be an indication of continuity of temperate woodlands through central Australia during the early Triassic.

Despite this regional variation in floras, the uniformity and low diversity of early Triassic floras is

impressive. It may be a lingering artifact of the Permian-Triassic life crisis. Extinctions of land plants have recently been shown to have been coeval with, and as severe as, the great dying of marine organisms (Retallack 1995). In addition, low diversity oligotrophic floras dominated by conifers and lycopods persisted for many millions of years after the Permian-Triassic boundary, with diversity of pteridosperm-dominated floras only attaining levels found in the Late Permian by Middle Triassic time with the Dicroidium odontopteroides flora of Gondwana and Scytophyllum flora of Laurasia. This low diversity oligotrophic interregnum was a time when there was no peat deposition anywhere in the world (Retallack et al. 1995). The record of land animals similarly shows a dramatic decline in diversity at the Permian-Triassic boundary followed by a cosmopolitan Lystrosaurus fauna of the early Triassic and then a diverse and provincial tetrapod fauna of the middle Triassic (Benton 1987). Similarly, in the sea, Early Triassic faunas were depauperate (Erwin 1994) and there are no known early Triassic reefs (Flügel 1994). These peculiarities of the early Triassic mark it as an unusual time. The big life crises in the history of life may indeed change the rules, making difficult the application of uniformitarianism in interpreting the past.

Systematic palaeobotany

CLASS LYCOPSIDA ORDER ISOETALES

GENUS *PLEUROMEIA* Corda for Germar 1852 *Pleuromeia dubia* (Seward) comb nov

Holotype. Stem cast (South African Museum 13727)

Type locality. Alcocks Quarry, near Aliwal North, South Africa; Burgersdorp Formation: Early Triassic (Anderson & Anderson 1985).

Description. The single leaf found at Culvida Soak (F9155, Fig 2E) is very similar to "Cylomeia undulata" (White 1981), but that name is unsuitable for a variety of reasons. The holotype of "C. undulata" is a fossil leaf identical to the Culvida fossil, called "Taeniopteris undulata" by Burges (1935). Its lateral wrinkles are probably due to compression or drying of a thick and fleshy lycopsid leaf (White 1981). I could not make out a supposed "very delicate" lateral venation spaced at "30 per cm" noted by Burges (1935) as evidence of cycadophytic affinities on either the type or Culvida material. Kimura (1959) was evidently not aware of this species when he erected the name Taeniopteris undulata for some quite different cycadophyte leaves of Upper Jurassic age in Japan. Confusion is now removed by the discovery of "Cylomeia undulata" leaves attached to lycopsid stems of "Gregicaulis" dubius in both the Newport Formation near Sydney Australia (Retallack 1973) and the Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985). Associated oval sporophylls with rounded tips have been found both in South Africa (Anderson & Anderson 1985) and in the Culvida Sandstone (White & Yeates 1976, Pl 12, Figs 44,45). Pleuromeiacean lycopsids are best identified according to reproductive structures

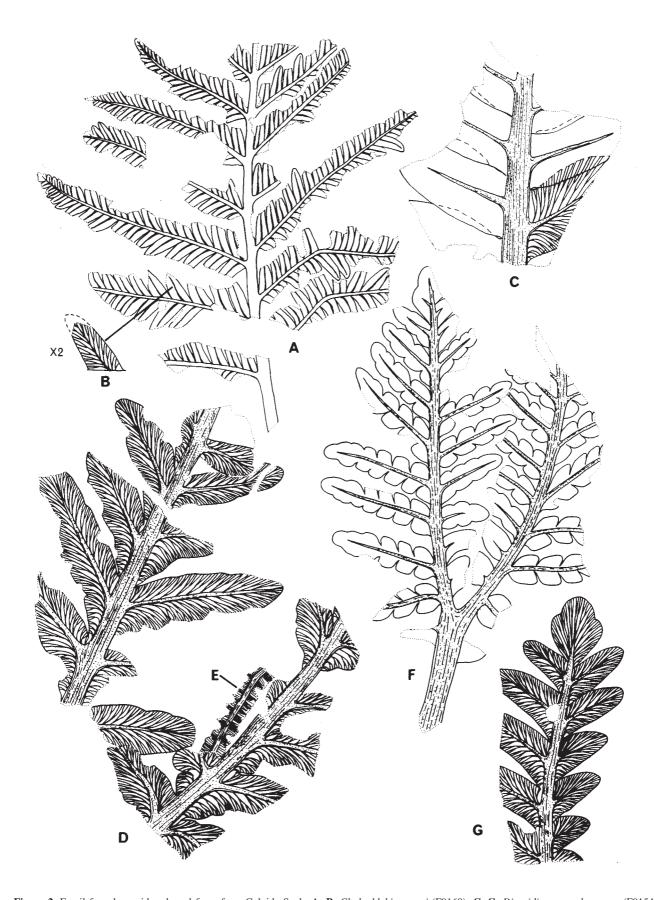


Figure 2. Fossil fern, lycopsid and seed ferns from Culvida Soak; **A, B**, *Cladophlebis carnei* (F9160); **C, G**, *Dicroidium narrabeenense* (F9154, F9149 respectively); **D**, *Dicroidium hughesii* (F9155); **E**, *Cylomeia undulata* (F9155); **F**, *Dicroidium zuberi* (F9144).

(White 1981; Sadovnikov 1982; Dobruskina 1985), and these sporophylls leave little doubt that "Gregicaulis" is a junior synonym of Pleuromeia, here taken in a stricter than usual sense. Pleuromeia dubia was originally described as "Stigmatodendron dubium" by Seward (1908), but that genus is based on remains of a Carboniferous arborescent lycopsid from Russia.

Distribution. Pleuromeia dubia is known from the Burgersdorp Formation of South Africa (Anderson & Anderson 1985) and the Newport Formation (Retallack 1973; White 1981) and Camden Haven Claystone (Holmes & Ash 1979) of southeastern Australia, all of late Early to early Middle Triassic age.

CLASS PTEROPSIDA

ORDER & FAMILY INCERTAE SEDIS GENUS *CLADOPHLEBIS* Brongniart emend Frenguelli 1947:12

Cladophlebis carnei Holmes & Ash 1979 (Figs 3A,B)

Holotype. Australian Museum partial frond F59425

Type locality. Camden Head near Laurieton, NSW; Camden Haven Claystone; late early to early Middle Triassic.

Description. One of the fossils from Culvida Soak (F9160, Fig 2A,B) has the characteristic falcate pinnules and singly forked lateral venation of this species. It is most similar to *Cladophlebis oblonga* Halle, which has somewhat blunter, wider pinnules and thicker rachis (Frenguelli 1947).

Affinities. Similar leaves are found with sporangia similar to those of *Asterotheca* in the Newport Formation of NSW (Retallack 1973, 1980a), Estratos del Alcázar of Argentina (Menendez 1957), and Burgersdorp Formation of South Africa (Anderson & Anderson 1985), so these leaves were probably marattialean ferns.

Distribution. In addition to the type locality, this species is known from the early Triassic Newport Formation near Sydney, NSW (Retallack 1973, 1980a), Estratos del Alcázar near Hilario, Argentina (Menendez 1957), Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985), and Middle Triassic Gunnee Beds near Delungra, N.S.W. (Bourke *et al.* 1977).

GENUS *CHIROPTERIS* Kurr emend Rühle von Lilienstern 1931:273

Chiropteris whitei sp nov (Figs 3F-J,4C) 1961 Ginkgoites antarctica White p 302, Pl 3, Fig 5

Holotype. The most complete leaf (F9158, Fig 4C), whose outline is reconstructed in Fig 3G.

Type locality. Culvida Soak, Canning Desert, Western Australia; Culvida Sandstone, late Early to early Middle Triassic.

Diagnosis. Reniform leaves, width about 40 mm (25-60 mm), with a petiole at least 12 mm long attached at a wide angle to the blade; leaf marine crenate and slightly recurved; venation fine, evenly radiating from petiole,

anastomosing and dichotomising throughout the leaf, obscured by interveinal woody striae.

Derivation. The specific epithet is from Mary E White, who pioneered paleobotanical studies of the Canning Basin and other outback Australian localities.

Comparison. Although very similar to the leaves of *Ginkgo*, these fossils (F9150, F9156-9) differ in their anastomosing venation (Fig 4C), reniform shape (Fig 3G) and angle of insertion of the petiole (reconstructed in Fig 3I). The venation is obscured by abundant woody interveinal striae, and the leaf texture was stiff enough for the conical shape of the leaf blade and a slightly recurved margin to have resisted compaction (Fig 4C). The leaf was also wrinkled in broad zones corresponding to growth ridges. These also are differences from ginkgoalean leaves.

There are two distinctive kinds of species within the genus Chiropteris now that the apetiolate woody species have been removed to Ginkgophytopsis (by Retallack 1980b). One group includes Chiropteris zeilleri (Seward 1903), and C. barrealensis (Frenguelli 1942) and has palmate, flabellate leaves with widely spaced clear venation, characteristically without anastomosis between the central two veins, unlike C. whitei. Another group includes the type species Chiropteris lacerata (Rühle von Lilienstern 1931), C. reniformis (Kawasaki 1925), C. kawasakii (Kon'no 1939) and C. harrisii (Archangelsky 1960). These are conical, circular or reniform leaves with dense venation and common interveinal striae, like C. whitei. Of these species, C. whitei is most like C. harrisii, which differs in being twice the size, with wider lateral lobes. These species have much less developed lateral lobes than in C. reniformis and C. kawasakii. The type species of the genus, C. lacerata is more strongly conical, cutinized and lignified than C. whitei, and has in addition a lamina more dissected and lobes not extending backward past a right angle to the petiole.

Affinities. Affinity of these plants with ginkgoaleans has long been thought unlikely, and Rühle von Lilienstern (1931) proposed that the type species was a dipteridacean fern on the basis of its reflexed conical leaf shape, anastomosing venation and supposed sori. These latter look more like insect domatia (of Stace, 1965) than sori and the details of the venation are quite unlike the nearly square meshes of typical dipteridacean Another possibility is that these ferns. progymnosperms allied to Archaeopteris as suggested for the similar Ginkgophytopsis by Retallack (1980b). A possible progymnosperm sporangial axis has been found in a New Zealand locality yielding Ginkgophytopsis (Pole & Raine, 1994), but both Gingkophytopsis and Chiropteris remain problematic.

CLASS PTERIDOSPERMOPSIDA

FAMILY CORYSTOSPERMACEAE Thomas 1933 GENUS DICROIDIUM Gothan emend. Townrow 1957:26.

Dicroidium hughesii (Feistmantel) Lele 1962a (Figs 2D, 4A)

Remarks. This large unipinnate leaf (F9155) was evidently forked, as two rachides converge on the slab (Figs

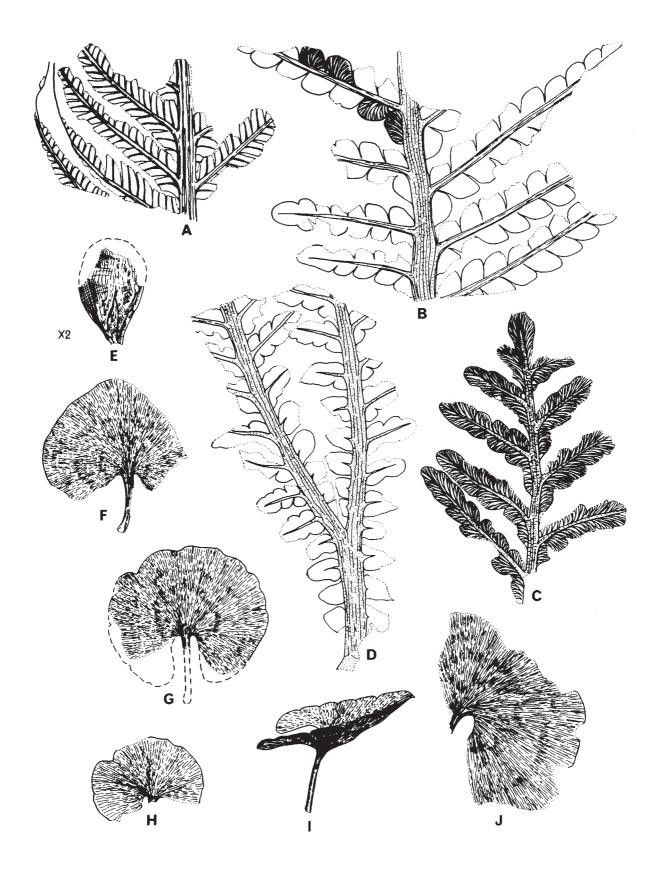


Figure 3. Fossil seed ferns and problematica from Culvida Soak; **A**, *Lepidopteris madagascariensis* (F9148); **B-D**, *Dicroidium zuberi* (F9151, F9143, F9152 respectively); **E**, *Umkomasia* sp indet (F9147); **F-J**, *Chiropteris whitei* (F9159, F9158, F9150, reconstructed leaf, F9156 respectively).

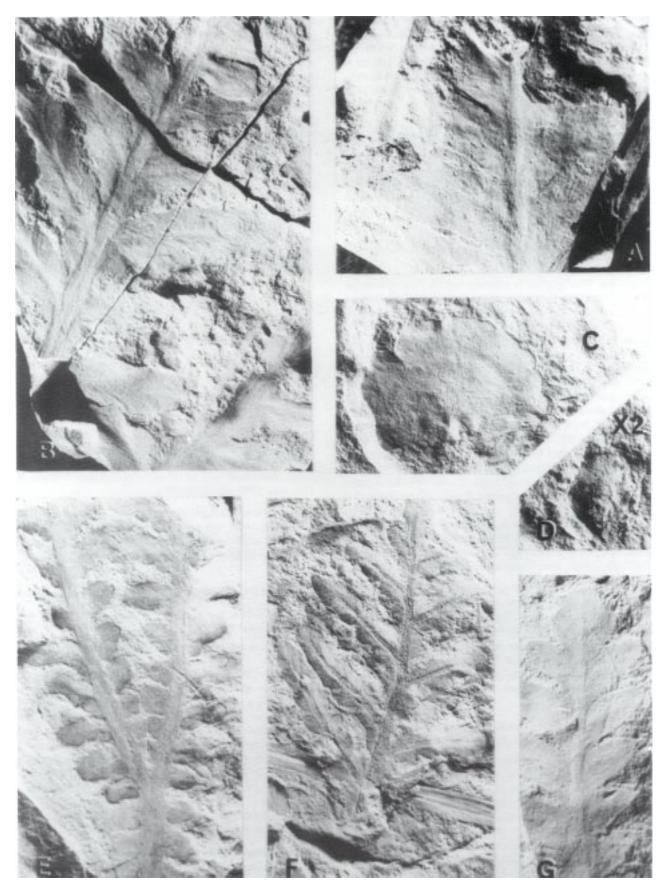


Figure 4. Fossil seed ferns and problematica from Culvida Soak: **A**, **G**, *Dicroidium narrabeenense* (F9154, F9149 respectively); **B**, *Dicroidium hughesii* and *Pleuromeia dubia* (F9155); **C**, *Chiropteris whitei* (F9158); **D**, *Umkomasia* sp (F9147); **E**, **F**, *Dicroidium zuberi* (F9152, F9143 respectively).

2D, 4A). It shows veins clearly, as well as basiscopic lobes to the pinnae that are the hallmarks of this species, distinguishing it from the otherwise similar *Dicroidium narrabeenense* Jacob & Jacob (1950). *Dicroidium eskense* is another comparable leaf distinguished by asymmetric pinnae, but in this case due to a deep acroscopic sinus in the pinnae (Retallack 1977).

Distribution. Dicroidium hughesii is well known from the Parsora Beds of India (Lele 1962a) and the Burgersdorp Formation of South Africa (Anderson & Anderson 1985). In both places, it is the dominant taxon, whereas only a few specimens were found at Culvida Soak [including material of White (1961) and White & Yeates (1976)].

Dicroidium narrabeenense (Walkom) Jacob & Jacob 1950 (Figs 2C-D,4B,G)

Remarks. This species is represented by two specimens (F9149, F9153-4). It is here interpreted in the broad sense of Anderson & Anderson (1983), who included bipinnatifid remains referred to "Dicroidium australe" by Jacob & Jacob (1950) as well as smaller leaves (Fig 2G) that formerly would have been referred to "Dicroidium lancifolium". However it has long been recognized that "D. lancifolium" is an extreme variant of D. odontopteroides (Retallack 1977), as well as of D. narrabeenense. The leaves similar to "D. lancifolium" associated with D. odontopteroides have pinna bases separated at the rachis, and are thin in texture, with clear venation, and thin cuticles with laterocytic stomata (Anderson & Anderson 1983), whereas leaves similar to "D. lancifolium" associated with D. narrabeenense have confluent to overlapping pinna bases, are so thick that veins are difficult to see, and have thick cuticles with cyclocytic stomata (Jacob & Jacob 1950; Retallack 1973). Although cuticles cannot be prepared from the Culvida Soak specimen similar to "D. lancifolium", it was thick with confluent pinna bases as in D. narrabeenense.

Distribution. Dicroidium narrabeenense has been found in the Newport Formation near Sydney (Retallack 1973, 1980a) and the Camden Head Claystone near Laurieton, NSW (Holmes & Ash 1979), both late Early to early Middle Triassic (Scythian-Anisian). Comparable leaves also have been found from the Parsora Beds of India (as "Dicroidium odontoperoides" of Lele 1962a), of the same age (Anderson & Anderson 1983).

Dicroidium zuberi (Szajnocha) Archangelsky 1968 (Figs 2F, 3B-D, 4E-F)

Remarks. This is a common, widespread and polymorphic species. One of the Culvida specimens is most like *D. zuberi* var *papillatum* (Townrow) Retallack (1977: F9145) which has rhomboidal pinnules, but most of them are like *D. zuberi* var *sahnii* (Seward) Retallack (1977: F9143-4, F9146-7, F9149-50, F9152) which has rounded pinnules that tend to coalesce into lobed outer pinnae. These varieties were intended as form-taxa. The frond size of the Culvida specimens is small and compact for this species (Retallack 1977, 1980a).

Artabe (1990) has proposed that Frenguelli's genus Zuberia be resurrected for bipinnate Dicroidium leaves

with rachis pinnules, so that the varieties of Retallack (1977) would become species of *Zuberia*. Many of these bipinnate *Dicroidium* leaves do have distinctive cyclocytic stomata (Townrow 1957; Anderson & Anderson 1983), but some have laterocytic stomata and cuticles otherwise identical to those of *Dicroidium odontopteroides* (Townrow 1957). Until more information is available on cuticular and other distinctive characters of the type Argentinian specimens of *Zuberia*, that genus is maintained as a junior synonym of *Dicroidium*.

Distribution. Very similar leaves to *D. zuberi* var papillatum have been found in the Newport Formation near Sydney, NSW (Retallack 1973, 1980a) and in the Erskine Sandstone at Derby, Western Australia (Antevs 1913; Townrow 1957). Dicroidium zuberi var sahnii is known from the Newport Formation near Sydney, NSW (Retallack 1973, 1980a) and from the Parsora Beds of the South Rewa Basin, India (Seward 1932; Lele 1962a).

GENUS UMKOMASIA (Thomas) emend Holmes 1987: 166.

Umkomasia sp indet (Fig 2E)

Remarks. This single cupule (F9147) is 8.3 x 6.2 mm in size, and appears identical to the more complete branching group of three cupules from Culvida Soak illustrated by White & Yeates (1976, Pl 13, Fig 49). They appear to have three or four cupule lobes. They thus have fewer lobes and are smaller in size than early Triassic *Umkomasia feistmantelii* (Holmes & Ash) Holmes (1987) and larger in size with more cupule lobes than other described species of middle and late Triassic age (Thomas 1933; Holmes 1987).

Distribution. The Culvida specimens are most like those associated with the type material of *Dicroidium zuberi* from the early Triassic Barreal Formation, near Barreal, Argentina (Frenguelli 1944a).

FAMILY PELTASPERMACEAE Thomas 1933 GENUS *LEPIDOPTERIS* Schimper emend Townrow 1956; 4.

Lepidopteris madagascariensis Carpentier 1935 (Fig 2A)

Remarks. Only one specimen was found (F9148), but it shows the distinctive rachis-pinnules, rounded pinnule apices and a conspicuous median ridge to the rachis that is distinctive for this species. The current specimen lacks the rounded pinnules and large blisters on the rachis of the Permian species *Lepidopteris stuttgardiensis* and *L. martinsii*, but has less pointed and lobed pinnules than the middle Triassic species *L. stormbergensis* (Townrow 1966). Its pinnules are not so large or coalescent as in *L. brownii* or *L. africana* (Anderson & Anderson 1989). Constricted pinnule bases distinguish *L. langlohensis* (Anderson & Anderson 1989).

Distribution. This species has been found in the Hawkesbury Sandstone and Newport Formation near Sydney, NSW (Townrow 1966), the Camden Haven Claystone near Laurieton, NSW (Holmes & Ash 1979), and the Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985), all of late

Early to early Middle (Scythian-Anisian) age. The type material was found at Amboriky in the early Triassic bed 3 of the Sakamena Group of Madagascar (Carpentier 1935).

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References

- Anderson J M & Anderson H M 1983 Palaeoflora of southern Africa Molteno Formation (Triassic). Vol 1 Part 1 Introduction. Part 2 Dicroidium. A A Balkema, Rotterdam.
- Anderson J M & Anderson H M 1985 Palaeoflora of southern Africa. Prodromus of South African megafloras, Devonian to Lower Cretaceous. A A Balkema, Rotterdam.
- Anderson J M & Anderson H M 1989 Palaeoflora of southern Africa. Vol 2 Gymnosperms (excluding *Dicroidium*). A A Balkema, Rotterdam.
- Antevs E 1913 Results of Dr E. Môjberg's Swedish scientific expeditions to Australia 1910-1913. V Some Mesozoic plants. Kungliga Svenska VetenskapsAkademien Handlingar 51:1-71.
- Archangelsky S 1960 "Chiropteris harrisii" nueva especies de la Serie La Golondrina, Provincia de Santa Cruz. Acta Geologica Lilloana 3:289-293.
- Archangelsky S 1968 Studies on Triassic fossil plants from Argentina. IV The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. Palaeontology 11:500-512.
- Artabe A E 1990 Revalidacion del genero triasico *Zuberia* Frenguelli 1943, familia Corystospermaceae. Revista del Museo de La Plata 9 Paleontologia 55:145-157.
- Benton M J 1987 Mass extinction among families of non-marine tetrapods: the data. Memoire de la Societé Géologique de France 150:21-32.
- Bose M N 1974 Triassic floras. In: Aspects and appraisal of Indian paleobotany (eds K R Surange, R N Lakhanpal & P C Baradwaj). Birbal Sahni Institute, Lucknow, 285-293.
- Bourke D J, Gould R E, Helby R, Morgan R & Retallack G J 1977 Floral evidence for a Middle Triassic age of the Gunnee Beds and Gragin Conglomerate, near Delungra, New South Wales. Journal and Proceedings of the Royal Society of New South Wales 110:33-40.
- Brunnschweiler R O 1954 Mesozoic stratigraphy and history of the Canning Desert and Fitzroy Valley, Western Australia. Journal of the Geological Society of Australia 1:35-54.
- Burges N A 1935 Additions to our knowledge of the flora of the Narrabeen Stage of the Hawkesbury Series in New South Wales. Proceedings of the Linnaean Society of New South Wales 60:257-264.
- Carpentier A 1935 Études paléobotaniques sur le groupe de la Sakoa et le groupe Sakamena (Madagascar). Annales Geologiques du Service de Mines Republic du Malagasy 5:1-32.
- Dobruskina I A 1985 Some problems of the systematics of Triassic lepidophytes. Paleontological Journal 19:74-88.
- Erwin D H 1994 The Permo-Triassic extinction. Nature 367:231-235
- Flügel E 1994 Pangean shelf carbonates: controls and paleoclimatic significance of Permian and Triassic reefs. In: Pangaea: paleoclimate, tectonics and sedimentation during accretion, zenith and breakup of a supercontinent (ed G de V Klein). Special Paper of the Geological Society of America 288:247-266.

- Foord A H 1890 Notes on the palaeontology of Western Australia. Geological Magazine 7:97-105.
- Frenguelli J 1942 Contribuciones al concimiento de la flora del Gondwana Superior en la Argentina. X *Chiropteris barrealensis* n sp. Notas de la Museo de La Plata 7 Paleontologia 51:341-353.
- Frenguelli J 1944a Las especies del genero "Zuberia" en la Argentina. Anales de la Museo de La Plata Paleontologia B Paleobotanica 2:1-74.
- Frenguelli J 1944b Contribuciones al concimiento de la flora del Gondwana superior en la Argentina XV La florula de la base de la Serie de Cacheuta en el Cerro de los Baños, Mendoza. Notas de la Museo de La Plata 9:271-310.
- Frenguelli J 1947 El genero *Cladophlebis* y sus representantes en la Argentina. Anales de la Museo de La Plata 2 Paleontologia 2:74 p.
- Frenguelli J 1948 Estratigrafia y edad de llamado retico en la Argentina. Gaea 8:159-309.
- Germar E F 1852 Sigillaria sternbergi Münster aus dem bunten sandstein. Deutsch Geologische Gesellschaft Zeitschrift 4:183-189
- Gorter J D 1978 Triassic environments in the Canning Basin, Western Australia. Bureau of Mineral Resources Journal of Australian Geology and Geophysics 3:25-33.
- Holmes W B K 1987 New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. Alcheringa 11:165-173.
- Holmes W B K & Ash S R 1979 An early Triassic megafossil flora from the Lorne Basin, New South Wales. Proceedings of the Linnaean Society of New South Wales 103:47-70.
- Jacob K & Jacob C 1950 A preliminary account of the structure of the cuticles of *Dicroidium (Thinnfeldia)* from the Mesozoic of Australia. Proceedings of the National Institute of Sciences India 16:101-126
- Kawaski S 1925 Some older Mesozoic plants in Korea. Bulletin of the Geological Survey of Chosen 4:71 p.
- Kimura T 1959 On the Tetori flora (Part II) Addition to the Mesozoic plants from the Kuzuryu Sub-group, Tetori Group, Japan. Bulletin of the Science High School Attached to Tokyo University of Education 2:104-120
- Kon'no E 1939 A new *Chiropteris* and other fossil plants from the Heian System, Korea. Japanese Journal of Geology and Geophysics 16:105-114.
- Lele K M 1962a Studies in the Middle Gondwana flora. 1 On Dicroidium from the South Rewa Gondwana Basin. Palaeobotanist 10:48-68.
- Lele K M 1962b Studies in the Indian Middle Gondwana flora. 2 Plant fossils from the South Rewa Gondwana Basin. Paleobotanist 10:69-83.
- Menendez C A 1957 Asterotheca hilariensis sp nov, del triásico superior de Hilario, San Juan. Ameghiniana 1:25-30.
- Parrish J T 1990 Gondwanan paleogeography and paleoclimatology. In: Antarctic paleobiology (eds T N Taylor & E L Taylor). Springer, New York, 15-26.
- Pole M S & Raine J I 1994 Triassic plant fossils from Pollock Road, Southland, New Zealand. Alcheringa 18:147-159.
- Rao A R & Lele K M 1963 On the cuticle of *Dicroidium* (*Thinnfeldia*) sahnii (Seward) with some observations on the genera *Thinnfeldia* and *Dicroidium*. Palaeobotanist 11:7-12.
- Retallack G J 1973 Stratigraphy, palaeobotany and environmental analysis of an area around Pittwater, north of Sydney, NSW. BSc Hons Thesis, University of New England, Armidale, NSW.
- Retallack G J 1975 The life and times of a Triassic lycopod. Alcheringa 1:3-29.
- Retallack G J 1977 Reconstructing Triassic vegetation of eastern Australasia: a new approach to the biostratigraphy of Gondwanaland. Alcheringa 1:247-277.

- Retallack G J 1980a Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In: A guide to the Sydney Basin (eds R J Helby & C Herbert). Bulletin of the Geological Survey of New South Wales 26:385-430.
- Retallack G J 1980b Middle Triassic megafossil plants and trace fossils from Tank Gully, Canterbury, New Zealand. Journal of the Royal Society of New Zealand 10:31-63.
- Retallack G J 1985 Triassic fossil plant fragments from shallow marine rocks of the Murihiku Supergroup, New Zealand. Journal of the Royal Society of New Zealand 15:1-26.
- Retallack G J 1995 Permian-Triassic life crisis on land. Science 267:77-80.
- Retallack G J, Renne P R & Kimbrough D L 1993 New radiometric ages for Triassic floras of southeast Gondwana. In: The non-marine Triassic (eds S G Lucas & M Morales). Bulletin of the New Mexico Museum of Natural History and Science 3:415-418.
- Retallack G J, Veevers J J & Morante R 1995 Global coal gap between Permian-Triassic extinction and Middle Triassic recovery of peat-forming plants. Bulletin of the Geological Society of America (in press).
- Rühle von Lilienstern H 1931 Über *Chiropteris*. Paläontogische Zeitschrift 13:253-277.
- Sadovnikov G N 1982 The morphology, systematics and distribution of *Tomiostrobus*. Paleontological Journal 16:100-109.
- Seward A C 1903 Fossil flora of Cape Colony. Annals of the South African Museum 4:1-122.
- Seward A C 1908 On a collection of fossil plants from South Africa. Quarterly Journal of the Geological Society of London 64:83-108.

- Seward A C 1932 On some fossil plants from the Parsora Stage, Rewa. Record of the Geological Survey of India 66:235-343.
- Stace C A 1965 Cuticular studies as an aid to plant taxonomy. Bulletin of the British Museum, Natural History, Botany 4:78 p.
- Thomas H H 1933 On some pteridospermous plants from the Mesozoic rocks of South Africa. Philosophical Transactions of the Royal Society of London B222:193-265.
- Townrow J A 1956 The genus *Lepidopteris* and its southern hemisphere species. Avhandlingar Norske Videnskaps Akademian Oslo Mathematische-Naturwissenschaften Klasse 2:1-28.
- Townrow J A 1957 On *Dicroidium* probably a pteridospermous leaf, and other leaves now removed from this genus. Transactions of the Geological Society of South Africa 60:1-36.
- Townrow J A 1966 On *Lepidopteris madagascariensis* Carpentier (Peltaspermaceae). Journal and Proceedings of the Royal Society of New South Wales 98:203-214.
- White M E 1961 Appendix 6. In: The geology of the Canning Basin (eds J J Veevers & A T Wells). Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia 60:291-310.
- White M E 1981 *Cylomeia undulata* (Burges) gen et comb nov, a lycopod of the early Triassic strata of New South Wales. Records of the Australian Museum 33:723-734.
- White M E & Yeates A N 1976 Plant fossils from the northeastern part of the Canning Basin, Western Australia. Records of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia 1976/18, 32 p.
- Yeates A N, Crowe R W A, Towner R R, Wyborn L A I & Passmore V L 1975. Geology of the Gregory Sub-basin and adjacent areas of the Canning Basin, Western Australia. Records of the Bureau of Mineral Resources Geology and Geophysics, Canberra, Australia 1975/77, 47 p.