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. hughesi 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) Archanglesky 1968 (White 1961)

C062 Taeniopteris sp indet (White 1961)

Dicroidium hughesi (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)
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)

Pleuroemia 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)

Taeiopteri 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 “Lingafofolium” 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 Pleuroemia 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 Parsona 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 sternbergii* (Münster) Corda in Germer (1852; see Foord 1890; Brunnschweiler 1954; White & Yeates, 1976, Pl 6, Fig 17b, Pl 8, Fig 29) as well as abundant *Dicroidium zuberi* (Szajnoca) 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 characteristic pollen-bearing and ovuliferous organs, whose presence is confirmed for the Culvida flora by its uniformity and low diversity of early Triassic floras is through central Australia during the early Triassic.

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 lycopsids 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 *Scythophyllum* 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 (P9155, Fig 2E) is very similar to "Clyomeia 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 Burgess (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 Burgess (1935) as evidence of cycadophyte 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 "*Clyomeia 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 "Stigmatoedendron 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 *Asterotherca* 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 Gunnec 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)

**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 distinct 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 pal- mate, 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. kawasakiii* (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. kawasakiii*. 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 reflected 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 ferns. Another possibility is that these are 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 *Ginkgophytopsis* and *Chiropteris* remain problematic.

### CLASS PTERIDOSPERMOPSIDA

#### FAMILY CORYSTOSPERMACAE 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 zubert (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 Parsiara 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* (Wallom) 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 australis" 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 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 PELTASPERMACEX** Thomas 1933

**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 early Triassic Barreal Formation, near Barreal, Argentina (Frenguelli 1944a).

**FAMILY PELTASPERMACEX** Thomas 1933

**GENUS LEPIDOPTERIS** Schimper emend Townrow 1956; 4.

**Lepidopteris madagascariensis** Carpenter 1935 (Fig 2A)

**Remarks.** Only one specimen was found (F9148), but it shows the distinctive rachis-pinules, 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 pinules than the middle Triassic species *L. stormbergensis* (Townrow 1966). Its pinules are not so large or coalescent as in *L. brownii* or *L. africana* (Anderson & Anderson 1989). Constricted pinnule bases distinguish *L. langloensis* (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 Amborky in the early Triassic bed 3 of the Sakamena Group of Madagascar (Carpentier 1935).

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References

Frenquelli J 1948 Estratigrafía y edad de llamado retico en la Argentina. Gaea 8:159-309.
Kimura T 1959 On the Tettoria flora (Part II) Addition to the Mesozoic plants from the Kuzuryu Sub-group, Tettoria Group, Japan. Bulletin of the Science High School Attached to Tokyo University of Education 2:104-120.
Rao A R & Lele K M 1963 On the cuticle of Dicroidium (Thinnfeldia) sahnii (Seward) with some observations on the genera Thinnfeldia and Dicroidium. Paleobotanist 11:7-12.


Thomas H H 1933 On some pteridospermous plants from the Mesozoic rocks of South Africa. Philosophical Transactions of the Royal Society of London B 222:193-265.


White M E 1981 Cylomeia undulata (Burges) gen et comb nov, a lycophytae of the early Triassic strata of New South Wales. Records of the Australian Museum 33:723-734.
