

Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland

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RETALLACK, G. J., 1977:10:28. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Aicheringa* 1, 247-277. *Aicheringa*-fiche 1, G1-J17. ISSN 0311-5518.

As is widely recognised, fossil florules are difficult to correlate because they appear to have been more controlled by environmental and ecological factors than uniform changes which reflect the passage of geological time. Here I present a worked example of a generally applicable approach to this problem in dating and mapping fossil plant associations.

Floral associations are best described and named by the classical methods of phytosociology. The three dimensional shape of an association in rocks and its palaeoecology can then be critically assessed. For example, during Middle Triassic time the following plant associations would have been encountered on a traverse from the coast to several hundred kilometres inland from the Pacific margin of Gondwanaland: *Pachydermophylletum* (mangrove scrub), *Linguifolietum* (coastal swamp woodland), *Dicrodium odontopteroidium* (floodplain forest), *Phoenicopsetum* (levee bank scrub), *Dicrodium odontopteroidium xylopterisum* (xerophytic woodland) and *Johnstonietum* (mallee-like woodland).

The fourth dimension of fossil plant associations (time) is best assessed from the evolution of a prominent group of plants. In conjunction with the ranges of other plant megafossils, evolutionary changes can be used to define Opperel-zones. For the Late Permian to Early Jurassic of eastern Australasia, I have used the evolution of *Dicrodium* and leaves of related pteridosperm plants together with other species of restricted stratigraphic range or prominent in the definition of the fossil plant associations. From this evidence four Opperel-zones can be recognised. '*Thinnfeldia*' *callipteroides* Opperel-zone (Chhidruan to Smithian, 250-230 x 10⁶ years), *Dicrodium zuberi* Opperel-zone (Smithian to Middle Anisian, 230-220 x 10⁶ years), *D. odontopteroides* Opperel-zone (Late Anisian to Ladinian, 220-210 x 10⁶ years) and *Yabeiella* Opperel-zone (Carnian to Rhaetian, 210-200 x 10⁶ years).

In a complete revision of the pteridosperm form-genera *Dicrodium*, *Johnstonia* and *Xylopteris*, a large number of new combinations and the following new taxa are proposed: *Dicrodium gouldii* sp. nov., *D. odontopteroides* var. *argenteum* var. nov., *D. odontopteroides* var. *moltenense* var. nov., *D. radiatum* sp. nov., *D. townrovi* sp. nov. and *Johnstonia coriacea* var. *obesa* var. nov.

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OBVIOUS features of megafossil plant collections can often be attributed to palaeoecological or palaeoenvironmental factors, but their age is best determined by other considerations once these factors have been removed. These practical obstacles to the correlation and interpretation of megafossil plant assemblages are widely recognised by palaeobotanists. Here I wish to indicate some simple methods of overcoming them. The classical methods of phytosociology are useful for labelling megafossil plant associations, interpreting their palaeoecological nature and mapping their three dimensional occurrence in rocks. For the fourth dimension (time) I have used Opperel-zones based largely on a postulated evolutionary lineage of the most prominent plants. My examples come from the suc-

cession of floral facies preserved in the upper part of the non-marine sequence in the Sydney Basin of New South Wales, and from other correlative florules in eastern Australia and New Zealand. However many of the conclusions are applicable throughout Gondwanaland.

Palaeoecological classification of fossil plant associations

Many of the problems of plant biostratigraphy can be overcome by naming fossil plant associations in the same way as modern plant associations. The life-form, palaeoenvironmental preferences, palaeosols, age and spatial relationships of the fossil association are then open to interpretation.

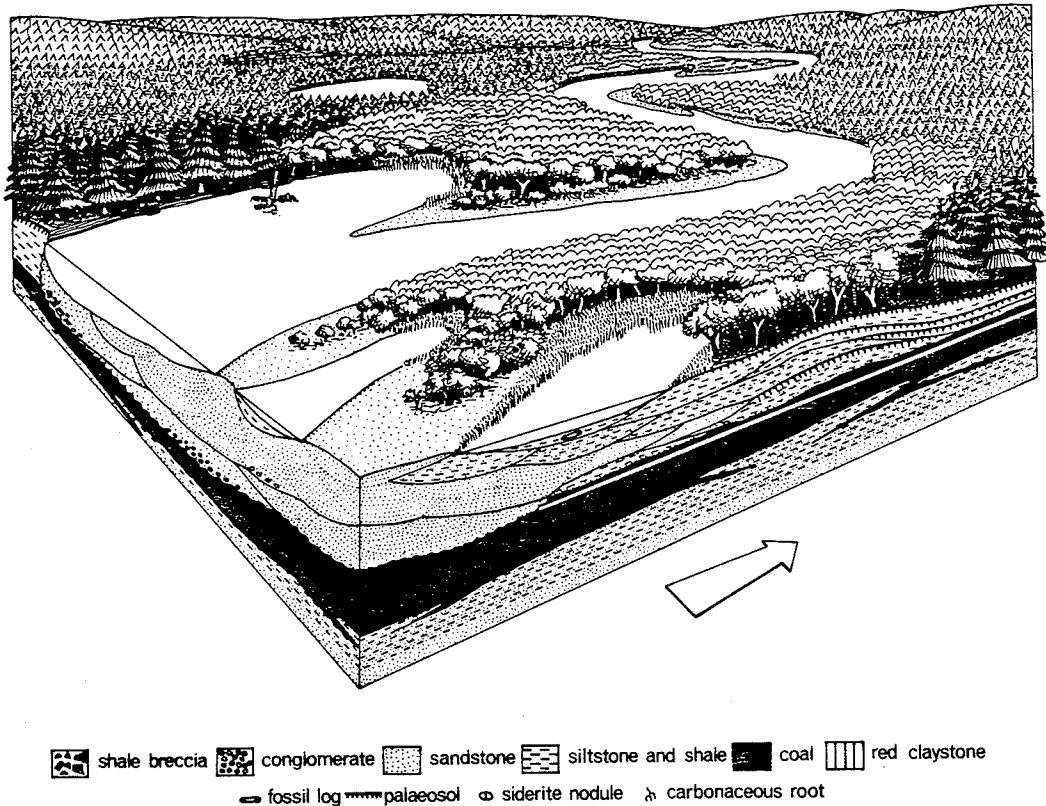


Fig. 1. A reconstruction of the 'Thinnfeldietum' callipteroidium (rounded bushes) and the Voltziopsetum (conical trees) in the Sydney Basin during latest Permian time. Idealised sedimentology based on the uppermost Illawarra Coal Measures (Bulli Coal) and lower Coalcliff Sandstone exposed near old Coalcliff jetty, south of Stanwell Park, on the Illawarra coast, and exposures of a similar stratigraphic interval, at the eastern end of Coxs Gap road tunnel, near Muswellbrook. The arrow indicates present north.

Modern phytosociological method. A modern plant association is a community of definite floristic composition and more or less uniform structure and habitat (Daubenmire, 1968; Braun-Blanquet, 1932). There are many conflicting ideas on how plant associations should be recognised and defined. According to Poore (1956) they are better defined by species which are large and prominent (*dominant*) and present in most stands of the association (*constant*) than those which are apparently restricted to the association (*faithful*). An association is better defined from a stand which is most distinct from others (*nodum*) than from where it intergrades. Traditionally, plant associations have been defined by direct observation and by tabulating species lists from different stands. Several authors (Williams & Lambert, 1960; Curtis &

MacIntosh, 1951) have devised more rigorous quantitative methods.

Associations are named from a characteristic species by adding the suffix '-etum' to the root of its genus name. If further precision is required, the specific epithet may also be used in the genitive case. For example, the *Dicroidietum odontopteroidium* is an association characterised by *Dicroidium odontopteroides*. Daubenmire (1968) and Braun-Blanquet (1932) have discussed additional ways of naming associations.

Associations are composed of smaller groups, including successional stages and groups of plants with similar life-forms and ecological requirements (*synusiae*). They may also be grouped into larger categories based on their life-form and habitat alone (*formation*) or by also considering their

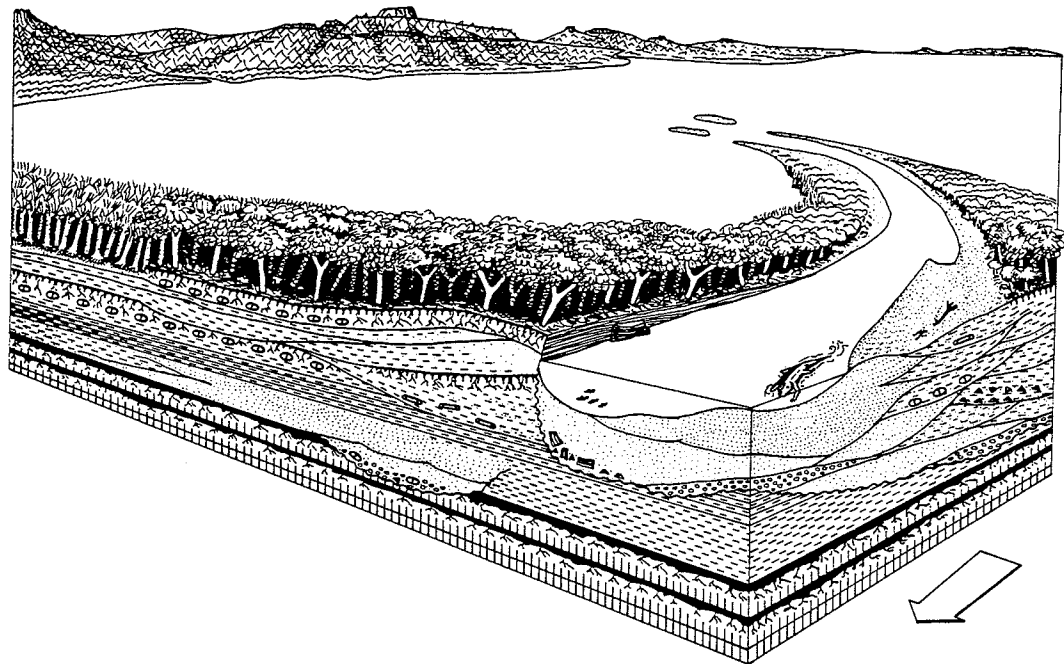


Fig. 2. A reconstruction of the *Dicroidietum zuberi* (foreground heath) and *Pleuromeietum* (left foreground meadows) on a lobe of the Gosford delta in the Sydney Basin during Smithian to Anisian time. Idealised sedimentology based on the southeast cliff-line of Turimetta Head, north of Narrabeen. The pre-delta palaeosols, which were forested by the *Dicroidietum zuberi* swamp woodland, were overlain by prodelta shales containing *Cylostrobus* and *Sigillariophyllum* and then successively larger distributary channels. The *Voltziopsetum coniferosum* forest (conical pattern) and *Dicroidietum zuberi* swamp woodland (undulose pattern) forested the old Gerringong volcanic ridge forming the horizon. The topography of this ridge is based on the magnetic anomaly map of Mayne *et al.* (1974). The arrow indicates present north. Lithological key as for Fig. 1.

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Palaeontological application. A fossil plant association is just such, rather than a reconstruction of former vegetation. It should bear the same relation to a modern association as a fossil species to a living one, or a palaeosol to a soil. To express the concept of ancient vegetation it is best to use the fossil plant association name together

with an indication of its likely type of formation, such as swamp woodland or heath, and use the past tense. The nodum of a fossil plant association is a collection from a reference locality. Thus the fossil plant association has an objective reality, regardless of effects such as differential preservation, collecting bias and so on, which are open to interpretation. Ideally this collection should be a subautochthonous, well-preserved, diverse accumulation of plant material, including leaves, fruits and logs. This facilitates further identification in the same way as a well-preserved holotype of a fossil species. There does not seem any more point in labelling fossil plant associations which have been very strongly modified during preservation and transport, such as accumulations of plant debris in marine rocks, than there is for creating a

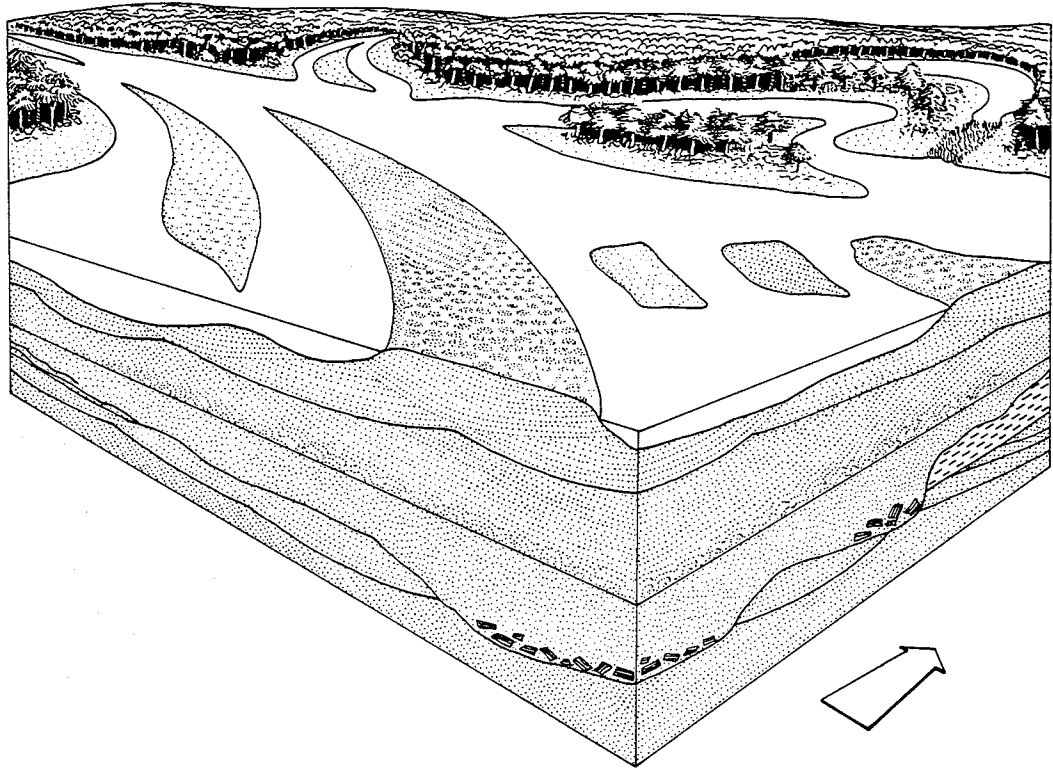


Fig. 3. A reconstruction of the *Dicroidietum zuberi* xylopterisum and braided streams in the Sydney Basin during Anisian time. Sedimentology after Conaghan & Jones (1975) and unpublished work in the area around Pittwater (Retallack, 1973). Sequences deposited in the waning phase of a stream flood cycle begin with massive sandstone, with possible antidunes (far left), an erosive base and local accumulations of shale breccia. This is overlain by huge cross-sets generated by channel-wide sand bars, then trough cross-bedded sandstone. Higher still, siltstone and shale beds are occasionally preserved. The arrow indicates present north. Lithological key as for Fig. 1.

separate species name for prismatic shell fragments of the bivalves *Inoceramus* and *Atomodesma*. It is extremely difficult, if not impossible, to obtain reliable quantitative information on the floristic composition of fossil plant associations. Thus, for the moment, fossil plant associations will have to be defined on the judgement of the palaeobotanist, with special regard for their potential usefulness, as in the pioneering days of modern plant synecology.

Equisetalean, filicalean and lycopod remains are probably more prominent in the fossil record than they ever were in life. They may form distinctive and even monodominant associations, such as the *Pleuromeietum* described here. However, where an assemblage largely of these plants contains a conspicuous component of seed plants, it is best to regard them as *synusia*

or successional stages of the seed plant association.

In his masterly treatment of plant palaeoecology, Krassilov (1972, translated 1975, p.141, 177-182) has mentioned a few Braun-Blanquet names, but he evidently intended these as a reconstruction of past vegetation, quite unlike the concept proposed here. Later (1974) he proposed a system of abbreviations to label fossil plant associations.

In the following sections I have characterised twelve fossil plant associations for the Late Permian to Middle Triassic of Gondwanaland. The evidence for my reconstructions is only briefly summarised here. More detailed documentation will be published elsewhere (Retallack, 1977, in press a,b). The sketches of vegetation types (Figs 1-4) are not meant to be an accurate

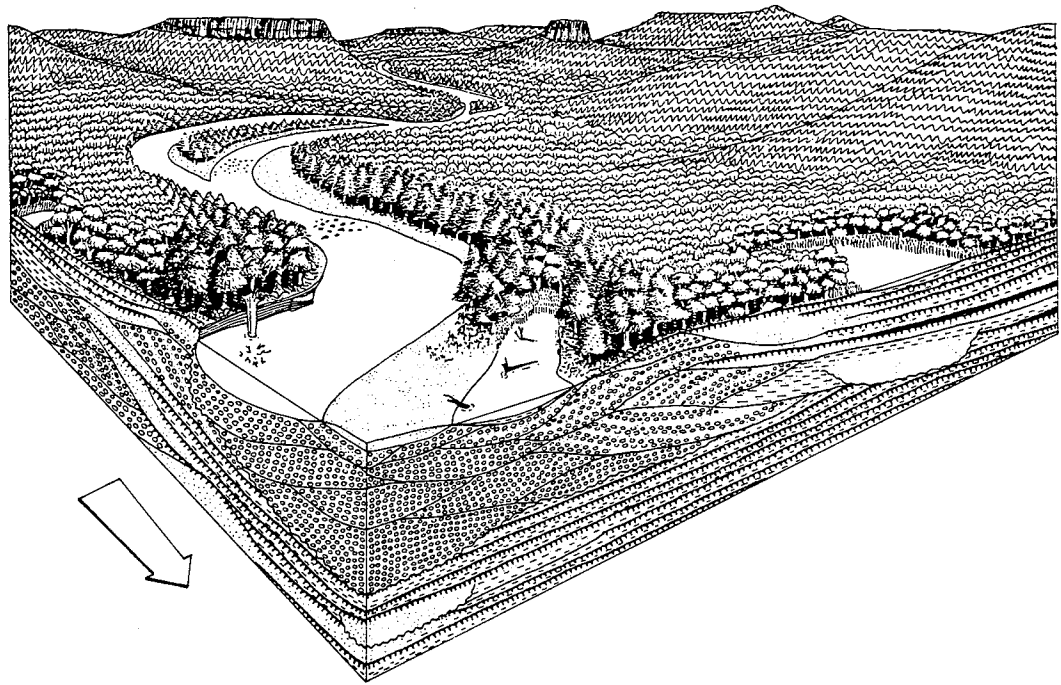


Fig. 4. A reconstruction of the *Dicrodium odontopteroidium* flood plain forest (rounded trees and undulose pattern), *Phoenicopsetum* levee scrub (dashed shading and conical pattern) and *Johnstonium* mallee-like woodland (serrated pattern on hillsides) in a Middle Triassic valley near the present town of Nymboida, north-eastern New South Wales. Sedimentology based on Fig. 5. Arrow indicates present north. Lithological key as for Fig. 1.

portrayal of the various elements of an association, nor 'an artist's impression', but rather a diagrammatic representation of the interpreted vegetation in its ancient environment based on the discussion given. The stratigraphic distribution of the associations is indicated in Figs 9-10. I have also discussed their distribution more comprehensively and given floral lists for the reference locality of each association on microfiche frames G4-G18.

'Thinnfeldietum' callipteroidium (levee bank scrub)

The 'Thinnfeldietum' callipteroidium is an association dominated by the distinctive pteridosperm '*Thinnfeldia*' *callipteroides* Carpentier 1935 (Fig. 6.1-3; see also Town-

row, 1966b). Common associates are *Schizoneura gondwanensis* Feistmantel 1876, large *Isoetes*-like leaflet groups, sterile cladophleboid fern fronds, and conifer shoots, including *Voltziopsis africana* Seward 1934 and undescribed remains similar to *Podozamites*. Assemblages with a similar specific composition and found at the same stratigraphic horizon, but in which the conifer remains are dominant, I here separate as the *Voltziopsetum*.

Several collieries in the southern coalfield of the Sydney Basin have made available maps of lowermost Narrabeen Group roof rocks. On these maps, localities of the 'Thinnfeldietum' callipteroidium occur in deposits of interbedded sandstone and shale. These levee and scroll bar deposits flank conglomeratic sandstone of palaeochannels, which meander through large areas of

blocky, clayey palaeosols. Equisetaleans, isoetaleans and filicaleans apparently thrived in and around ponds in the area of these levees and scroll bars. '*Thinnfeldia*' *callipteroides* is commonly abundant and well-preserved in these pond deposits, but few conifer leaves and no large fossil logs have been found in them. Large carbonised logs, in riffle-bar conglomerate and intraformational breccia at the base of the fluvial palaeochannels, were probably provided by local erosion of the Voltziopsetum, which is closely associated with palaeosols at other localities on the same stratigraphic level. To this evidence may be added the large spreading fronds of '*Thinnfeldia*' *callipteroides*, and Roselt's (1962) reconstruction of a ?related plant (*Callipteris scheibei*). All these lines of evidence suggest that the 'Thinnfeldietum' callipteroidium was a bushy scrub vegetation, colonising scroll bars and levees of meandering streams, as diagrammatically shown in Fig. 1. I have drawn the Voltziopsetum overtopping the 'Thinnfeldietum' callipteroidium and rooted in the lower slope of the levee. This is conjecture, as there is no way of evaluating the exact location and sharpness of the ecotone from the fossilised remains.

The 'Thinnfeldietum' callipteroidium and Voltziopsetum were probably derived from *Callipteris* and conifer dominated associations, now widely fossilised in Permian redbeds of the northern hemisphere (see Schopf, 1973; Read & Mamay, 1964). Carpentier (1935) regarded these two associations in Madagascar as a more xerophytic vegetation of crystalline uplands coeval with low-lying peat-swamps, wooded largely by *Glossopteris*. They probably colonised the emerging uplands of eastern Australia in Late Permian time. Then they became widespread in depositional areas of the Sydney Basin as alluvium was disconformably laid over the *Glossopteris*-bearing coal measures, following a period of uplift and erosion. This depositional hiatus is more marked towards and beyond the northern margin of the basin.

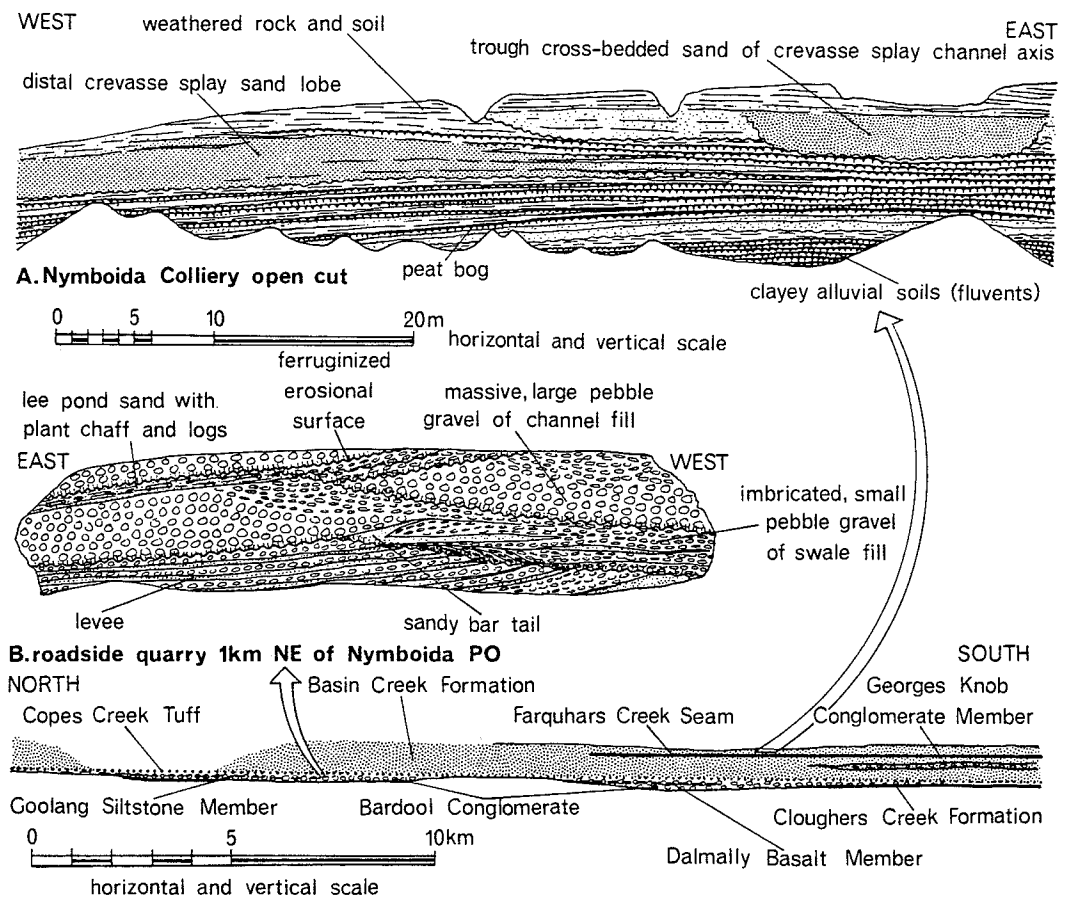
Voltziopsetum (coniferous forest)

The Voltziopsetum is used not only for assemblages of conifer remains dominated by *Voltziopsis*, but also for other assem-

blages of fragmentary conifer twigs and log accumulations found in the same stratigraphic interval as *Voltziopsis*. This association is poorly represented by megafossil remains. It can also be mapped by the *Protohaploxylinus reticulatus*, *P. samoilovichii* and *Lunatisporites pellucidus* palynological Assemblages of Helby (1973) in the Sydney Basin.

In the middle and lower Narrabeen Group of the Sydney Basin, dispersed conifer-shoot remains of the Voltziopsetum are rare, and often poorly preserved and fragmentary. Large fossil logs are common in some channel sandstones. Associated palaeosols, similar to humic gley and grey-brown podzolic soils, often show well-humidified organic horizons and A horizons densely penetrated by carbonised roots and reduced root mottles. All these features suggest active decay of leaf-litter among closely-spaced trees with a closed canopy. The shoot of *Voltziopsis* (Townrow, 1967b; Retallack, 1976) is so similar to that of modern New Zealand rimu (*Dacrydium cupressinum*), that it is tempting to reconstruct it similarly as conical juvenile and crown-forming mature trees with pendulous shoots. However I have chosen a relatively stylised representation for Fig. 1. The Voltziopsetum was apparently similar to low-diversity evergreen forests now growing in the cool temperate zone of the northern hemisphere (Strahler, 1969).

In the Sydney Basin these forests apparently preferred mineralogically-immature soil materials, partly derived from an eastern volcanic ridge. They persisted through a cycle of high base level, during which they were penetrated locally by coastal lagoons. The Dicroidietum zuberi gradually gained ascendancy over the Voltziopsetum from the west, with more widespread siliceous substrate and a lowering of base level. However, the conifers apparently persisted on an eastern volcanic ridge. They made a last advance, into the Dicroidietum zuberi, on grey-brown podzolic (ferrod) palaeosols now preserved in the Bald Hill Claystone in the area around Sydney. This was at a time of very low base level, when erosion and soil formation prevailed over deposition. The Voltziopsetum is not found at higher stratigraphic levels, where the eastern volcanic source of the Bald Hill Claystone and Garie Formation no longer contributed sediment to the onshore Sydney Basin.



C. reconstructed cross-section of Triassic valley deposits around Nymboida

Fig. 5. Interpreted sedimentology of the Nymboida Coal Measures near Nymboida, northeastern New South Wales.

Dicroidietum zuberi (broadleaf forest and heath)

Diverse broadleaf floras dominated by *Dicroidium* are most characteristic of the Gondwanaland Triassic. The *Dicroidietum zuberi* is dominated by *Dicroidium zuberi* (Szajnocha) Archangelsky 1968 (Fig. 6.11-16). This and the *Dicroidietum odontopteroides* were probably two ecologically similar associations. In the absence of reliable quantitative data, I have arbitrarily distinguished these two associations by the presence of *Dicroidium odontopteroides* (Morris) Gothan 1912 (Fig. 6.37-42). The *Dicroidietum zuberi* commonly includes a variety of equisetaleans (notably (*Neo-*

calamites), filicaleans (*Cladophlebis*), pteridosperms (*Lepidopteris* and *Pachydermophyllum*), cycadophytes (*Taeniopteris*) and the characteristically large corystosperm reproductive structures attributed to *Dicroidium zuberi* (Fig. 7).

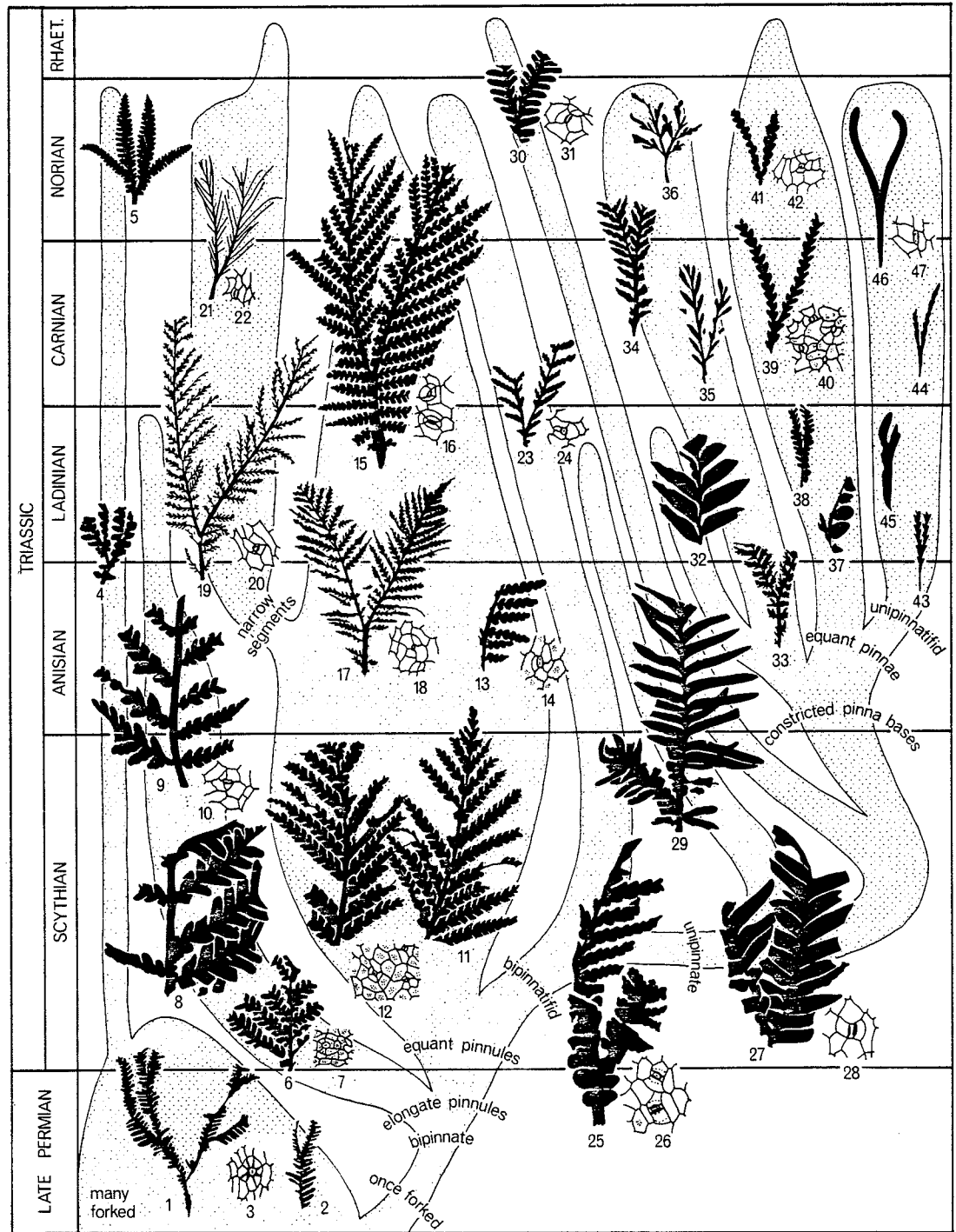
During deposition of the upper Narrabeen Group north of Sydney, the *Dicroidietum zuberi* was both a delta-top heath and a lagoon-margin swamp woodland at different times and places (Fig. 2). The swamp woodland grew on humic gley (fibrist) soils between the Voltziopsetum and a large coastal lagoon at a time of high base level. Large logs and well-humidified remains of the *Dicroidietum zuberi* can be observed in the organic horizon of one of these

palaeosols in the lowermost Garie Formation at Turimetta Head. Remains of this association are better preserved in the adjacent sediments. Equisetaleans (*Neocalamites*) preserved in growth position in the lower organic and upper A horizon of this same palaeosol, were probably a preliminary stage in an hydrarch succession at the lagoon margin. During deposition of the overlying Newport Formation at Turimetta and North Avalon Heads, the *Dicrodium zuberi* probably grew as a heath on thin gleyed-podzolic (aquod and ochrept) and alluvial (aquent) soils of deltas infilling the northern portion of the lagoon. This heath interpretation is based on the absence of large fossil logs in these rocks; the small diameter of radiating root systems, egg-cup podzols, and cradle knolls observed in the palaeosol A horizons; the similarity of the palaeosols to modern soils supporting heath and the relatively coriaceous nature of associated *Dicrodium* leaves compared to those of other localities on a similar stratigraphic horizon. The *Dicrodium zuberi* may have had a different habit, such as a floodplain forest, at other localities in the upper Narrabeen Group, such as the lowermost

Bald Hill Claystone north of Garie, the Gosford Formation below the Skillion near Terrigal, and the Wentworth Falls Claystone Member of the Banks Wall Sandstone at Mt Piddington.

The *Dicrodium zuberi* probably differentiated from the 'Thinnfeldium' callipteroidium. A transitional assemblage has not been found in the Sydney Basin, but is very closely approached in the assemblage collected near Nidpur, India (Bose & Srivastava, 1971). In the Sydney Basin the *Dicrodium zuberi* displaced the *Voltziopsetum* from the west and north when a stable to slightly-lowering base level caused the substrate to be reworked to a greater mineralogical maturity. The megafossil plant association from Nymboida open cut (microfiche frames G11-G13) is a *Dicrodium odontopteroidium* very close to the transition from the *Dicrodium zuberi*, as *Dicrodium zuberi* is still very common there. In the Sydney Basin, this later transition is obscured by the *Taeniopteretum lentriculiformis* and the *Dicrodium zuberi xylopterosum* and a marked change in depositional environment (Fig. 10).

Fig. 6. Permian and Triassic evolution of *Dicrodium* and related leaves in Gondwanaland. All silhouettes are one sixth natural size and all cuticles magnified by fifty. Individual specimens are not necessarily opposite the age of the rocks in which they were found, but are within the stratigraphic range of the species they represent. The drawings are from published figures and from specimens in the Geology Dept. Univ. New England (prefixed UNEF-). 1-3, '*Thinnfeldia*' *callipteroides* Carpentier 1935, after Retallack (in press b, fig. 22.5B-D). 4-5, *Tetraptilon heteromerum* Frenguelli 1950; 4, after Flint & Gould (1975, pl.3, fig. 10); 5, after Frenguelli (1950, fig. 2). 6-8, *Dicrodium brownii* var. *brownii* (Seward) comb. nov.; 6-7, after Bose & Srivastava (1971, figs 4H,5B); 8, UNEF13944, Newport Formation, N.S.W. 9-10, *Dicrodium brownii* var. *barrealense* (Frenguelli) comb. nov., UNEF13957, Newport Formation, N.S.W. 11-12, *Dicrodium zuberi* var. *papillatum* (Townrow) comb. nov.; 11, after Feistmantel (1890, pl.23, fig.1); 12, after Townrow (1957, fig. 11A). 13-14, *Dicrodium zuberi* var. *sahnii* (Seward) comb. nov., after Thomas (1933, figs 50, 52b). 15-16, *Dicrodium zuberi* var. *zuberi* (Szajnocha) Archangelsky 1968; 15, after Frenguelli (1944a, pl.4); 16, after Jacob & Jacob (1950, fig. 17). 17-18, *Dicrodium townrovii* sp. nov., after Townrow (1957, figs. 8A,7F). 19-20, *Xylopteris tripinnata* (Jones & de Jersey) Schopf 1973, after Retallack (in press b, fig. 22.10A,C). 21-22, *Xylopteris elongata* var. *rigida* (Dun) comb. nov.; 21, after Retallack (in press b, fig. 22.10D); 22, after Townrow (1962b, fig. 1E). 23-24, *Dicrodium dubium* var. *dubium* (Feistmantel) Gothan 1912; 23, after Feistmantel (1890, pl.26, fig.3); 24, after Jones & de Jersey (1947, pl.4, fig.3). 25-26, *Dicrodium dubium* var. *australe* (Jacob & Jacob) comb. nov.; 25, UNEF13945, Newport Formation, N.S.W.; 26, after Jacob & Jacob (1950, fig. 21). 27-28, *Dicrodium narrabeenense* var. *narrabeenense* (Dun in Walkom) Jacob & Jacob 1950; 27, UNEF13950, Newport Formation, N.S.W.; 28, after Jacob & Jacob (1950, fig.8). 29, *Dicrodium narrabeenense* var. *bursellii* (Lacey) comb. nov., UNEF13952, Newport Formation, N.S.W. 30-31, *Dicrodium lancifolium* var. *lancifolium* (Morris) Gothan 1912; 30, after Walkom (1925b, pl.26, fig.2); 31, after Walkom (1917a, fig. 6C). 32, *Dicrodium eskense* (Walkom) Jacob & Jacob 1950, after Flint & Gould (1975, pl.2, fig.3). 33, *Dicrodium radiatum* sp. nov., after Plumstead (1969, pl.19, fig.5). 34, *Dicrodium incisum* (Frenguelli) Anderson & Anderson 1970, after Du Toit (1927, fig. 8A). 35, *Dicrodium prolungatum* (Menendez) comb. nov., after Menendez (1951, pl.14, fig.5). 36, *Dicrodium gouldii* sp. nov., after Gould & Retallack (in Bourke *et al.*, 1977, fig. 3.12). 37, *Dicrodium odontopteroides* var. *argenteum* var. nov., after New Zealand Geological Survey specimen B1095.1, Tank Gully Formation, Mt. Potts Group, New Zealand. 38, *Dicrodium-odontopteroides* var. *remotum* (Szajnocha) Retallack (in Retallack, Gould & Runnegar, 1977), after Frenguelli (1944c, pl.1, fig.1). 39-40, *Dicrodium odontopteroides* var. *moltenense* var. nov.; 39, after Feistmantel (1890, pl.26, fig. 2); 40, after Townrow (1957, fig.6B). 41-42, *Dicrodium odontopteroides* var. *obtusifolium* Johnston 1886, after Townrow (1966a, figs. 1E,2E). 43, *Johnstonia stelzneriana* var. *stelzneriana* (Geinitz) Frenguelli 1943, after Frenguelli (1941). 44, *Johnstonia stelzneriana* var. *serrata* var. nov., after Walkom (1925a, fig.8). 45, *Johnstonia coriacea* var. *obesa* var. nov., after Townrow (1967a, fig.2E). 46-47, *Johnstonia coriacea* var. *coriacea* (Johnston) Walkom 1925a; 46, after Frenguelli (1943, fig. 28a); 47, after Archangelsky (1968, pl.97, fig.5).



Pleuromeietum (marine and lagoonal bay meadows)

The Pleuromeietum is an almost monospecific lycopod association. In the Sydney Basin it includes *Pleuromeia longicaulis* (Burges) Retallack 1975, its supposed cones (*Cylostrobus sydneyensis* (Walkom) Helby & Martin 1965 *s.l.*), and leaves *Sigillariophyllum* of Vogellehner, 1968). In various parts of the world it formed dense meadows around coastal lakes, lagoons and protected seashores (Fig. 2; see also Retallack, 1975). Although it could thrive in salinities intolerable to other plant associations, its landward spread was probably checked by factors other than salinity, such as interspecific competition, spore dispersal mechanisms, and germination requirements. The Pachydermophylletum apparently displaced *Pleuromeia* from the seashores of Gondwanaland during Anisian time.

Taeniopteretum lentriculiformis (coastal scrub)

This association is characterised by abundant leaves of *Taeniopteris lentriculiformis* (Etheridge) Walkom 1917a, but may also contain rare elements of the Dicroidietum zuberi. It is found at several localities in the upper Narrabeen Group in the eastern Sydney Basin and, as drift fragments, in Anisian marine rocks of the Murihuku Supergroup in New Zealand (New Zealand Geological Survey collections B191, B1075). At North Avalon, near Sydney, the Taeniopteretum lentriculiformis is associated with grey clay (fluvent) palaeosols developed on levee deposits. Here *Taeniopteris lentriculiformis* has been found attached to and associated with slender many-branched axes. Thus it was probably a diffuse shrub growing on slightly higher, better drained and more exposed areas. The Taeniopteretum lentriculiformis apparently formed a distinctive coastal scrub which was succeeded by the Linguifolietum swamp woodland during Ladinian time.

Dicroidietum zuberi xylopterium (xerophytic woodland)

This association contains many of the species of the Dicroidietum zuberi, but is characterised by a conspicuous component

of *Xylopteris* (Fig. 6.19-22). The Dicroidietum zuberi xylopterium is a very similar association to the Dicroidietum odontopteroidium xylopterium, but for the presence in this latter of *Dicroidium odontopteroides* and other species found in the Dicroidietum odontopteroidium.

A drier palaeoenvironment, suggested by the xerophytic *Xylopteris* leaves, is also supported by other associated narrow-leaved species of *Sphenobaiera*, *Czekanowskia* and *Dicroidium*. A more extreme type of xerophytic association containing *Xylopteris*, such as that described from Rhaetian rocks near Paso Flores in Argentina by Frenguelli (1937), could be termed a 'Xyloptero-Czekanowskietum'. Xerophily of *Xylopteris* is indicated primarily by its reduced leaf area compared with closely-related *Dicroidium* leaves. The relatively wider, more obscure and irregular midrib of compressed pinnae, compared to that of naturally macerated and oxidized leaves is probably due to lignification of the leaf interior. Xerophily is also suggested by comparing the cuticle of *Xylopteris* with that of coexisting *Dicroidium* leaves (Townrow, 1962a).

In the Sydney Basin during the deposition of the Hawkesbury Sandstone, the growth of the Dicroidietum zuberi xylopterium was probably retarded by high water stress and low fertility of the sandy, siliceous substrate. This substrate was the result of a relatively stable base level and the emergence of the Lachlan Fold Belt, to the south and west, as a (partial) source area. Conaghan & Jones (1975) have suggested that the Hawkesbury Sandstone was deposited by braided streams of a size and type comparable to the modern Brahmaputra River. The Antarctic Ellsworth Mountains (Elliot, 1975), may have been the Triassic source of highly seasonal discharge, comparable with the modern Himalaya. However, sparse vegetation was probably also a significant factor in braiding and irregular discharge (see Schumm, 1968). Accumulations of moderate-sized logs in sandstone palaeochannels and megafossil plant assemblages in shale lenses, such as the one near Brookvale, indicate that these sandy floodplains and channel bars were wooded by shrubs and small trees of the Dicroidietum zuberi xylopterium. Equisetaleans of this association flourished locally around abandoned channels and floodplain lakes, along with less common filicaleans



Fig. 7. A reconstruction of *Dicroidium zuberi* (Szajnocha) Archangelsky 1968; leaf (black); microsporophyll, '*Pterorrachis*' *barrealensis* Frenguelli 1942b, better regarded as *Pteruchus* (left); dehiscent megasporophyll, *Umkomasia* sp. (right); pollen, *Alisporites* sp. 2 of de Jersey (1962) (upper inset); seed (lower inset). These reproductive structures are attributed to this type of leaf on the basis of their similar cuticles, common association (sometimes in almost monospecific assemblages) and their general similarity to other supposed corystosperm fructifications and leaves (Frenguelli, 1944a; Townrow, 1962a; Retallack, 1973). The reproductive structures are natural size and the leaves range from smaller than this to about 1 m long.

and liverworts (Fig. 3). Considering the close relation of the *Dicroidietum zuberi* xylopterisum to the *Dicroidietum zuberi*, this latter may have contemporaneously forested the less-disturbed floodplain.

Dicroidietum odontopteroidium (broadleaf forest)

This is a similar diverse association to the *Dicroidietum zuberi*, but by definition must contain at least one unequivocally-forked specimen of *Dicroidium odontopteroides*. Also present in the association are equisetaleans (*Neocalamites*, *Phyllothea*), filicaleans (*Asterotheca*, *Cladophlebis*, 'Coniopteris', *Dictyophyllum*), pteridosperm leaves (*Lepidopteris*, *Pachydermophyllum*, *Dicroidium*, *Johnstonia*, *Tetraptilon*), smaller corystosperm reproductive structures (*Pteruchus* and *Pilophorosperma* of Thomas, 1933, and Townrow, 1962a, 1962c), ginkgoales (*Sphenobaiera*, *Ginkgoites*, *Phoenicopsis*), conifers (*Rissikia*), cycadophytes (*Taeniopteris*, *Pterophyllum*, *Pseudoctenis*) and several plant remains of uncertain affinity (variously referred to *Glossopteris*, *Anthrophyopsis*, *Chiropteris* and *Yabeiella*).

The reference locality for the *Dicroidietum odontopteroidium* is the Nymboida Colliery open cut, in northeastern New South Wales. Apart from the sedimentary petrology necessary for geological mapping (McElroy, 1963), little work has been done on the Nymboida Coal Measures with a view to reconstructing the Triassic environment. In the next few paragraphs I briefly attempt this as an example of the kind of evidence necessary for understanding megafossil plant associations.

The variation in the thickness of the Bardool Conglomerate underlying the Copes Creek Tuff (Fig. 5C), suggests that it is a valley fill conglomerate. Its clasts are largely acid volcanics, with local layers of abundant greywacke and schist clasts (McElroy, 1963). Thus this extensive valley system had cut through widespread volcanics of the source area into deformed Palaeozoic basement. Although a basalt flow and a tuff are interbedded with Triassic sediments, the main period of volcanic activity in the source area ceased some time before the cooling of the New England Batholith, which has been

radiometrically dated at 225-250 x 10⁶ years (Wilkinson, 1974). During Middle Triassic time, active volcanoes are indicated by Late Triassic granitic intrusions southeast of Nymboida on the present coast (McDougall & Wellman, 1976) and north of Nymboida, near and beyond the present Queensland border (Webb & McDougall, 1967; McKenzie, 1972; Green & Webb, 1974). Thus I have reconstructed the Triassic terrain west of Nymboida as a dormant volcanic tableland which has been eroded since the Late Permian (Fig. 4).

The sedimentary structure of the Bardool Conglomerate (Fig. 5B) is most similar to that of modern braided streams described by Bluck (1967), Boothroyd (1972), and Williams & Rust (1969). A Trask sorting coefficient of 2.46, estimated from 500 pebbles of the lowest conglomerate in Fig. 5B, indicates that it was deposited by a river, rather than in an alluvial fan or lakeside shingle beach (compare values given by Emery, 1955). Considering the general similarity of the Triassic palaeogeography (Fig. 4) to that prevailing at present around Nymboida, these Triassic streams probably had both meandering and braided reaches like the modern conglomeratic channels of the Nymboida River. Conglomeratic channel deposits are also common within the Basin Creek Formation. As far as can be seen, they are of a similar type to those of the Bardool Conglomerate, although somewhat smaller in average grain size.

The wedge and trough-shaped sandstone bodies in overbank deposits of the Basin Creek Formation are best interpreted as crevasse splay deposits (Fig. 5A). These resemble small deltas which burst through breaches in the levee during floods (Allen, 1970). Crevasse splays may generate a variety of stratigraphic sections (McKee, Crosby & Berryhill, 1967). Generally they are coarser towards their base and closer to the channel.

Shaly overbank deposits often contain many superimposed, thin (10-20 cm), clayey alluvial (fluvial) palaeosols. An especially characteristic fossil root of these palaeosols consists of dense bundles of adventitious roots along thicker axes. Similar remains have been described and figured by Frenguelli (1942a) as '*Czekanowskia rigali*'. Larger roots, stumps and logs are also found.

The large logs and roots found in

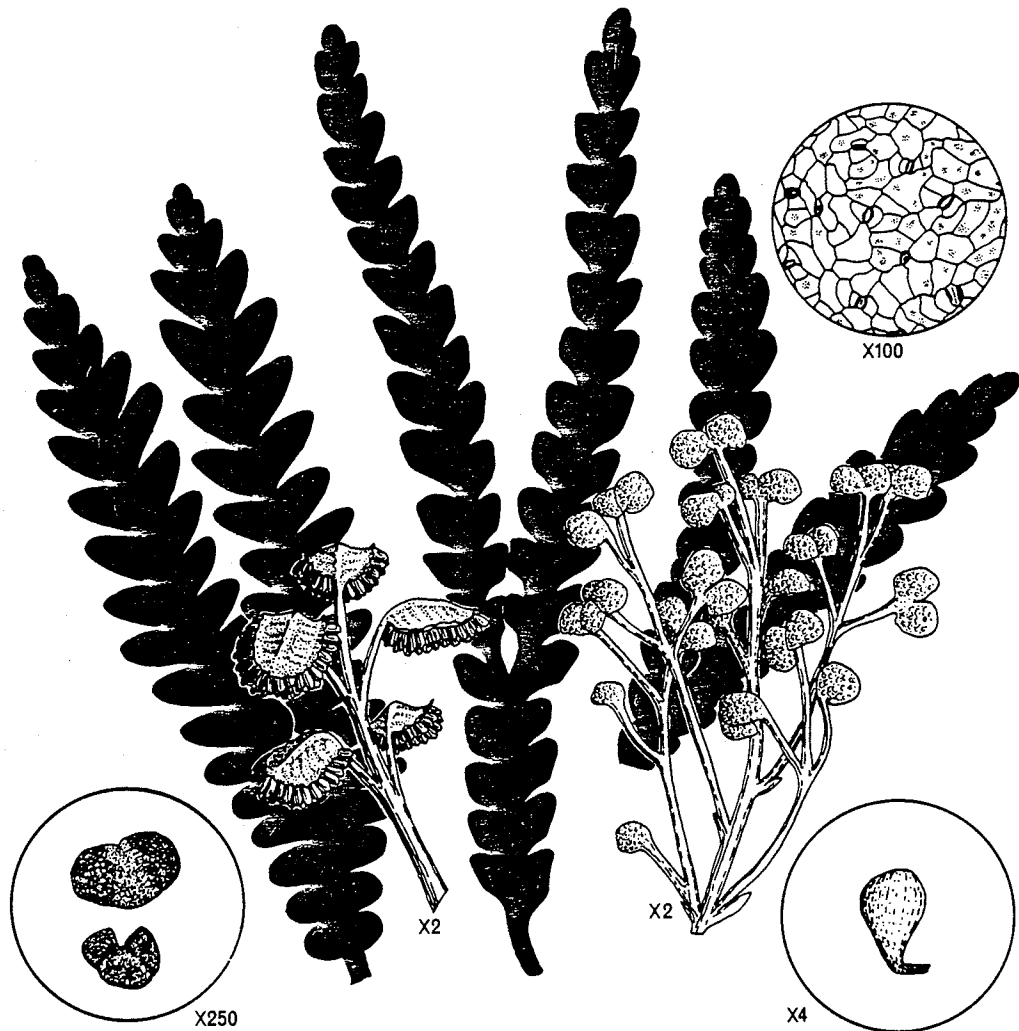


Fig. 8. A reconstruction of *Dicroidium odontopteroides* (Morris) Gothan 1912; leaves (black), showing the variation I accept for this species, including var. *odontopteroides* (Morris) Gothan 1912 (left), var. *moltenense* var. nov. (centre) and var. *obtusifolium* Johnston 1886 (right); microsporophyll, *Pteruchus johnstonii* (Feistmantel) Townrow 1962c (left); megasporophyll, *Pilophorosperma* sp. (right); pollen, *Alisporites australis* de Jersey 1962 (lower left inset); seed (lower right inset); cuticle (upper right inset). After Carruthers (1872), Thomas (1933) and Townrow (1957, 1962a, 1962c, 1966a). Drawings are natural size unless otherwise indicated.

Nymboida Colliery open cut indicate that the *Dicroidietum odontopteroidium* was a forest association there. Individual layers of shale from this quarry may show local abundance of equisetaleans, filicaleans, *Lepidopteris*, cycadophytes, *Taeniopteris* and 'Anthrophyopsis'. Considering likely reconstructions of these types of plants

(Delevoryas, 1975; Townrow, 1960), the forest was probably composed of a great variety of structural elements, including reed-like, herbaceous and shrubby plants and probably several layers of trees. I only recognise the local abundance of *Phoenicopsis*, usually in orange-weathered sandstone here, as a separate association.

Phoenicopsetum (levee-bank scrub)

This consists largely of *Phoenicopsis* leaves, together with very few remains of plants also found in the Dicroidietum odontopteroidium. In the Nymboida Colliery open cut (Fig. 5A) this association is found in the lower part of the crevasse splay sandstones. This suggests that it was a levee and point bar scrub or woodland (Fig. 4) whose leaf litter was scoured out during floods.

Johnstonietum (mallee-like woodland)

This association is dominated by *Johnstonia*, most commonly *Johnstonia coriacea* (Johnston) Walkom 1925a (Fig. 6.43-47). It may also include species found in the Dicroidietum odontopteroidium, although pteridophytic remains are not usually present.

The Johnstonietum is found near Toongra and Delungra in New South Wales and in Victoria Land, Antarctica (microfiche frames G15). All these places were probably inland of a coastal dividing range during Triassic time (Elliot, 1975; Bourke *et al.*, 1977). Near Delungra the Johnstonietum thrived over westward draining valleys in granitic basement. It is preserved there in a black shale. The relative rareness of partly decomposed and clumped leaves, suggests that the organic component of this shale is a resorted mull humus (a type of soil organic horizon described by Bridges, 1970). There is also a conspicuous absence of equisetalean and filicalean remains, large fossil logs and root systems at this locality. Like *Xylopteris*, *Johnstonia* had a relatively smaller leaf area, more lignified leaf interior (especially in *J. stelzneriana* (Geinitz) Frenguelli 1943), and more xerophytic cuticle than coexisting *Dicroidium* leaves (compare Townrow, 1957, and Archangelsky, 1968). Taken together, all these features suggest that the Johnstonietum was a well-spaced woody

association of moderate height with a sparse, loose leaf litter. These features are also characteristic of modern plant formations such as the Australian mallee scrub (see Eyre, 1968) and the northern hemisphere chapparal (see Daubenmire, 1968, p.65). As can be seen from the lists of fossil plants given by Gould & Retallack (in Bourke *et al.*, 1977), several examples of the Dicroidietum odontopteroidium have also been found near Delungra. These and thin coal seams probably accumulated locally where the water table was perched by impervious clay or irregularities in the crystalline basement.

Dicroidietum odontopteroidium xylopterisum (xerophytic woodland)

The Dicroidietum odontopteroidium xylopterisum was probably ecologically analogous to the Dicroidietum zuberi xylopterisum. It contains at least one and commonly several specimens each of *Xylopteris* and *Dicroidium odontopteroides*, together with various species also common in the Dicroidietum odontopteroidium. Both the Dicroidietum zuberi xylopterisum and the Dicroidietum odontopteroidium xylopterisum probably formed partly xerophytic woodlands. They are both more floristically balanced than the Johnstonietum, so were probably communities of more complex structure.

Pachydermophylletum (mangrove scrub)

This is an almost monospecific association of *Pachydermophyllum* leaves. It is very similar to the northern hemisphere Jurassic plant association described by Harris (1966), as a coastal mangrove scrub.

One kilometre east of Benmore Dam wall, New Zealand, the reference locality of the Pachydermophylletum is found 6 m above

Fig. 9. Stratigraphic ranges of selected species in some better known Gondwanaland sequences spanning at least one Opper-zone boundary. In order to be consistent with the ammonoid-based time scale used in the Triassic (after Tozer, 1971), I have used the Permian time scale of Furnish (1973) rather than the brachiopod-based system of Waterhouse (1976). Abbreviations: H. S. = Hawkesbury Sandstone; W. G. = Wianamatta Group; T. G. = Toogoolawah Group. Karroo Basin zones A-E after Du Toit (1927). The Middle Triassic '*Otozamites queenslandii*' Walkom 1917b from the Toogoolawah Group (Hill, Playford, & Woods, 1975) is regarded as generically distinct from *Otozamites*.

* new oppel-zones ⇨

- Glossopteris spp.
- "Thinnfeldia" callipteroides
- Voltziopsis spp.
- "Danaeopsis" hughesii
- Dicroidium brownii
- D. zuberi
- D. dubium var. australe
- D. narrabeenense
- D. lancifolium
- Pleuromeia spp.
- Pachydermophyllum spp.
- Taeniopteris lentriculiformis
- Xylopteris spp.
- Dicroidium odontopteroides
- D. odontopteroides var. remotum
- D. eskense
- Rissikia spp.
- Johnstonia spp.
- Linguifolium spp.
- Yabeiella spp.
- Pterophyllum multilineatum
- Sphenobaiera tenuifolia
- Otozamites spp.

	LATE PERMIAN		TRIASSIC											EARLY JURASSIC														
	GUADALUPI	DZHULF.	EARLY			MIDDLE				LATE				LIASSIC														
			SCYTHIAN																									
	WORDIAN	CAPTANIAN	AMARASSIAN	ARAKSIAN	CHHIDRUAN	CHANGSINGIAN	EARLY GRIESBACHIAN	LATE GRIESBACHIAN	DIENERIAN	SMITHIAN	SPATHIAN	EARLY ANISIAN	MIDDLE ANISIAN	LATE ANISIAN	EARLY LADINIAN	LATE LADINIAN	EARLY CARNIAN	LATE CARNIAN	EARLY NORIAN	MIDDLE NORIAN	LATE NORIAN	RHAETIAN	HET TANGIAN	SINEMURIAN	PLIENSCHACHIAN	TOARCICAN		
					"Thinnfeldia" callipteroides						Dicroidium zuberi			D.odontopteroides			Yabeiella											
Glossopteris spp.																												
"Thinnfeldia" callipteroides																												
Voltziopsis spp.																												
"Danaeopsis" hughesii																												
Dicroidium brownii																												
D. zuberi																												
D. dubium var. australe																												
D. narrabeenense																												
D. lancifolium																												
Pleuromeia spp.																												
Pachydermophyllum spp.																												
Taeniopteris lentriculiformis																												
Xylopteris spp.																												
Dicroidium odontopteroides																												
D. odontopteroides var. remotum																												
D. eskense																												
Rissikia spp.																												
Johnstonia spp.																												
Linguifolium spp.																												
Yabeiella spp.																												
Pterophyllum multilineatum																												
Sphenobaiera tenuifolia																												
Otozamites spp.																												
Sydney Basin	Illawarra Coal Meas.				Narrabeen Gp				H.S.			WG.																
Esk, Ipswich & Moreton Basins													T.G.				Ipswich Coal Measures								Bundamba Gp			
Barreal-Hilario Basin														Barreal Fm.														
Cacheuta-Potreriillos Basin														Las Cabras Formation		Potr. Fm.		Cach. Fm.										
Karoo Basin	Lower				Beaufort Group				Upper-B					Molteno Formation									Red Beds			Cave Sandstone		

the base of a unit of coal and carbonaceous shale and mudstone, which has some of the features of a tidal flat deposit. The coaly unit is underlain by calcareous pebbly sandstone containing the remains of codiacean algae, which suggest the sea was nearby. The coaly unit is overlain by lenticular and irregularly coalescing, 5 to 15 m thick, conglomerate beds. These are imbricated and cross-bedded and fine upwards from subrounded blocky pebbles up to 60 cm long to fine sandstone and siltstone. Five hundred measured pebbles from the base of the conglomerate overlying the coaly unit have a Trask sorting coefficient of 1.76 (compare values of Emery, 1955). All these features suggest that they are stream-flood conglomerates of a braided stream debouching into an estuary. A more detailed treatment of Triassic floras and environments of New Zealand is in preparation for publication elsewhere.

Linguifolietum (coastal-swamp woodland)

This association is dominated by *Linguifolium*, but commonly contains *Cladophlebis*, '*Chiropteris*' (of Arber, 1917) and *Phoenicopsis*.

The Linguifolietum is best known in coal measures associated with Ladinian marine rocks and as fossil plant chaff and flotsam in shallow marine rocks in New Zealand. Several authors (Arber, 1917; Campbell & Warren, 1965; Campbell & Force, 1972) have published accounts of the geology and palaeobotany of Tank Gully near Mt Potts in New Zealand. In the coal measures there, I have observed abundant *Linguifolium* leaves associated with large fossil logs showing seasonal growth rings and roots penetrating up to a metre of sediment. A coaly unit containing the Linguifolietum is conformably overlain by sandstone containing marine shell fragments similar to marine fossil assemblages higher in the sequence. Near Benmore Dam, coaly layers, largely formed of *Linguifolium* leaves, separate 5 to 10 cm carbonaceous mudstone bands containing rolled and twisted remains of

other plants. These coaly layers were probably formed by autumn leaf fall. Steinmann (1921) reached the same conclusion after examining a Linguifolietum from the Bio Bio River in Chile. Thus the Linguifolietum was probably a deciduous coastal forest which replaced the *Taeniopteretum lenticuliformis* during early Ladinian time.

Evolving pteridosperm lineages

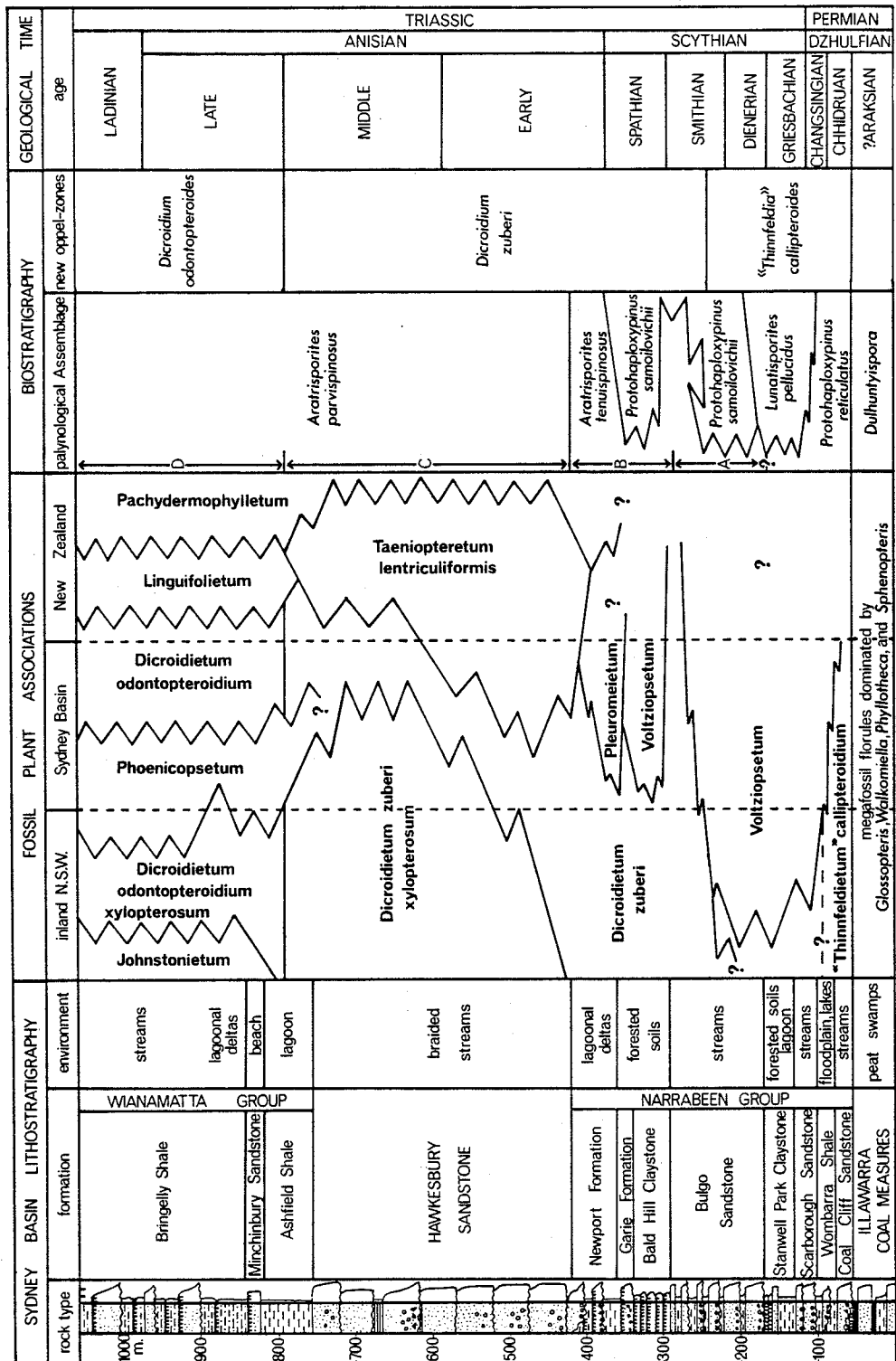
Pteridosperm leaves are the most prominent and distinctive plant fossil remains found in Triassic rocks of Gondwanaland. I have tried to reconstruct an evolutionary lineage from some of these fossils, and this is supported by their reproductive structures, where known. This lineage together with selected taxon ranges may be used to postulate a series of biostratigraphic zones.

Genera of southern pteridosperm leaves

I have found it convenient to consider these fossil leaves in nine generic groupings: '*Supaia*' complex, '*Thinnfeldia*' *callipteroides* complex, *Tetraptilon*, *Lepidopteris*, *Pachydermophyllum*, *Parsophyllum*, *Dicroidium*, *Xylopteris* and *Johnstonia*.

The '*Supaia*' complex includes several types of leaves whose taxonomy is confused. They are most similar to *Dicroidium* because their rachis is forked once, but they differ from *Dicroidium* in their larger size, straighter, more erect and denser secondary venation, transversely undulose pinnae with entire margins and their strongly decurrent or lobed basiscopic pinna margins. *Compsopteris* and *Glenopteris* (see Boureau & Doubinger, 1975) are very similar to leaves of the '*Supaia*' complex but differ from most members of the complex in being unforked. Contrary to Sze (1955), the leaves I here refer to the '*Supaia*' complex (including his material) should remain distinct from *Protoblechnum* until more is known about the type material of *Protoblechnum*. The cuticle of the '*Supaia*' complex, where known, is characterized by haplocheilic stomata (Lele, 1961a). The '*Supaia*' complex is best known from the Permian of Arizona

Fig. 10. Megafossil plant Opperl-zones and associations and palynological Assemblage Zones in eastern Australasian rocks which correlate with the Sydney Basin sequence (left hand three columns). Grain size scale on the rock section divided, from left, into shale, sandstone and conglomerate. The rock section is idealised from descriptions and maximum thicknesses given by Bunny & Herbert (1971), Herbert (in press), McElroy (1969), Loughnan (1963), and Retallack (1973). Palynology after Helby (1973).



in North America (White, 1929; Read & Mamay, 1964). In Gondwanaland these leaves have almost invariably been identified or compared with '*Danaeopsis hughesii* Feistmantel 1882. These are most common in Late Permian or Early Triassic rocks in India (Lele, 1961a) and South Africa (Seward, 1908; Du Toit, 1927) and may have persisted until the Late Triassic in Queensland (Walkom, 1917a).

The '*Thinnfeldia callipteroides* complex (Fig. 6.1-3) is a group of leaves found in latest Permian rocks of Gondwanaland, which have been loosely referred to this species by Carpentier (1935) and Townrow (1966b). They are quite unlike '*Thinnfeldia*' and '*Pachypteris*', which latter now includes '*Thinnfeldia*' (Doludenko, 1971). The multiple-forked rachis of '*Thinnfeldia callipteroides*' is most like the northern Permian genus '*Callipteris*'. Its pinnules may be lobed, long and narrow, or short and semicircular. Its stomata are surrounded by a massive cutin structure which radiates outward between the walls of an even ring of 4 to 6 subsidiary cells (haplocheilic; see Townrow, 1966b; Retallack, in press b). I would also tentatively include within this complex some remains from Parsora, Nidpur and Daigaon localities, South Rewa Basin, India (described by Feistmantel, 1882, as '*Thinnfeldia* comp. *odontopteroides*'; by Lele, 1961a, as '*Dicroidium* sp.', and figs 2B,4, pl. 1, figs 2,5,6 only as '*Dicroidium odontopteroides*'; and by Bose & Srivastava, 1971, as '*Dicroidium gopadensis*'). These fragments have a slender dichotomizing rachis, barely visible secondary venation with a definite midrib and haplocheilic stomata with a massive cutin rim.

Tetraptilon (Fig. 6.4-5) was erected by Frenguelli (1950) for leaves with several (usually three) dichotomies of the rachis and pinnae similar to those of '*Dicroidium odontopteroides*' (Morris) Gothan 1912 (Fig. 6.37-42). Its cuticle is not known. Some authors (Jones & de Jersey, 1947a; Townrow, 1966a) have regarded these as sports of '*Dicroidium*'. However, I have seen two specimens showing three of these leaves laid one over the other on a single slab of rock (UNEF13988 from UNEL1582 near Bryden in Queensland, and UNEF13336 from UNEL1489 in Nymboida Colliery open cut, N.S.W., housed in the Dept. of Geology, Univ. New England). This suggests

that at least one plant was entirely clothed in such leaves. This and the relatively more conservative pinnule shape known in '*Tetraptilon*' compared with the large variety in '*Dicroidium*', induces me to keep these two genera separate. '*Tetraptilon*' has been found in Middle (Flint & Gould, 1975, pl.3, fig. 10) and Late (Frenguelli, 1950) Triassic rocks.

Lepidopteris leaves are characteristically unforked, bipinnate, bipinnatifid, or tripinnatifid, with narrow, elongate pinnules and a conspicuously blistered rachis (Townrow, 1956, 1960). Its stomata are haplocheilic, with the stomatal pit usually overhung by a papilla or cutin lappet on each of the 4 to 6 similarly sized, subsidiary cells. In Gondwanaland, earlier Triassic species had relatively large pinnules (*Lepidopteris indica* Srivastava 1974; '*Callipteridium africanum* Du Toit 1927, pl.27 only), which became narrower (*Lepidopteris madagascariensis*; see Townrow, 1966b) and finally pointed (*L. stormbergensis*; see Townrow, 1960) by Middle Triassic time.

Harris (1964) has submerged '*Pachydermophyllum*' (of Thomas & Bose, 1955) within '*Pachypteris*', but I would prefer it reinstated as a separate genus. '*Pachydermophyllum*' is once pinnate and unforked like '*Pachypteris*'; but it differs from '*Pachypteris*' in having elss basally constricted, broader and, often, more crowded pinnae and pinnules. The cuticle of '*Pachydermophyllum*' is most like that of '*Lepidopteris*' and quite different from that of '*Pachypteris*' (see Boureau & Doubinger, 1975, p.687; Townrow, 1966b). In '*Pachydermophyllum*' the cuticle is amphistomatic and haplocheilic with characteristic papillae or cutin lappets on the subsidiary cells overhanging the stomatal pit. I would include the following Gondwanaland material in '*Pachydermophyllum*': '*Rienitsia*' (of Jones & de Jersey, 1947a, and Douglas, 1969), '*Pachypteris pinnata*' (of Townrow & Jones, 1969), '*Odontopteris dubiae*' (of Burges, 1935, and Townrow, 1957), '*Thinnfeldia praecordillerae*' (of Frenguelli, 1944b), '*Dicroidium* sp.' (of Archangelsky, 1968), '*Danaeopsis gracilis*' (of Lele, 1961b) and the unipinnate fronds only of '*Lepidopteris stormbergensis*' (of Townrow, 1960). These remains range from Early to Late Triassic in age.

Parsorophyllum (of Lele, 1969) is based on a single specimen from Late Permian or Early Triassic rocks of India. Its cuticle and

forking pattern are unknown. Its outline is very similar to a fragment of *Dicroidium zuberi* (Szajnocha) Archangelsky 1968, but the pinnules have a distinct midvein.

The Early to Late Triassic *Dicroidium*-like group includes *Dicroidium* (Fig. 6.6-18, 23-42), *Xylopteris* (Fig. 6.19-22) and *Johnstonia* (Fig. 6.43-47). These are three very similar genera all with a single dichotomy of the rachis. Their amphistomatic cuticles mainly contain stomata with asymmetric lateral subsidiary cells (a type I here term 'pseudosyndetocheilic'), but there may be varying proportions or even a predominance of haplocheilic stomata. Frenguelli (1943) proposed *Xylopteris* for leaves with linear leaf segments. Walkom (1925a) proposed *Johnstonia* for pinnatifid or entire leaves. These two genera appear to have been more xerophytic than coexisting *Dicroidium* leaves. They had a much reduced leaf area, an occasionally marked lignification of the leaf interior and tended to have cuticles with much thicker and straighter cell outlines and sunken stomata overhung by cutin flanges or a continuous cutin flange also covering the guard cell poles (Archangelsky, 1968; Townrow, 1962a). These cuticular features may be found in the '*Thinnfeldia*' *callipteroides* complex and in some Early Triassic *Dicroidium* leaves (see Townrow, 1957; 1966b). In view of the distinctive external morphology of *Xylopteris* and *Johnstonia*, and these other differences, I find it convenient to keep these genera separate from *Dicroidium*. However, I agree with Townrow (1957), Bonetti (1966) and Archangelsky (1968), that Frenguelli's (1943) other genera for *Dicroidium*-like leaves (*Diplasiophyllum*, *Dicroidiopsis* and *Zuberia*) should be resubmerged within *Dicroidium*. Similarly the genus *Hoegia* (of Townrow, 1957) is also a junior synonym of *Dicroidium* (Archangelsky, 1968).

Generic relationships

Plants producing leaves similar to those of the '*Supaia*' and '*Thinnfeldia*' *callipteroides* complexes were widespread on Permian uplands of both northern and southern hemispheres. Larger-leaved members of these complexes, which succeeded *Glossopteris*-dominated floras on the lowlands of Gondwanaland, were probably ancestral to the *Dicroidium*-like group and *Tetraptilon* (Fig. 6). The flora from Parsora in India may be one of these larger-leaved

forerunners of *Dicroidium*-dominated floras. It contains a variety of plants, including the pteridosperms '*Danaeopsis hughesii*' Feistmantel 1882 (abundant), *Parsorophyllum indicum* Lele 1969 and some fragments of larger and broader pinnules, otherwise similar to '*Thinnfeldia*' *callipteroides* Carpentier 1935 (figured by Feistmantel, 1882; Lele, 1961a).

Lepidopteris and *Pachydermophyllum* have very similar cuticles, which could have derived from the massive cutin structure of '*Thinnfeldia*' *callipteroides*. As leaves similar to *Callipteris* and *Lepidopteris* are now known from Late Permian rocks of both the northern and southern hemispheres (see Carpentier, 1935; Townrow, 1960), we can no longer be sure where *Lepidopteris* differentiated. The relationships of Mesozoic leaves referred to *Lepidopteris*, *Pachydermophyllum* and *Pachypteris* are still unclear.

Evolution of the *Dicroidium*-like group

It is worth considering the *Dicroidium*-like group in more detail as a basis for the oppel-zones proposed in the following sections. A taxonomic revision of the genera *Dicroidium*, *Johnstonia* and *Xylopteris* is summarised in the last section of this paper. More details and illustrations may be found on microfiche frames G23-J16.

Overall, the leaves form a reduction series. Early Triassic leaves are mostly large and bipinnate and have thick cuticles containing a greater proportion of haplocheilic stomata (Figs 6,7). Late Triassic leaves are mostly small and unipinnate and have thinner cuticles containing a greater proportion of pseudosyndetocheilic stomata (Figs 6,8). These changes are parallel to those in the likely reproductive structures of these leaves (Figs 7-8). This evolutionary scheme is not supported by the variety of reproductive structures which Indian workers (Pant & Basu, 1973; Bose & Srivastava, 1973a, 1973b; Srivastava, 1974, 1975) have recently attributed to *Dicroidium* leaves from the Late Permian or Early Triassic Nidpur plant locality. Contrary to these workers, I believe that the cuticles of these fructifications and their various other features, indicate a closer relation to remains of *Lepidopteris*, *Rhabdotaenia*, *Glossopteris*, and *Glottolepis* also found at Nidpur (Srivastava, 1969, 1971; Bose & Srivastava, 1969). Similarly, the

fructifications '*Umkomasia cacheutensis* Frenguelli (1942c) and *Karibacarbon* and *Sengwacarbon* of Lacey (1976) are unrelated to *Dicroidium*. They most likely belong to *Peltaspermum*, the supposed megasporophyll of *Lepidopteris* (Townrow, 1960).

The oldest *Dicroidium* leaves had elongate pinnules and mainly haplocheilic stomata (*Dicroidium brownii* (Seward) comb. nov.). These are best known from the Late Permian or Early Triassic Nidpur plant locality in the South Rewa Basin, India (Bose & Srivastava, 1971), where they are associated with *Glossopteris* (Srivastava, 1969, 1971), *Lepidopteris* (Srivastava, 1974) and some likely examples of the '*Thinnfeldia*' *callipteroides* complex ('*Dicroidium gopadensis*' of Bose & Srivastava, 1971). *Dicroidium brownii* also persisted into younger assemblages (Fig. 6. 8-10).

A slight shortening in the length of the pinnules gave rise to *Dicroidium zuberi* (Szajnocha) Archangelsky 1968 (Fig. 7) which dominates Smithian to Middle Anisian broadleaf associations. These are known from the Newport Formation of the Narrabeen Group in the Sydney Basin (Walkom, 1925b; Jacob & Jacob, 1950; Retallack, 1973) and the Chicharia locality, South Rewa Basin, India (Seward, 1933; Lele, 1961a). At this level a limited diversity of pinnatifid (*Dicroidium dubium* var. *australe* (Jacob & Jacob) comb. nov.; Fig. 6.25-26) and unipinnate (*D. narrabeenense* (Dun in Walkom) Jacob & Jacob 1950, Fig. 6.27-29, and *D. lancifolium* (Morris) Gothan 1912, Fig. 6. 30-31) leaves had also differentiated.

The *Dicroidium zuberi* xylopterium of the Brookvale shale lens of the Hawkesbury Sandstone in the Sydney Basin (microfiche frame G10) includes the oldest specimens of *Xylopteris* known in Gondwanaland. Judging from the more abundant bipinnate leaves in this association and the evidence of cuticles, it is perhaps a little more likely that *Xylopteris* developed from the very similar *Dicroidium townrovii* sp. nov. (Fig. 6.17-18), than from the unipinnate *D. lancifolium* var. *lineatum* (Tenison-Woods) comb. nov. However, one should not overlook the possibility of a polyphyletic origin of *Xylopteris* at various times and places of drier conditions, from both these species, as well as from *Dicroidium natalense* (Frenguelli) comb. nov., *D.*

superbum (Shirley) Townrow 1957 and *D. gouldii* sp. nov.

By Middle Triassic time *Dicroidium* reached its greatest diversity of species and unipinnate leaves came to dominate broadleaf associations. The products of this evolutionary radiation are best known from the Nymboida Coal Measures of New South Wales (microfiche frames G11-G13) and from Little Switzerland and Upper Umkomaas localities in the Molteno Formation of South Africa (Anderson & Anderson, 1970; Anderson, 1974). Three groups are recognisable in these unipinnate leaves. The '*eskense*' species group have constricted pinna bases and clearly marked secondary venation at a very acute angle to the pinna midrib. These include *Dicroidium eskense* (Walkom) Jacob & Jacob 1950 (Fig. 6.32), *D. gouldii* sp. nov. (Fig. 6.36), *D. incisum* (Frenguelli) Anderson & Anderson 1970 (Fig. 6.34), *D. prolongatum* (Menendez) comb. nov. (Fig. 6.35) and *D. radiatum* sp. nov. (Fig. 6.33). A second group includes the varieties of *D. odontopteroides*, which all have relatively equant pinnae (fig. 6. 37-42). Lastly, the species of *Johnstonia* form a pinnatifid to entire group (Fig. 6.43-47).

Several species of *Dicroidium* became extinct at different times during the Carnian and Norian, very few species survived into the Rhaetian, and none into the Jurassic. The supposed Rhaeto-Liassic floras of Townrow (1964, 1966a) are more likely Anisian to Norian (Anderson & Anderson, 1970; de Jersey, 1975). The only reliably dated *Dicroidium*-bearing rocks of Rhaetian age are the Aberdare Conglomerate and Raceview Formation of the Bundamba Group in Queensland (Jones & de Jersey, 1947a; de Jersey, 1975; Day, Cranfield, & Schwarzböck, 1974) and at Paso Flores and Malacara in Argentina (Frenguelli, 1948). These contain *Dicroidium odontopteroides* (Morris) Gothan 1912, *D. lancifolium* (Morris) Gothan 1912, *Xylopteris argentina* (Kurtz) Frenguelli 1943 and *X. elongata* (Carruthers) Frenguelli 1943. A Liassic record of *Dicroidium lancifolium* (Frenguelli, 1937) is based on an indeterminate apical fragment. Townrow (1957) also believed that this species was figured by Arber (1917, pl. 5, fig. 2) from Middle Jurassic rocks at Owaka Creek in New Zealand (Speden, 1958). In this specimen, which I have examined, the

supposed 'dichotomy' of the rachis is sympodial and formed by the accidental juxtaposition of two robust pinnae of *Cladophlebis*. Several records of Australian Jurassic pteridosperm leaves (Walkom, 1921; Jones & de Jersey, 1947b; Jones, 1948), which could be confused for *Dicroidium*, are best referred temporarily to '*Thinnfeldia*' *talbragarensis* Walkom 1921. These have much broader, and commonly coalescing pinnules, compared with the Langlosh material Townrow (1965) referred to '*Pachypteris crassa*' and with the doubtfully identical type material of that species ('*Scleropteris crassa*' of Halle, 1913). The cuticle of '*Thinnfeldia*' *talbragarensis* is not yet known, but my own extensive collection of the type locality, the overall frond shape and abscission scars (Australian Museum specimen F2664), confirm that the frond was unforked, unlike *Dicroidium*.

Oppel-zones of megafossil plants for Gondwanaland

In the following sections I have characterised four Oppel-zones for the pteridosperm-dominated Triassic floras of Gondwanaland. These succeeded *Glossopteris*-dominated floras during Late Permian time, and were followed by *Otozamites*-dominated floras in the Early Jurassic (see Gould, 1976; Herbst, 1968). The stratigraphic distribution of these Oppel-zones is detailed on microfiche frames G19-G22.

The boundaries of the zones are theoretically delineated by five events which affected mesophytic communities of the coastal plain: the migration of the '*Thinnfeldia*' *callipteroides* complex into Gondwanaland, the differentiation of *Dicroidium zuberi* and then of *D. odontopteroides*, the appearance of *Yabeiella*, and the extinction of *Dicroidium*. By themselves, these taxa are insufficient to characterise the intervening zones. They may persist into zones younger than the one they characterise, and they did not grow or become preserved everywhere when they lived. Thus the zones are more confidently identified by also using associated taxa. The ranges of all these taxa are interpreted within the limits of resolution of the zones in Fig. 9.

In concept, these zones are most similar to 'Oppel-zones' as defined by Hedberg (1971). Although commonplace in marine

biostratigraphy, this method has not previously been used for correlating megafossil plant associations. Most authors, for example Read & Mamay (1964), Douglas (1969) and Gould (1976), have distinguished successive 'floras' in any way possible, regardless of the palaeoecology or taxonomic relationships of the 'index fossils'. Some, such as Jones & de Jersey (1947a) and Menendez (1951), have correlated megafossil floras by the percentage of shared species. Others, such as Banks (1968), have postulated lineages, without formalising them into zones. The proposals of Krassilov (1974) are theoretically similar to mine, although quite different in their formal structure.

I have heeded the warning of Stipanovic & Bonetti (1969), that determining the age of sedimentary formations from the evolution of vertebrate fossils may be misleading. The palaeoecology and genotypic variation of tetrapod and fish populations was probably much more complex than that of plant and marine life. The ages of the zones proposed here have been determined mainly from associated marine fossils, mainly ammonoids (Furnish, 1973; Tozer, 1971) rather than brachiopods (Waterhouse, 1976), and from the extrapolation of isotopic dates from extrusive rocks. Nevertheless, these new zones overcome previous conflicts between palaeobotanists and vertebrate palaeontologists, outlined by Sill (1967).

'*Thinnfeldia*' *callipteroides* Oppel-zone (Chhidruan to Smithian, 250-230 x 10⁶ years)

Recognition. The most characteristic fossil floras of this zone are dominated by '*Thinnfeldia*' *callipteroides* Carpentier 1935. Common within the zone and also found in younger zones, are *Voltziopsis* spp., '*Danaeopsis*' *hughesii* Feistmantel 1882 and *Dicroidium brownii* (Seward) comb. nov., which also distinguish this zone from underlying floras dominated by *Glossopteris*.

The reference collections of the 'Thinnfeldietum' *callipteroidium* and *Voltziopsetum* (on microfiche frames G4-G5) are good examples of the zone. However, the *Voltziopsetum* does not always contain enough diagnostic taxa to distinguish this from the succeeding Oppel-zone.

For the moment, the broader-leaved fossil floras of the Nidpur and Parsora localities, South Rewa Basin, India, are included in the upper part of this zone. These contain some likely members of the 'Thinnfeldia' *callipteroides* complex, with 'Danaeopsis' *hughesii*, *Dicroidium brownii*, *Parsorophyllum indicum* and *Lepidopteris indica*, as discussed in previous sections. This fossil plant association could be termed a 'Danaeopsetum' *hughesii*, and may prove characteristic of an additional oppel-zone if ever found in clear stratigraphic succession with fossil floras of the other oppel-zones.

Geological setting. Megafossil floras of the zone are commonly found in sandy and silty river deposits overlying either crystalline basement or *Glossopteris*-bearing coal measures.

Marine biostratigraphic age. In Madagascar, megafossil floras of this zone occur at a stratigraphic horizon between Chhidruan and Late Griesbachian to lower Dienerian ammonoid faunas (Embleton & McElhinny, 1975; Anderson & Amderson, 1970; Tozer, 1971; Furnish, 1973). However, Waterhouse (1976) believes this lower fauna could be as old as the Amarassian of Furnish (1973). In the Sydney Basin, megafossil floras of this zone overlie Late Permian coal measures, containing abundant *Glossopteris* leaves, which in turn overlie rocks with marine fossils whose precise international correlation is uncertain (Clarke & Banks, 1975; Runnegar & McClung, 1975). These floras of the zone underlie sediments containing a palynological assemblage which may be correlated with that of Lower Griesbachian marine rocks (Balme, 1969). Some distinctive elements of the palynological assemblage found with megafossil floras of this zone have also been found in Chhidruan marine rocks of the Salt Range, West Pakistan (Balme & Helby, 1973).

Radiometric age. This zone spans the Permian-Triassic boundary, which Green & Webb (1974) accept as 240 x 10⁶ years ago. In the Sydney Basin, megafossil floras of the zone are certainly much younger than the Gerringong Volcanics, which have yielded isotopic dates of 246-260 x 10⁶ years (Raam, 1969; Runnegar, Roberts & Kleeman, pers. comm.). These floras lived through a cycle of low base level when a great number of

isotopically dated granitic intrusions were emplaced in eastern Australia (see Veevers & Evans, 1975, fig. 40.18).

Dicroidium zuberi Oppel-zone (Smithian to Middle Anisian, 230-220 x 10⁶ years)

Recognition. Fossil floras of this zone are distinguished from those of older zones by their abundant leaves of *Dicroidium zuberi* (Szajnoch) Archangelsky 1968, and its likely reproductive structures: 'Pterorrachis' *barrealensis* Frenguelli 1942b and a large cupulate organ similar to *Umkomasia* (of Thomas 1933; see Fig. 7). These leaves range into the Norian (Fig. 9; Azcárate & Fasola, 1970; Archangelsky, 1968), but the reproductive structures are not yet known from rocks demonstrably older or younger than this zone. *Dicroidium dubium* var. *australe* (Jacob & Jacob) comb. nov., *Pleuromeia* spp. and its supposed cones *Cylostrobos* spp. are apparently restricted to this zone. *Dicroidium narrabeenense* (Dun in Walkom) Jacob & Jacob 1950 is more abundant in this than the succeeding zone. The presence of *Voltziopsis* spp., distinguishes this from younger zones and the following distinguish it from older zones: *Xylopteris* spp., *Pachydermophyllum* spp., *Dicroidium lancifolium* (Morris) Gothan 1912 and *Taeniopteris lentriculiformis* (Etheridge) Walkom 1917a.

The reference collection of the *Dicroidietum zuberi* (microfiche frames G6-G7) is a typical fossil flora, probably of the central part, of this zone. Its polymorphic, large, coriaceous *Dicroidium* leaves and low species diversity, compared to younger *Dicroidium*-dominated floras, are characteristic. The zone can be less confidently identified in the *Dicroidietum zuberi* xylopterium and apparently also includes the *Taeniopterium lentriculiformis* and *Pleuromeietum*.

Geological setting. Megafossil floras of this zone are commonly found in silty, sandy and conglomeratic river deposits, occasionally with conspicuous redbed interpolations.

Marine biostratigraphic age. The *Pleuromeietum* occurs in the middle of the sedimentary sequence containing broadleaf floras of this zone in the Sydney Basin. This fossil association includes Smithian to

Anisian marine faunas in the U.S.S.R. and Japan (Retallack, 1975). The *Taeniopterum lentriculiformis*, found in the upper part of the sequence containing floras of the zone in the eastern Sydney Basin, is prominent in later Malakhovian to Etalian (Anisian) shallow marine rocks of New Zealand (Retallack, in press b). In the Sydney Basin, floras of the zone appear after a period of high base level, which may be correlated with the eastern Australian, and possibly global, transgression during Smithian time postulated by McTavish & Dickins (1974).

Radiometric age. I know of no volcanic flows interbedded with floras of this zone. So the zone may correlate with an isotopically-dated lull in the igneous activity of eastern Australia (Veevers & Evans, 1975, fig. 40.18).

Dicroidium odontopteroides Oppel-zone (Late Anisian to Ladinian, 220-210 x 10⁶ years)

Recognition. Fossil floras of this zone are distinguished from those of older zones by containing *Dicroidium odontopteroides* (Morris) Gothan 1912 and its likely reproductive structures: *Pteruchus johnstonii* (Feistmantel) Townrow 1962c and *Pilophorosperma* spp. (of Thomas, 1933; see Fig. 8). All these probably ranged through the succeeding Oppel-zone to the end of the Triassic (Jones & de Jersey, 1947a, p.71). Other taxa useful for recognising this zone are *Dicroidium eskense* (Walkom) Jacob & Jacob 1950, and *D. odontopteroides* var. *remotum* (Szajnocha) Retallack (in Retallack, Gould & Runnegar, 1977). *Johnstonia* and *Linguifolium* are restricted to this and the succeeding Oppel-zone. Several little-known species appear to be regionally diagnostic of this zone (see Retallack, Gould & Runnegar, 1977).

This zone is easiest to recognize within the *Dicroidietum odontopteroidium*, such as is found in Nymboida Colliery open cut, northeastern New South Wales (on microfiche frames G11-G13). Here a great diversity of associated taxa dispel confusion with older or younger zones, which may arise from the occasional abundance of *Dicroidium zuberi* within this zone, and the possibility that the diagnostic taxa of the

Yabeiella oppel-zone had a restricted geographic distribution. The *Phoenicopsetum* and *Diicroidietum odontopteroidium xylopterisum* usually contain enough associated taxa to identify the zone. However, it is not certain how many, if any, of these and the diagnostic taxa of the succeeding *Yabeiella* Oppel-zone, ever lived within the coeval *Johnstonietum*, *Linguifolietum* and *Pachydermophylletum*.

Geological setting. Megafossil plants of this zone are commonly found in river sediments, often with a prominent calcareous matrix and with interbedded extrusive volcanics.

Marine biostratigraphic age. A *Dicroidietum odontopteroidium* of this zone has been found in coal measures conformably underlying Kaihikuan (Ladinian) marine rocks in Tank Gully near Mt Potts in New Zealand (Retallack, in press b).

Radiometric age. A basalt flow, stratigraphically sandwiched between two floras of the zone near Nymboida in New South Wales, has yielded a K-Ar isotopic age of 211 x 10⁶ years (Retallack *et al.*, 1977). I have visited the 'Jimmy Jimmy flow', which Dulhunty (1976) has had dated at 216 x 10⁶ years. It is an intrusion which has uparched the underlying Permian coal measures in the same way as the nearby 'Barigan laccolites' described by Carne (1903). Florules of this zone in the New Zealand Geological Survey collections (NZGSB820, B823, B825; see Townrow, 1967a) from the upper Fremouw and lower Falla Formations of the Beardmore Glacier area, Antarctica, underlie by some distance a tuff, dated at 203 x 10⁶ years (Barrett, 1972). In Argentina, floras of the zone are considerably younger than volcanics dated at 225 x 10⁶ years (Stipanovic, 1969). In the Italian Alps, K-Ar ages of 220 x 10⁶ years have been gained from Aniso-Ladinian flows, and of 215 x 10⁶ years from Ladinian intrusions (Ferrara & Innoncenti, 1974).

Yabeiella Oppel-zone (Carnian to Rhaetian, 210-200 x 10⁶ years)

Recognition. *Yabeiella* leaves, and their likely fructification *Fraxinopsis*, are relatively constant and faithful to fossil floras of this zone, but are not usually abundant (see Anderson, 1974, table 3).

Other taxa useful for identifying the zone are *Sphenobaiera tenuifolia* (Johnston) Jain & Delevoryas 1967 and *Pterophyllum multilineatum* Shirley 1897. Several taxa surviving from older zones may be abundant in fossil floras of this zone: *Xylopteris* spp., *Linguifolium* spp., *Pachydermophyllum* spp., *Johnstonia* spp., *Dicroidium odontopteroides* (Morris) Gothan 1912 and *D. zuberi* (Szajnocha) Archangelsky 1968.

The *Yabeiella* Opperl-zone is most easily distinguished from the preceding Opperl-zone within the *Dicroidietum odontopteroidium*, *Phoenicopsetum* and *Dicroidietum odontopteroidium xylopterisum* associations. The best single collection of this last type known to me, is that collected by Wieland from Minas de Petroleo in the Potrerillos Formation of the Cacheuta Group in Argentina and described by Jain & Delevoryas (1967). I do not know of any examples of the *Johnstonietum*, *Linguifolietum* or *Pachydermophylletum* which could be assigned to this zone on their floral composition alone. However, marine fossils associated with the *Pachydermophylletum* in the Jurassic of Yorkshire (see Harris, 1966) and with the *Linguifolietum* in the Murihuku Supergroup of New Zealand (New Zealand Geological Survey collection B131), suggest that at least these two coastal assemblages persisted within this zone.

Geological setting. Sedimentary rocks containing megafossil floras of this zone are generally finer grained, less conglomeratic, and lack the calcareous matrix of older alluvial sequences in the same areas. The youngest of these, where not eroded away, include thick redbeds.

Marine biostratigraphic age. *Yabeiella marayesiaca* (Geinitz) Oishi 1931 has been recorded from the largely marine Norian sequence of coastal Chile (Villegas, 1937a, 1937b; Cecioni & Westermann, 1968; Azcárate & Fasola, 1970). However this is impossible to assess from the poor published figures of the specimens. Solms-Laubach (1899) also identified *Y. marayesiaca* from La Ternera in Chile, in coal measures which apparently underlie, by some distance, Liassic marine rocks (Steinmann, 1899). Floras of this zone in Argentina (Frenguelli, 1948; Jain & Delevoryas, 1967), also underlie Liassic rocks containing Sinemurian marine faunas (Stipanovic, 1969).

Radiometric age. I have here followed Green & Webb (1974), who placed the Triassic-Jurassic boundary at 200×10^6 years ago.

Synthesis: Opperl-zones and associations in time and space

Fig. 10 shows the relationships between the stratigraphy of the Sydney Basin and the associations and Opperl-zones defined here. Each fossil plant association has a four dimensional shape in space and time. Its age is best assessed by dating the formation in which it occurs by means of the Opperl-zones (Fig. 9) or by other methods.

In eastern Australasia during Late Permian to Middle Triassic time, the Sydney Basin was a coastal plain area, inland New South Wales was an inland area, and New Zealand was a coastal to shallow marine area. The distribution of the plant associations over this landscape was probably more complex than I have shown. However by attempting to reconstruct this distribution, even plant associations which are poorly dated, offer some constraints for the dating of sedimentary formations. This distribution gives a better idea of facies control and evolution in palynological assemblages. Finally and foremost, it also gives a clearer phytogeographical picture of ancient vegetation.

Systematic palaeobotany

This is a checklist of the new and accepted species and varieties of the pteridosperm form-genera *Dicroidium*, *Johnstonia* and *Xylopteris*, including their type specimens, a brief diagnosis, and their stratigraphic range. A more detailed treatment, including illustrations, synonymies, discussion, and a taxonomic key is given on microfiche frames G23-J16.

1. *Dicroidium brownii* (Seward) comb. nov.; for '*Odontopteris browni*' of Seward (1908, pl.7). Bipinnate and tripinnatifid fronds; pinnules more than twice as long as wide; commonly with some rachis pinnules and some more equidimensional pinnules (as those of *D. zuberi*) in places. (? latest Permian) Scythian to Ladinian.

2. *D. brownii* var. *barrealense* (Frenguelli) comb. nov.; for '*Zuberia barrealensis*' of Frenguelli (1944a, pl.13). Some pinnule margins lobed. Smithian to Ladinian.

3. *D. brownii* var. *brownii* (Seward) comb. nov. Pinnule margins entire. (? latest Permian) Scythian to Middle Anisian.
4. *D. dubium* (Feistmantel) Gothan 1912; for '*Gleichenites dubius*' of Feistmantel (1878, pl.15, fig.8). Bipinnatifid fronds; pinna bases unstricted; secondary venation, often obscure, curving to an angle of about 45° to the pinna margin. Smithian to Norian.
5. *D. dubium* var. *australe* (Jacob & Jacob) comb. nov.; for '*Dicroidium australis*' of Jacob & Jacob (1950, figs 20-24). Medium to large, irregularly bipinnatifid fronds; secondary venation relatively obscure and dense; thick coriaceous lamina. Smithian to Ladinian.
6. *D. dubium* var. *dubium* (Feistmantel) Gothan 1912. Small to medium fronds; pinna lobes inclined towards the pinna apex; secondary venation obscure, sparse; leaf substance thick. Late Anisian to Norian.
7. *D. dubium* var. *tasmaniense* (Anderson & Anderson) Retallack (in Retallack, *et al.*, 1977); for '*Dicroidium tasmaniensis*' of Anderson & Anderson (1970, chart 9). Small to medium fronds; pinnae broad and short, with rounded apices; pinna lobes rounded, more or less symmetrical and erect. Late Anisian to Norian.
8. *D. eskense* (Walkom) Jacob & Jacob 1950; for '*Thinnfeldia eskensis*' of Walkom (1928, pl.28, fig.1). Medium to large unipinnate fronds; pinna base characteristically constricted, often with a deep narrow sinus in the basal acroscopic margin; secondary venation clearly visible and at a very acute angle to the pinna midrib and margins; pinna apex acute. Late Anisian to Ladinian.
9. *D. gouldii* sp. nov.; for '*Dicroidiopsis* sp.' of Gould & Retallack (in Bourke *et al.*, 1977, fig. 3.12). Bipinnate fronds; pinnules and pinnae oblanceolate with rounded apices; secondary venation clearly visible and at a very acute angle to the pinna midrib; pinnules in the apical half of the pinna usually coalescing. Late Anisian to Norian.
10. *D. incisum* (Frenguelli) Anderson & Anderson 1970; for '*Pachypteris incisa*' of Du Toit (1927, fig. 8A). Bipinnatifid fronds; pinna bases constricted; pinna apices acute; pinna lobes inclined towards the pinna apex; secondary venation clearly visible and at a very acute angle to the pinna midrib. Late Anisian to Norian.
11. *D. lancifolium* (Morris) Gothan 1912; for '*Pecopteris odontopteroides* var. *lancifolia*' of Morris (1845, pl.6, fig.4). Small to medium, unipinnate fronds; pinnae with unstricted bases, more than three times longer than wide, usually less than 1 cm wide or 5 cm long. Smithian to Rhaetian.
12. *D. lancifolium* var. *lancifolium* (Morris) Gothan 1912. Pinnae relatively even in width, with rounded apices. Smithian to Rhaetian.
13. *D. lancifolium* var. *lineatum* (Tenison-Woods) comb. nov.; for '*Gleichenia lineata*' of Tenison-Woods (1883, pl.3, fig. 6). Pinnae elongate, narrow, tapering to an acute apex, touching at their base but well spaced for most of their length. Anisian to Norian.
14. *D. narrabeenense* (Dun in Walkom) Jacob & Jacob 1950; for '*Thinnfeldia narrabeenensis*' of Walkom (1925b, pl. 28, fig.4). Large unipinnate fronds; pinnae longer than 5 cm or wider than 1 cm; pinna bases unstricted; thick coriaceous lamina. Smithian to Ladinian.
15. *D. narrabeenense* var. *bursellii* (Lacey) comb. nov.; for '*Dicroidium bursellii*' of Lacey (1976, fig.1). Pinnae elongate, narrow, tapering to an acute apex, almost touching at their base but well-spaced for most of their length. Smithian to Middle Anisian.
16. *D. narrabeenense* var. *narrabeenense* (Dun in Walkom) Jacob & Jacob 1950. Pinnae broad, often closely spaced or overlapping; pinna apices obtuse or bluntly pointed. Smithian to Ladinian.
17. *D. natalense* (Frenguelli) comb. nov.; for '*Stenopteris elongata*' of Du Toit (1927, fig. 12E). Bipinnatifid fronds; pinnae and pinnules with narrower and more elongate apical portions. Late Anisian to Norian.
18. *D. odontopteroides* (Morris) Gothan 1912; for '*Pecopteris odontopteroides*' of Morris (1845, pl.6, fig.3). Small to medium unipinnate fronds; pinnae more or less equidimensional, no longer than three times their length. Late Anisian to Rhaetian.
19. *D. odontopteroides* var. *argenteum* var. nov.; for New Zealand Geological Survey specimen B1095.1 (Fig. 6.37). Pinnae erect, subcircular or subrhombic, basally constricted. Ladinian to Norian.
20. *D. odontopteroides* var. *crassum* (Menendez) comb. nov.; for '*Dicroidiopsis crassa*' of Menendez (1951, pl. 14, fig. 3).

- Pinnae subrhombic, narrow, basally constricted, at an acute angle to the rachis. Late Anisian to Norian.
21. *D. odontopteroides* var. *moltenense* var. nov.; for '*Thinnfeldia odontopteroides*' of Feistmantel (1890, pl. 26, figs 2, 2a). Pinnae subtriangular, semicircular or subrhombic, with unrestricted bases. Late Anisian to Rhaetian.
22. *D. odontopteroides* var. *obtusifolium* Johnston 1886; for '*Dicroidium obtusifolium*' of Townrow (1966a, pl. 1, fig. 2). Pinnae rounded, coalescing at the base, broader than long by at least one fifth; leaf substance thick and coriaceous so that secondary venation is barely visible. Late Anisian to Norian.
23. *D. odontopteroides* var. *odontopteroides* (Morris) Gothan 1912. Pinnae two to three times as long as wide, sometimes with an impersistent midrib in the basal third of their length. Late Anisian to Norian.
24. *D. odontopteroides* var. *remotum* (Szajnocha) Retallack (in Retallack, et al., 1977); for '*Neuropteris remota*' of Szajnocha (1888, pl. 2, fig. 3a). Basal pinnae subcircular to subtriangular, with constricted bases; outward facing pinnae about twice as long as wide, with rounded apices, and closely spaced to overlapping near the apex of the frond; inward facing pinnae elongate and at a very acute angle to the rachis. Late Anisian to Ladinian.
25. *Dicroidium pinnis-distantibus* (Kurtz) Frenguelli 1943; for '*Thinnfeldia lancifolia* var. *pinnisdistantibus*' of Kurtz (1921, pl. 20, fig. 283). Unipinnate fronds; pinnae long, narrow, distantly spaced so that adjacent pinna margins are separated by more than one pinna width along the rachis. Smithian to Norian.
26. *D. prolungatum* (Menendez) comb. nov.; for '*Dicroidiopsis crassa* var. *prolungata*' of Menendez (1951, pl. 14, fig. 5). Unipinnate fronds; pinnae elongate, lanceolate, with constricted or subpetiolate bases; secondary venation clearly visible and at an acute angle to a weak or impersistent pinna midrib. Late Anisian to Norian.
27. *D. radiatum* sp. nov.; for '*Dicroidium incisa*' of Anderson & Anderson (1970, chart 9, N-U.U.1). Bipinnatifid fronds; pinnae irregularly lacinate, flaring apically. Late Anisian to Ladinian.
28. *D. superbum* (Shirley) Townrow 1957; for '*Sphenopteris superba*' of Shirley (1898, pl. 8). Tripinnatifid fronds; pinnules more or less equidimensional, partly split into two or three lobes, each supplied with an equal number of clearly visible and well-spaced secondary veins. Late Anisian to Norian.
29. *D. townrovii* sp. nov.; for '*Dicroidium superbum*' of Townrow (1957, figs 7E-G, 8A, 10A-B). Bipinnate fronds; pinnae taper to an elongate narrow apex; pinnules multiveined, narrower than 5 mm, with a subacute apex. Smithian to Ladinian.
30. *D. zuberi* (Szajnocha) Archangelsky 1968; for '*Cardiopteris zuberi*' of Szajnocha (1888, pl. 2, fig. 1). Bipinnate fronds; pinnules more or less equidimensional and entire. Smithian to Norian.
31. *D. zuberi* var. *feistmantelii* (Johnston) comb. nov.; for '*Thinnfeldia odontopteroides*' of Feistmantel (1879, pl. 9 (27), figs 2, 2a). Pinnules subtriangular, very slightly longer than wide, their midline at an angle of about 45° to the pinna rachis, with a subacute apex. Smithian to Ladinian.
32. *D. zuberi* var. *papillatum* (Townrow) comb. nov.; for '*Thinnfeldia odontopteroides*' of Feistmantel (1879, pl. 11 (29), figs 1, 1a, 1b). Pinnules rhomboidal, weakly lobed, split or frayed around the margins, generally large and a little broader than long; leaf substance thin and/or secondary venation clearly visible; rachis pinnules sometimes more markedly lobed than other pinnules. Smithian to Ladinian.
33. *D. zuberi* var. *sahnii* (Seward) comb. nov.; for '*Thinnfeldia sahnii*' of Seward (1933, pl. 8). Pinnules rounded, erect on the pinna rachis, sometimes coalescing in the apical third of the pinna. Smithian to Ladinian.
34. *D. zuberi* var. *zuberi* (Szajnocha) Archangelsky 1968. Pinnules subrhombic, with parallel lateral margins and apical margin parallel to the pinna rachis. Smithian to Norian.
35. *Johnstonia coriacea* (Johnston) Walkom 1925a; for '*Rhacophyllum coriaceum*' of Johnston (1888, pl. 26, fig. 9). Entire or slightly wavy leaf margin; secondary venation at a very acute angle to the rachis and leaf margin. Late Anisian to Norian.
36. *J. coriacea* var. *coriacea* (Johnston) Walkom 1925a. Leaf blade no wider than 8 mm. Late Anisian to Norian.
37. *J. coriacea* var. *obesa* var. nov.; for '*Dicroidium dutoitii*' of Townrow (1967a,

- fig. 3E). Leaf blade no narrower than 8 mm; rachis below fork often longer than that above the fork. Late Anisian to Ladinian.
38. *J. dutoitii* (Townrow) comb. nov.; for '*Johnstonia coriacea*' of Du Toit (1927, fig. 12D). Pinnatifid fronds; lobes broad, rounded, more or less symmetrical; secondary veins meeting the margin at about a 45° angle. Late Anisian to Norian.
39. *J. stelzneriana* (Geinitz) Frenguelli 1943; for '*Pachypteris Stelzneriana*' of Geinitz (1876, pl.2, fig.7). Pinnatifid fronds; lobes elongate, narrow, entire, and at a very acute angle to the rachis; secondary veins arising from the rachis well below the lobe in which they end. Late Anisian to Norian.
40. *J. stelzneriana* var. *serrata* var. nov.; for '*Johnstonia coriacea*' of Jones & de Jersey (1947a, fig.11). Lobes low, asymmetric steps, with very shallowly incised apical margins. Late Anisian to Norian.
41. *J. stelzneriana* var. *stelzneriana* (Geinitz) Frenguelli 1943. Lobes well incised, elongate, narrow, at an acute angle to the rachis. Late Anisian to Norian.
42. *J. trilobita* (Johnston) Walkom 1925a; for '*Thinnfeldia trilobita*' of Johnston (1887, pl.14, fig.6). Pinnatifid fronds; each lobe in turn bilobate or trilobate. (?) Late Anisian to Norian.
43. *Xylopteris argentina* (Kurtz) Frenguelli 1943; for '*Sphenopteris elongata* var. *argentina*' of Kurtz (1921, pl.16, fig.200). Unipinnate fronds; less than four distantly spaced pinnae on each side of the rachis. Late Anisian to Rhaetian.
44. *X. elongata* (Carruthers) Frenguelli 1943; for '*Sphenopteris elongata*' of Carruthers (1872, pl.27, fig.1). Unipinnate fronds; more than four pinnae on each side of the rachis. Anisian to (?) Rhaetian.
45. *X. elongata* var. *elongata* (Carruthers) Frenguelli 1943. Pinnae numerous, closely spaced, separated laterally by less than four pinna widths. Late Anisian to Norian.
46. *X. elongata* var. *rigida* (Dun) Stipanovic & Bonetti (in Stipanovic, 1957); for '*Stenopteris rigida*' of Dun (1909, pl. 50, fig.1). Pinnae fewer, well spaced, laterally separated by more than four pinna widths. Anisian to (?) Rhaetian.
47. *X. spinifolia* (Tenison-Woods) Frenguelli 1943; for '*Trichomanides spinifolium*' of Tenison-Woods (1883, pl.3, fig.7). Bipinnate to bipinnatifid fronds; one or more univeined pinnules per pinna. Late Anisian to Norian.
48. *X. tripinnata* (Jones & de Jersey) Schopf 1973; for '*Stenopteris elongata*' of Walkom (1917a, pl.6, fig.1 only). Tripinnate and tripinnatifid fronds; pinnules pinnate or trilobate; ultimate segments more or less linear and univeined. Anisian to Norian.

Acknowledgments

This paper has been greatly improved by constructive discussions with many people. I especially thank Mr W. B. K. Holmes, Drs R. E. Gould, N. J. de Jersey, E. T. Tozer and R. J. Helby, and Assoc. Profs B. Runnegar and S. R. Ash. I am also grateful to those who allowed access to fossil collections of various institutions; Mr G. Z. Foldvary (Sydney Univ., Dept. of Geology and Geophysics), Dr J. Pickett (Mining Museum, Geological Survey of N.S.W.), Dr A. Ritchie and Mrs M. E. White (Australian Museum), Assoc. Prof. J. D. Campbell (Otago Univ., Geology Dept.), Mr D. C. Mildenhall and Dr C. A. Fleming (New Zealand Geological Survey, Lower Hutt) and Drs R. A. Kyle and P. J. Barrett (Victoria Univ. Wellington, Geology Dept.). My own reference collections (now housed in the Geology Dept., Univ. New England) have been supplemented with specimens collected by Mr J. C. E. Flint, Mr H. R. Butler and Dr R. E. Gould. The work was supported by a Commonwealth Post-graduate Award and the resources of the Geology Department, University of New England. Finally, I am indebted to Mrs R. K. Vivian, who typed several drafts of this manuscript and the final sheets for microfiche reproduction.

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