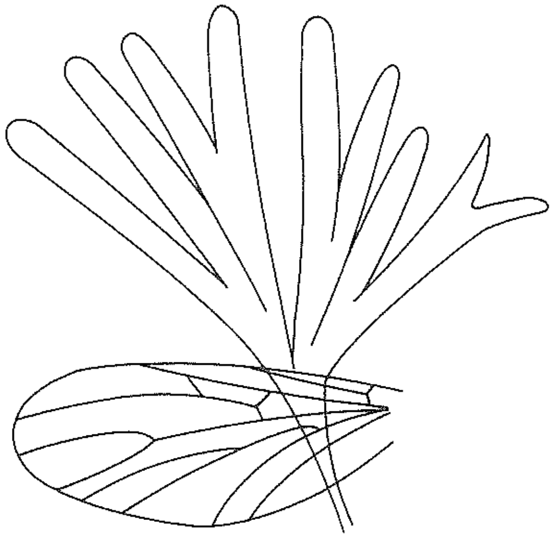
Plants and invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria



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Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria

ANDREW N. DRINNAN AND T. CARRICK CHAMBERS

DRINNAN, A.N., & CHAMBERS, T.C., 1986: 7:10. Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Mem. Ass. Australas, Palaeontols 3*, 1-77. ISSN0810-8889.

An excavation of the Koonwarra Fossil Bed within the Korumburra Group on the South Gippsland Highway south of Leongatha in February 1981 yielded a major collection of fossil plants including new records and other botanically significant specimens associated with fossil fish and invertebrates. Together with previous collections from the same site and supplementary material from other contemporaneous Victorian localities the plant material is the basis for the present study. The Early Cretaceous age of the flora is based on microfloral, megafloral and fission track data.

The plant remains consist of foliage, unattached fertile organs, and isolated cone scales and seeds, representing most of the major taxonomic groups from the Bryophyta to the Coniferophyta. No angiosperms have been recorded. The Pteridophyta is the most diverse and abundant group. Fifty-six separate plant taxa are recognized, of which thirty-five are foliage. Twenty-seven of the foliage types are classified to the level of genus. It is suggested that the flora was dominated by a forest of *Ginkgo* and several conifers, over an understorey of pentoxylaleans, ferns, sphenophytes and bryophytes, in a cool, possibly montane environment.

New species described are *Riccardia koonwarriensis, Dendroceros victoriensis, Hepaticites undulatus, Isoetes bulbiformis, Cladophlebis biformis* and *Podostrobus elongatus*. Other species revised or treated taxonomically include *Phyllotheca wonthaggiensis* (Chapman) comb. nov. emend., *Sphenopteris warragulensis* McCoy, *Sphenopteris travisi* Stirling, *Gleichenites nanopinnatus* (Douglas) comb. nov., *Adiantites lindsayoides* Seward emend., *Onychiopsis paradoxus* Bose & Dev, *Aculea bifida* Douglas, *Phyllopteroides lanceolata* (Walkom) Medwell, *Taeniopteris daintreei* McCoy, *Sahnia laxiphora* Drinnan & Chambers, *Ginkgo australis* (McCoy) comb. nov., *Bellarinea barklyi* (McCoy) Florin, and *Brachyphyllum gippslandicum* McCoy.

A.N. Drinnan and T.C. Chambers, School of Botany, University of Melbourne, Parkville, Victoria, Australia 3052: *received 1 August 1985.*

THE KOONWARRA FOSSIL BED, located on the South Gippsland Highway between Leongatha and Tarwin, 142km by road southeast from Melbourne (Fig. 1) yielded the majority of the fossil plants forming the basis of this study. It is within that part of the Korumburra Group of Stirling (see Talent, 1965) (= Strzelecki Group of Medwell (1954a) and Douglas (1976)) that has been dated as Early Cretaceous within megafloral zone C (*Ginkgoites australis* Zone) by Douglas (1969) and the microfloral *Dictyotosporites speciosus* Zone by Dettmann (1963); it lies within the upper unit of the microfloral *Cyclosporites hughesii* Subzone (M.E. Dettmann pers. comm. 1985) and therefore, may be ascribed to the latter half of the Aptian (Dettmann & Douglas, 1976) or possibly earliest Albian (Dettmann, this memoir).

Fission track ages of volcanogenic apatites separated from two samples, one 7m above the Fossil Bed and the other immediately below, were determined as 115 ± 6 my and 118 ± 5 my respectively (Lindsay, 1982). Lindsay (1982) noted that petrographic evidence suggested negligible reworking of the sediments which must have been deposited soon after eruption, thus the fission track dates may be taken as the age of deposition. They represent a maximum age for the Fossil Bed which is consistent with the Aptian determination suggested by the palynology.

The Fossil Bed is represented by 8m of fine-grained mudstone interbedded between two fluviatile arkosic sandstones. The mudstones consist of graded laminae of various thicknesses composed of alternate layers of claystone and siltstone and strike 230-235° with a dip of 35-40°; they represent a lacustrine environment in the predominantly fluviatile sediments of the Victorian Lower Cretaceous. Although the enclosing strata are known to be widespread the extent of the Koonwarra Fossil Bed is unknown.

Discovered in 1961 by Country Roads Board workmen, this locality has yielded abundant specimens of the fossil fauna and flora showing superb imagery but unfortunately the plant material has little or no anatomical preservation. The fish were studied by Waldman (1971); the invertebrates are described by Jell & Duncan (this memoir); several feathers were noted by Talent *et* *al.* (1966); a conchostracan was described by Talent (1965) and a xiphosuran by Riek & Gill (1971). A brief summary of some of the plant material was provided by Douglas as an addendum to the fish studies (Waldman, 1971, p. 93). Douglas (1969, 1973) included 19 fossil plant taxa from this site in his treatment of the Mesozoic flora of Victoria.

For this study a new excavation of the Koonwarra site was made in February 1981 to collect fossil plant remains and to determine the probable palaeoecology. This extensive new collection and most earlier collections are housed in the palaeontological collections of the Museum of Victoria (indicated by prefix NMVP appended to registration numbers); collections of the Geological Survey of Victoria (GSV) and the private collection of Mr Peter Duncan have now been registered in the Museum of Victoria collection; other material is housed in the Department of Geology, University of Melbourne (MUGD). Unless otherwise stated material used in this paper was collected at NMVPL425 — the Koonwarra Fossil Bed site on the South Gippsland Highway. Fertile and sterile material from elsewhere in the Victorian Lower Cretaceous has been used in some cases to supplement Koonwarra specimens. In all such cases the locality of the specimen, its repository and its registered number are listed. Precise details concerning many of the localities collected last century are unavailable. The most important localities for this paper have been entered in the locality register of the Museum of Victoria (prefix NMVPL) with Grid References to the 1:250 000 Topographical Map Series R502 (1st edn), Division of National Mapping; they are as follows:—

NMVPL425 Koonwarra Fossil Bed on South Gippsland Highway between Koonwarra and Tarwin at GR397246 on Warragul sheet SJ55-10.

NMVPL426 Cape Horn — quarry on Binn's Road north of Cape Otway near Apollo Bay at GR170226 on Colac sheet SJ55-12.

NMVPL427 Whitelaw — road cutting near old Whitelaw railway siding at GR436250 on Warragul sheet SJ55-10 (see also Douglas, 1973, p. 183, map 5, locality 122P).

NMVPL428 Cape Paterson — shore platform between Eagle's Nest and Inverloch at GR370253 on Warragul sheet SJ55-10 (see also Douglas, 1973, p. 185, map 8).

NMVPL429 Boola Boola Forest — locality 14 of Douglas (1969, map 4) on Exalt Creek in Boola Boola Forest north of Traralgon at GR446301 on Warragul sheet SJ55-10.

NMVPL430 Balook — at GR448258 on Warragul sheet SJ55-10 (Douglas, 1973, p. 184, map 6, locality 137P).

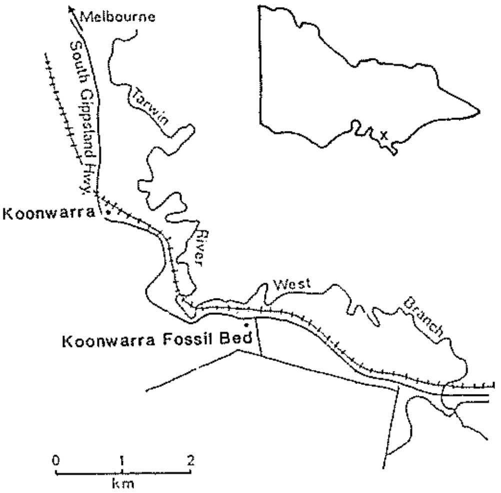

Fig. 1. Locality map showing fossil site on South Gippsland Highway. North is up the page.

Methods

As most of the Koonwarra specimens are preserved only as colour stains on the cleaved matrix surface, or at best as particles of compressed cleated carbon, considerable weight has been placed on preserved colour when interpreting the probable nature of a tissue. Dark coloured carbonaceous remains are taken as indicating a woody habit (e.g. *Podostrobus elongatus* sp. nov. Fig. 33A-F) and light brown impressions are accepted as suggesting a herbaceous texture, (e.g. leaves and fern fronds). The Koonwarra Fossil Bed sediments are buff yellow in colour. The additional specimens collected from Cape Horn are preserved as black coalified compressions in grey rock, but remain only as a cleated carbonaceous film which disintegrates when the rock is treated with hydrofluoric acid.

Excepting some peels and transfer preparations the only method used for enhancement of specimens was careful degaging with mounted needles and a Desoulter pneumatic engraving pen with a modified chisel tip. Transfers were made by painting a solution of PRIMAL AC-234 (water-based acrylic polymer) on the specimen, removing with needles when dry, and dissolving away the adhering matrix particles in 40% hydrofluoric acid (the acrylic appears to be HF resistent). The resulting acrylic peels with plant remains embedded were mounted for light microscopy.

All specimens were photographed dry, as immersion in low surface tension liquids caused the remaining carbon to disperse. An OLYMPUS OM-1 camera with a 50mm macro lens (and

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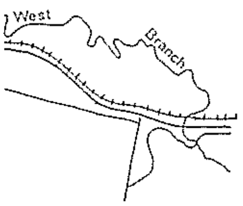

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Victorian Lower Cretaceous geology — a summary

Lower Cretaceous strata were laid down in southern Victoria in two major sedimentary basins (Otway and Gippsland Basins) in a mostly fluviatile, freshwater environment. These sediments have considerable outcrop and subsurface distribution, extending westward as far as Robe, South Australia, eastward to about Lakes Entrance, and southward under Bass Strait (Fig. 2). To the north they do not occur beyond 37° south latitude and in the east-west direction they are interrupted only by the Mornington Peninsula Palaeozoic High. Major outcrop sectors (Fig. 2) belong to several different rock units; those of the Merino and Otway Ranges Highs and the Barrabool Sandstone belong to the Otway Group whereas those of the Strzelecki Ranges High and the Tyers Apron belong to the Korumburra Group. A minor exposure of the Otway Group occurs at Sunnyside Road Beach, Mornington.

Opinions as to the age of the strata have varied considerably. Concerned originally with the coal seams and associated macrofossils, the dating was the centre of a dispute between the Reverend W.B. Clarke and Professor F. McCoy which can be followed in the Transactions of the Royal Society of Victoria (1860, *et seq.*). McCoy used the newly found leaf *Taeniopteris daintreei* McCoy 1860 to argue an inferior Oolite age similar to the well documented European fossil floras, while Clarke insisted on a late Palaeozoic age equivalent to the coalfields of New South Wales. Description of the flora by Seward (1904), resulted in several of the components being assigned to Yorkshire Jurassic species and an overall comparison with the fossil flora of the Rajmahal Series, India. Later investigations by Medwell (1954a) led to the strata being generally accepted as Lower-Middle Jurassic.

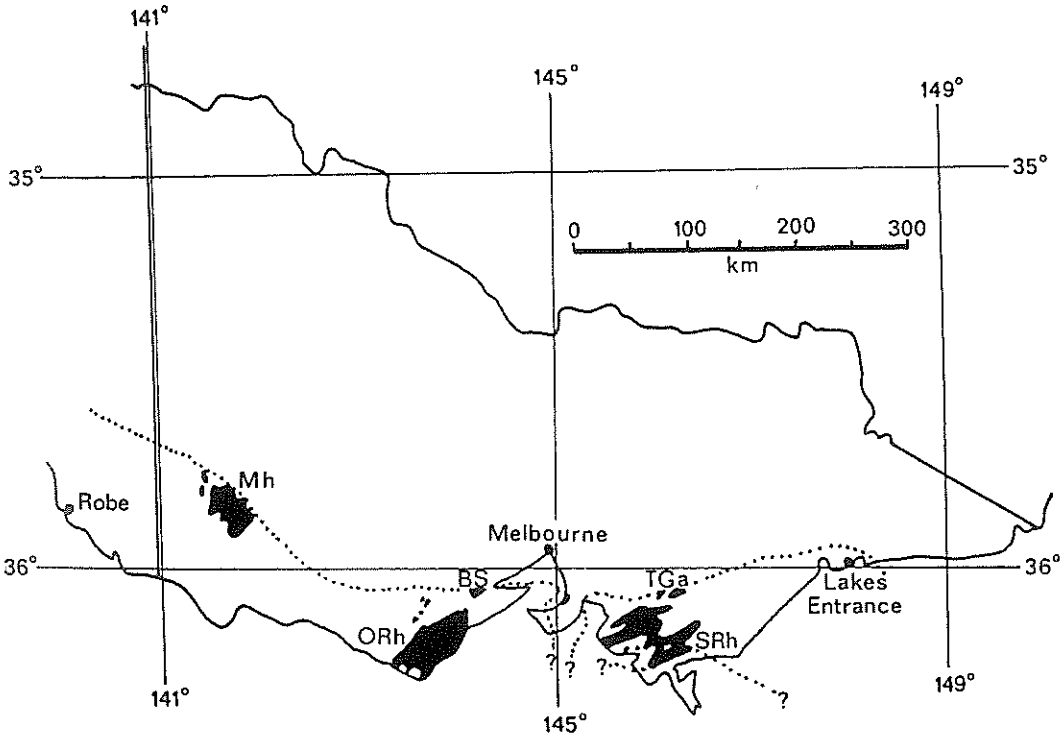


Fig. 2. Map of Victoria showing outlines (dotted lines) of major late Mesozoic-Tertiary coastal sedimentary basins, namely the Otway Basin west of the one hundred and forty-fifth meridian and the Gippsland Basin to the east; the outcrop of Cretaceous sedimentary rocks (black) and some structural features. BS — Barrabool Sandstone; Mh — Merino high; ORh — Otway Ranges high; SRh — Strzelecki Ranges high; TGa — Tyers Group apron.

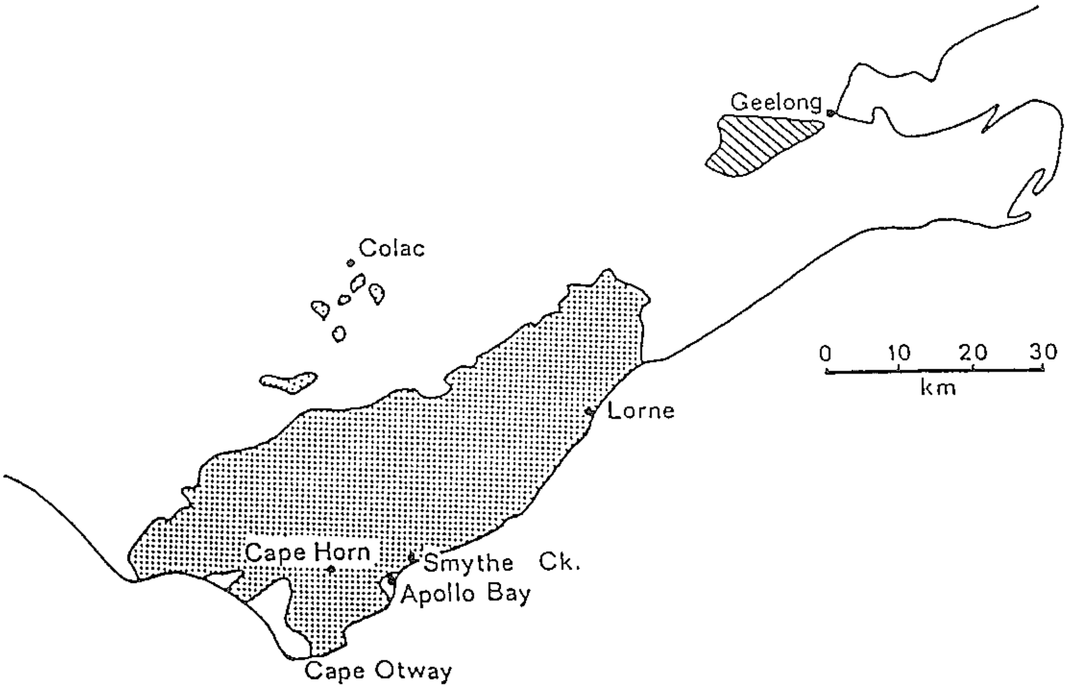


Fig. 3. Outcrop distribution map of Cretaceous sediments of Otway Ranges high (stippled) and of Barrabool Sandstone (diagonally lined).

Dettmann (1963) provided palynological evidence of three biostratigraphic pollen assemblages spanning the Lower Cretaceous in these strata in Victoria; they conform approximately to the early Neocomian, late Neocomian — early Albian, and middle Albian ages (Dettmann & Playford, 1969). Dettmann (1963) further noted the distinction of Seward's 'Yorkshire' species from those of the English Middle Jurassic (Harris, 1961) and the determination of a probable Early Cretaceous (Neocomian) age for the Rajmahal Formation (Arkell, 1956). Agreeing with Dettmann's Early Cretaceous age Douglas (1969) used plant macrofossil evidence to divide the sediments into four biostratigraphic zones which are recognizable in boreholes. Recent dating of volcanic constituents of Otway Group outcrop sediments using the fission-track method gives ages in the latter half of Early Cretaceous time (Gleadow & Duddy, 1980).

The Otway Basin

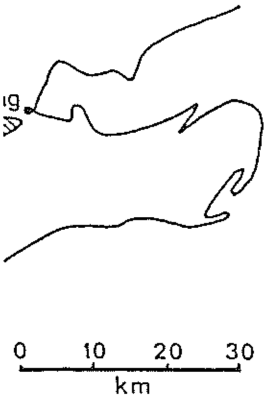
The Otway Basin was formed during the early stages of continental rifting between Antarctica and Australia marking the site of later separation of the two continents during the Eocene. The initial depositional phase is represented by 3km of Lower Cretaceous nonmarine sediments outcropping over 2600km^2 as the Otway Ranges and Merino High (Figs 2,3).

The Gippsland Basin

The Gippsland Basin formed at the same time as the Otway Basin in much the same tectonic framework. The initial deposition consisted of vast thicknesses of fluviatile nonmarine sediments over an extensive area of what is now southeastern Victoria from Western Port to Lakes Entrance and southward under Bass Strait. The main outcrop, the Strzelecki Ranges High (Figs 2,4) consists of block-faulted volcanogenic sandstone interbedded with mudstones and coal seams. Unweathered rock is exposed only along the sea cliffs and shore platforms between Cape Paterson and Inverloch and in occasional deep road cuttings. The lithologies are identical to the Otway sediments, and this, together with the uniform palaeontological sequences, indicates synchronous sedimentation and a common provenance for the sedimentary grains.

Taxonomic summary of the flora

Some of these plants compare closely with extant taxa, a few of which no longer occur in the



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The liverworts, particularly *Dendroceros victoriensis* sp. nov., *Riccardia koonwarriensis* sp. nov. and some of the leafy liverworts, on the basis of their thallus form, appear to be closely allied to extant genera. Likewise, shapes of the few mosses are similar to extant species, although there is little evidence of their systematic position within the Bryophyta.

Isoetes bulbiformis sp. nov. was apparently a robust plant with a substantial corm and, although its anatomical structure is unknown, its external morphology is consistent with extant *Isoetes* L. Only one, somewhat uncertain, stem fragment is recorded as belonging to the Lycopodiales, although Dettmann (1963, this memoir) reported several quite common lycopod spore species in the Victorian Lower Cretaceous.

Mesozoic equisetaleans were virtually cosmopolitan and none of the extant species of *Equisetum* L. are indigenous to Australia. The two species from Koonwarra are vegetatively similar to living horsetails, but equisetaceous fertile structures are unknown from Koonwarra. *Phyllotheca wonthaggiensis* (Chapman 1914) comb. nov. had a habit very similar to extant *Equisetum* (in particular the rhizome and tuber system), but differs noticeably in leaf morphology. The leaf ends of living *Equisetum* nodal sheaths are typically reduced, membraneous and non-chlorophyllose, as opposed to the expanded, free, probably photosynthetic leaf ends of *P. wonthaggiensis*. Fertile organs attributable to *P. wonthaggiensis* were not found, but based on the similarities in vegetative habit to *Equisetum*, noted above, they could be expected to more closely resemble cones of *Equisetum* than those of the Permian *Phyllotheca australe* Brongn. 1828 and *P. indica* Bunbury 1861 which have branched sporangiophores (Townrow, 1955). *Phyllotheca wonthaggiensis* is probably an intermediate form close to *Equisetum* which has retained free leaf ends.

Despite the abundance of sterile fern-like foliage, there is an almost total absence of the same foliage in the fertile condition. *Sphenopteris warragulensis* McCoy 1892 is one of the most abundant fossils at Koonwarra, yet not one fertile piece was recovered. However, at Cape Horn

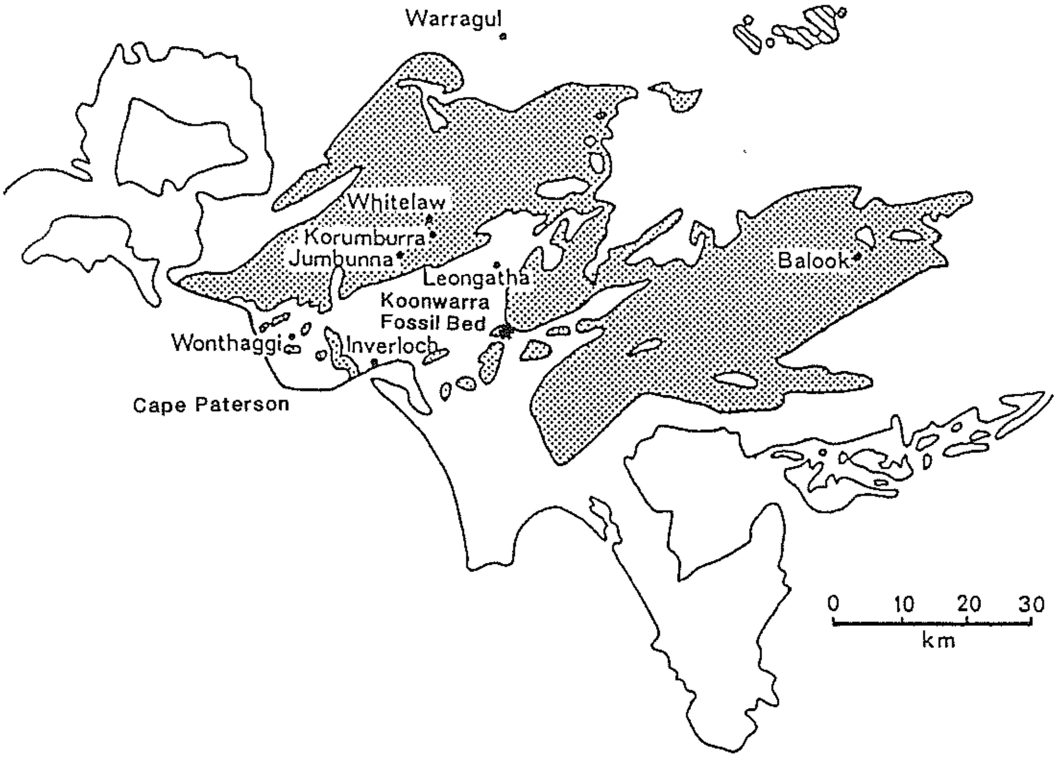

Fig. 4. Outcrop distribution map of Cretaceous sediments of Strzelecki Ranges high (stippled) and Tyers Group apron (diagonally lined).

250km away fertile *S. warragulensis* is common. Similarly *Adiantites lindsayoides* Seward 1904 emend. and *Aculea bifida* Douglas 1973 are both common in the fertile condition at Cape Horn, but no fertile *Adiantites lindsayoides* and only two pieces of fertile *Aculea bifida* were recovered at Koonwarra. The only other Koonwarra fertile fern specimens are one frond of *Sphenopteris travisi* Stirling 1900 and a small piece of *Onychiopsis paradoxus* Bose & Dev 1961. It is possible that the absence of fertile foliage at Koonwarra relates to the season in which fossilization regularly occurred being a time when most plants were not fertile. Fortunately, fertile material of some species (e.g., *Sphenopteris warragulensis, Adiantites lindsayoides*, and to a lesser extent *Onychiopsis paradoxus*) from other localities has allowed a more complete description and also permitted interpretation of several of these species as being related to extant leptosporangiate ferns. In particular, *Sphenopteris warragulensis, S. travisi* and *Adiantites lindsayoides* all have small leptosporangia (approx. 250μm diameter) with an approximately vertical annulus and trilete spores. As noted below, the spores of the latter two species have previously been allied to the Cyathaceae.

The prevalence of sterile foliage which by itself cannot be placed with any certainty in a particular fern order causes sizeable gaps in the taxonomic story of the flora. No fertile foliage representing the eusporangiate ferns or the more primitive leptosporangiate ferns belonging to the Schizaeaceae have been recorded from the Victorian Lower Cretaceous, yet vegetative material of the form-genus *Cladophlebis* Brongn. is abundant. In the Yorkshire Jurassic *Cladophlebis* foliage has been attributed to both groups (*Todea* Willd. (Osmundaceae) and *Klukia* Raciborski (Schizaeaceae)) by Harris (1961). Consequently the three types of *Cladophlebis* foliage from Koonwarra may represent either the Osmundaceae, the Schizaeaceae, or even both. Supporting evidence for the presence of both these families in the Victorian Lower Cretaceous includes *Osmundites* Jaeger stems (Medwell, 1954a), and several schizaeaceous spore species belonging to the spore form-genera *Cicatricosisporites* Potonié & Gelletich and *Klukisporites* Couper (Dettmann, 1963).

Although *Gleichenia*-like ferns are well documented in Cretaceous and other Mesozoic sediments of the Northern Hemisphere (Abbott, 1954; Andrews, 1961; Surange, 1966), and several species of *Gleichenia* Smith are reasonably common components of the present Victorian flora, only one Koonwarra species is tentatively allocated to the '*Gleichenia*-like' form-genus *Gleichenites* Goeppert. The relationships of the other fern species, *Sphenopteris* sp., *Aculea bifida, Onychiopsis paradoxus*, and the two specimens compared to the Marsileales, are uncertain.

One of the more interesting discoveries is the evidence linking *Taeniopteris daintreei* McCoy 1874 to the Pentoxylales. Hitherto a little known order of gymnosperms from the Indian Jurassic and one locality in New Zealand, it now appears that they were widespread and quite abundant in mid-Mesozoic times. Present records suggest they ranged from Toarcian (Late Jurassic) until late in the Aptian (Early Cretaceous) (Drinnan & Chambers, 1985).

The Ginkgophyta, which had a world-wide distribution in Mesozoic times, is represented in the Koonwarra flora by leaves of *Ginkgo australis* (McCoy 1892) comb. nov. and isolated male strobili. The leaves are more dissected than those of the only extant species *Ginkgo biloba* L. 1771 which is indigenous to Chekiang Province, China. *Ginkgo australis* probably had a deciduous habit similar to that of *G. biloba*. Associated ginkgoalean pollen organs from Koonwarra which probably belong to *G. australis*, closely resemble those of the extant species.

Four foliage types attributed to the Coniferales are preserved, but only the one attributed to the Podocarpaceae by Florin (1952) is assigned confidently at family level. The pollen cone specimens ascribed to *Podostrobus elongatus* sp. nov. are also attributed to the Podocarpaceae.

The Araucariaceae is represented by at least one cone scale type, two seed cone axes and one or possibly two foliage types, all of which conform to the *Eutacta* Endl. *emend.* Wilde & Eames 1952 section of *Araucaria* A.L. Juss.

The conifer *Brachyphyllum gippslandicum* McCoy 1892 is interpreted as belonging to the Podocarpaceae but may represent a taxodiaceous type.

The remaining seeds, cone scales, and seed bearing structures are all isolated fragments with questionable affinities. Although most are listed in the Coniferophyta, some may belong to other gymnosperm groups.

Notable absences from the Koonwarra flora

Although not particularly diverse the Koonwarra flora includes a wide representation of the major plant groups with the exception of the angiosperms. There are however, several notable absences. Eusporangiate ferns are lacking. The Polypodiaceae s.s. appears to be absent; this is not totally unexpected as current concepts of the evolution of these advanced ferns place their development about the time of or subsequent to the rise of the angiosperms, and reports of pre-

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Late Cretaceous polypodiaceous ferns are treated with reservation (Lovis, 1977).

Seedferns reached their peak between the Late Carboniferous and early Mesozoic (e.g. in the Permian *Glossopteris* flora) but probably existed until the end of the Early Cretaceous. At Koonwarra, however, there is little foliage attributable to that group. It is unlikely that they were a major component of the flora. This is possibly because their ecological niche was extensively utilized by *Taeniopteris daintreei* (Pentoxylales). This reason may also account for the absence of the Cycadophyta which are prevalent in other Mesozoic floras and represented in the extant flora of eastern Australia.

The Bennettitales were a major component of the slightly older Zone B flora, together with *Pachypteris austropapillosa* Douglas 1969 and *Reinitsia? variabilis* Douglas 1969 (Douglas, 1969). They are not present at Koonwarra or in any Zone C sediments.

The small awned seeds (Fig. 36U,V) and the two small cruciform structures (Fig. 36Q,R) are the only possible indications of angiosperms, but the evidence is unsatisfactory. No leaf remains resembling angiosperms (and only *Hausmannia* sp. (Douglas, 1973) with definite reticulate venation) are reported from Zone C; it is improbable that angiosperms formed a significant part of the flora. Dettmann (this memoir) records angiosperm-like pollen which she attributes to '*Ascarina* or its precursors' as possibly indicating 'the presence of shrubby angiosperms within the vegetation'. Elsewhere angiospermous pollen appears in the fossil record about the Barremian (Early Cretaceous) (Dettmann, 1981), and is closely followed by angiosperm megafossil remains.

In some respects the Victorian Early Cretaceous flora appears to be a remnant, or at least a late developing flora, e.g. the persistence of the Pentoxylales, and the apparent rarity of angiosperms. This is parallelled by the vertebrate fauna e.g. by the dinosaur *Allosaurus* Marsh which disappeared from the Northern Hemisphere during the Jurassic (T. Rich pers. comm. 1983). However, the invertebrate fauna is much more similar to extant faunas of the region than it is to typical early Mesozoic insect faunas of eastern Australia (P.A. Jell pers. comm. 1985).

Comparison of the Koonwarra flora with other middle Mesozoic Gondwana floras

The Australian Cretaceous flora was reviewed with a palynological emphasis by Dettmann (1981). Although not dealing with Douglas's (1969) megafloral zones in any great detail, Dettmann collectively likened them to the Bennettitales floras of Jabalpur and Cutch (India), and of Patagonia (South America). The similarity of the Victorian Zone B bennettitaleans to those of the Indian fossil floras noted above and also the ?Jurassic flora of the Rajmahal Series is marked; they possibly shared some species. However, it is the succeeding Zone C megaflora with which this study is concerned.

Comparisons with other middle Mesozoic floras may not be strictly relevant because of dating uncertainties and abundance of sterile foliage types which can be compared only on gross morphology. The Koonwarra flora, however, includes several forms allowing useful comparisons with some other Mesozoic floras. These comparisons are considered here collectively with respect to their phytogeographical and chronological significance.

The most similar generic and possibly even specific comparison appears to be with the flora of the Rajmahal Series of India. This Series consists of a number of lava traps and intertrappean beds, of which the basal five are fossiliferous. The flora of the lower three beds is dominated by Bennettitales and Filicales, while the fourth and fifth intertrappean beds contain mostly pteridophytes and conifers (Zeba-Bano *et al.*, 1979). Rajmahal plants comparable to Koonwarra species (the latter indicated by brackets) include *Ginkgo rajmahalensis* (Sah & Jain 1965) Zeba-Bano *et al.* 1979 (*G. australis*), *Thinnfeldia indica* Feistmantel 1876 (*Thinnfeldia* sp. cf. *T. indica*), *Sphenopteris hislopi* Oldham & Morris 1863 (*S. warragulensis*), *Cladophlebis indica* (Oldham & Morris 1863) Sahni & Rao 1933 (*C. biformis* sp. nov.; *C.* sp. cf. *C. oblonga* Halle 1913), *Nipaniophyllum raoi* Sahni 1948 (*Taeniopteris daintreei*), *Sahnia nipaniensis* Vishnu-Mittre 1953 (*S. laxiphora* Drinnan & Chambers 1985), *Brachyphyllum mammilare* Brongn. 1828 (*B. gippslandicum*) and *Araucarites cutchensis* Feistmantel 1876 (*Araucaria* cone scale).

The fossil association of *Ginkgo rajmahalensis* and *Ptilophyllum* Morris fronds in the Indian beds suggests those floras are transitional between the Victorian Zones B and C. In Victoria *Ptilophyllum boolensis* Douglas 1969 and *Ginkgo australis* are accepted guide fossils for their respective zones and have not been found together.

Considered to be Middle-Late Jurassic by Indian palaeobotantists, the age of the Rajmahal Series has long been disputed. Neocomian ammonites from Cutch (Spath, 1933), which date a flora similar to that of the Rajmahal Series, led Arkell (1956) to conclude an Early Cretaceous age. Playford & Cornelius (1967) considered palynological data from the Rajmahal Hills (Sah & Jain, 1965) to be indicative of a Neocomian (and possibly post-Barremian) age. McDougall & McElhinny (1970) determined a K-Ar age of between 100 and 105 my for lava traps stratigraphically contiguous with the plant deposits. The megaflora of the Rajmahal Series shows a close affinity to the Victorian Early Cretaceous floras which have been dated by microfloral analysis and fission track techniques. It appears that the Rajmahal flora may be of Early Cretaceous (Neocomian) age. The Jabalpur flora (India) does not differ greatly from that of the Rajmahal Series and shares with the Koonwarra flora the fern species *Onychiopsis paradoxus*.

The fossil flora of the Talbragar Fish Bed in New South Wales is similar to that from Koonwarra but the number of plant types shared with Talbragar is fewer than with the Rajmahal Series. Types shared with Talbragar (Koonwarra comparison in brackets) include *Thinnfeldia talbragarensis* Walkom 1921 (*Thinnfelida* sp. cf. *T. indica*), *Taeniopteris spatulata* McClelland 1850 (*T. daintreei*), *Coniopteris hymenophylloides* Brongn. 1849 (*Sphenopteris travisi*), and *Brachyphyllum* sp. (*B. gippslandicum*). *Thinnfeldia pinnata* Walkom 1921 is very similar, and possibly identical, to *Reinitsia*? *variabilis* from the Victorian Zone B. Most notably, *Ginkgo* leaves are absent at Talbragar. Walkom (1921) compared the Talbragar flora closely with the Victorian Early Cretaceous flora (then thought to be Jurassic) and assigned a Jurassic age to the Talbragar beds on the basis of the preserved megaflora. Based on the slightly more advanced development of the teleost fish *Leptolepis koonwarri* Waldman 1971 than its Talbragar equivalent *L. talbragarensis* Woodward 1895, Waldman (1971) considered the Koonwarra Fossil Bed slightly younger. The most probable reason for the close similarity of the floras from the two sites is the presumed similarity in ecological habitat (i.e. lake or river edge). It is also possible that these plants existed for a considerable time span. The age of the Talbragar Beds is generally considered late Early Jurassic (Hind & Helby, 1969; Loughnan & Evans, 1978).

The Lower Cretaceous Burrum and Styx River Series in Queensland have several similar plant types, notably araucarian cone scales, *Phyllopteroides lanceolata* (Walkom 1919) Medwell 1954 and *Sphenopteris* and *Cladophlebis* foliage types. The Queensland Jurassic Walloon flora shares only one form, *Taeniopteris spatulata* (similar and possibly identical to *T. daintreei*), with the Koonwarra flora. The Triassic Ipswich flora is quite different and has a considerable *Dicroidium* Gothan component.

Sediments from Port Waikato, New Zealand which were deposited during the Middle Tithonian (Late Jurassic) have revealed a plant association consisting largely of *Taeniopteris daintreei*, but also with *Coniopteris hymenophylloides*, several *Cladophlebis* types and the fructification *Carnoconites cranwellii* Harris 1962.

The Early Cretaceous Ticó flora of Patagonia, Argentina has two *Ginkgo* leaf types which are very similar to *G. australis*.

Of the contiguous Victorian floras the Koonwarra flora has more in common with the underlying one (Zone B). Several species and forms overlap, including *Taeniopteris daintreei*, *Aculea bifida*, *Phyllopteroides lanceolata*, and some *Thinnfeldia* Ettingshausen, *Cladophlebis*, *Coniopteris* and conifer types, but there are some notable differences. *Sphenopteris warragulensis* and *Ginkgo australis* are both common at Koonwarra and elsewhere in Zone C but are absent from Zone B, while the dominant Zone B floral components such as the Bennettitales, *Pachypteris austropapillosa* and *Reinitsia*? *variabilis* are not present in Zone C. The younger Zone D has only a few similar *Cladophlebis*, *Aculea*, and *Phyllopteroides*-like foliage types in common with Koonwarra.

The most notable difference to the Koonwarra flora shown by the above contemporaneous 'Koonwarra-like' floras, (i.e. Talbragar (N.S.W.), Victorian Zones B and D, Port Waikato (N.Z.), is the apparent absence of *Ginkgo* leaf types. *Ginkgo* leaves are common at Koonwarra, and present in the Indian Rajmahal Series and other Jurassic and Early Cretaceous floras of the world. It is impossible to determine whether the absence of *Ginkgo* is due to insufficient collecting at these other localities, some major phytogeographical significance, or to local ecology.

Palaeoenvironment — climatic and depositional

The Koonwarra Fossil Bed flora does not contain positive evidence for any particular palaeoclimate, but is consistent with the indication of the environment suggested by the invertebrate fauna also preserved. Extrapolation from the environments of their extant relatives gives an indication of the probable conditions in which these invertebrates lived.

Based on the evidence provided by the invertebrate fauna Jell & Duncan (this memoir) conclude that the Koonwarra Fossil Bed represents the sediments of a small marginal basin of an ancient, cold, freshwater lake.

The climate was probably cool, perhaps montane (possibly sub-alpine, but not alpine). The Victorian Lower Cretaceous sediments have undergone periods of upthrust and subsidence (e.g. sediments of Zone C age extend to almost 2000m below ground level in the Heathfield no. 1 bore in western Victoria (Douglas, 1969), and to a similar depth below the sea floor under Bass Strait (J.G. Douglas pers. comm.), and thus their present altitude bears no relation to their altitude at the time of deposition. A cool climate is consistent with the two major components of the preserved flora, *Ginkgo australis* and *Taeniopteris daintreei*. Both taxa are large, simple, petiolate leaves which were abscised complete, and were probably borne on deciduous plants.

The undisturbed, finely graded laminae, which do not contain any particles larger than a medium grained sand, indicate a still water environment receiving periodic influxes of sediment; the clay settled during periods of little or no water movement. Such sediments are usually deposited in reasonably deep water where disturbance of silt is minimal. The absence of large mineral particles (coarse sand, pebbles) and the sparse distribution of plant fossils (which consist mainly of leaves and other foliar fragments; wood and other substantial material is absent) suggest the site excavated was of sufficient distance or permanently isolated from the water entry point for the heavy debris to have settled out and the lighter material dispersed.

The laminae toward the base of the Fossil Bed (basal 2m) are very narrow (often only a few millimetres), and contain the highest concentration of plant and invertebrate fossils but only a few fish. This is possibly because the site was further from the water inlet at the time of deposition of these layers (and had received less sediment) and closer to the edge of the lake (inclusion of plant material from lake edge vegetation and invertebrates living in the shallows). In the 5.5–7.5m part of the section where most of the fish are preserved, the laminae are much thicker (usually at least several centimetres) and plant and insect remains are less common.

Available evidence suggests a cold, freshwater lake of reasonable size (possibly several kilometres across) which existed over a considerable period of time. The lake received periodic influxes of water and silt, and supported an aquatic ecosystem which included several species of fish and a rich assortment of immature aquatic insects. The surrounding vegetation appears to have been a forest dominated by *Ginkgo* and several members of the Coniferales, with an understorey of *Taeniopteris* (Pentoxylales), pteridophytes, equisetaleans, and bryophytes.

Systematic palaeobotany

The fossil plants from Koonwarra are isolated impressions of often incomplete portions of sterile foliage and fertile structures, unfortunately with no preserved anatomical structure or spore detail; gross morphology and careful comparative study are therefore the only bases for their systematic position. As external appearance (especially of foliage) is not particularly useful for classification within some plant groups (e.g. ferns, conifers), only tentative taxonomy is possible.

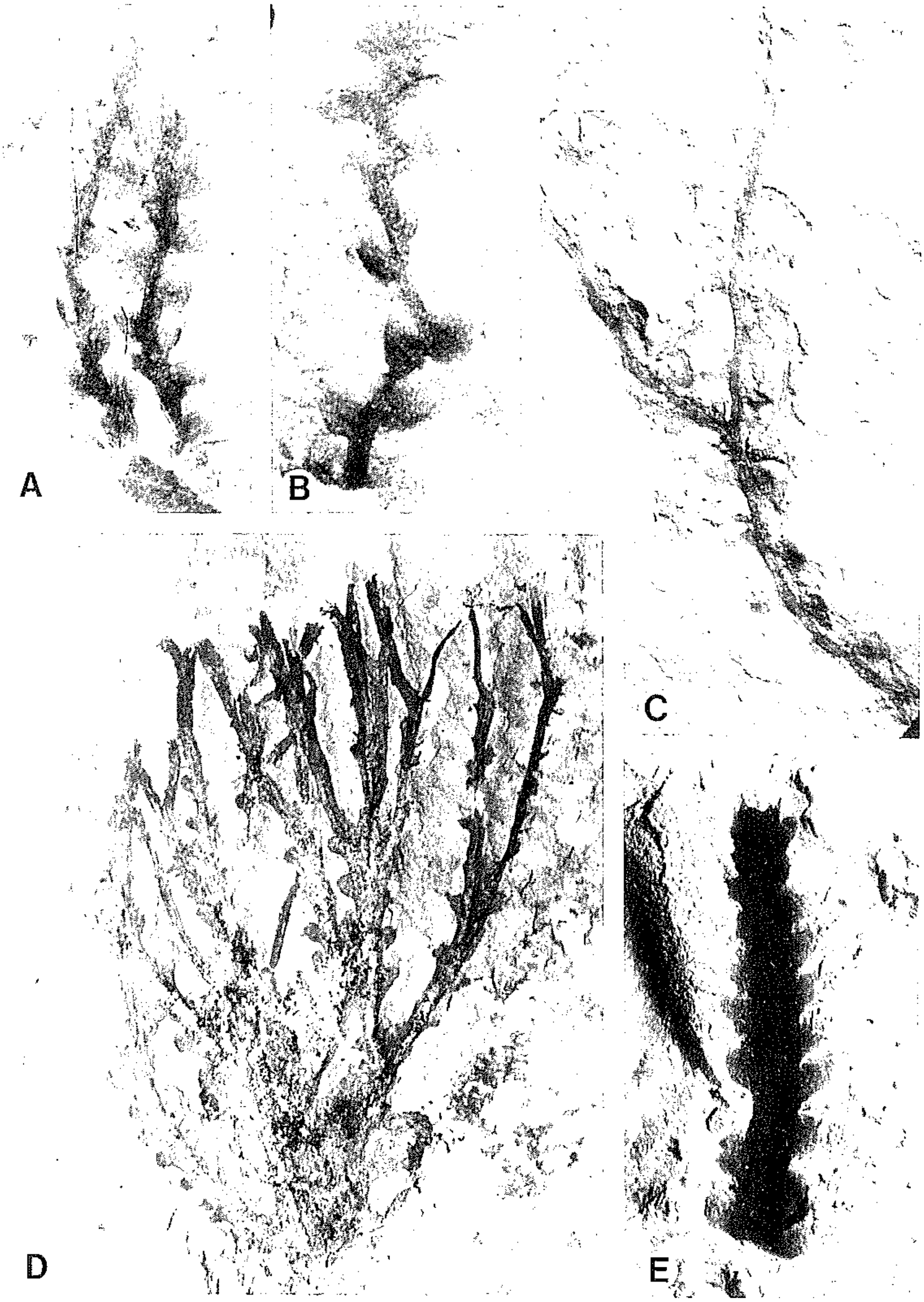
For comprehensive floral study a large sample must be taken, and caution must be exercised in interpreting the significance of the absence of a particular plant group or the abundance of a particular fossil type. Abundance of a fossil taxon does not necessarily reflect true abundance in the flora, (e.g., deciduous trees which are at leaf fall at the time of deposition will be better represented in the fossil flora than evergreens).

The extensive collection made at Koonwarra in 1981 sampled the total vertical thickness of the Fossil Bed (approx. 8m) which may have spanned a considerable period, possibly as long as 1000 years. It is possible that not all the fossilized plant taxa present were collected, but the range of plants recovered — from liverworts to conifers — supports the assumption that the sample examined for the present study is representative of an Early Cretaceous flora at or near to that site.

The synonomy lists for each species contain only those references which are significant to the name applied to the taxon concerned (e.g. initial mention of taxon, change of name, description, or illustration), and the literature which merely lists or mentions an already existing species name has been omitted. Similarly, material listed for each taxon represents only additional and previously unrecorded specimens, and previously collected specimens that have been of significance in the present study; this is essentially a collection from Koonwarra. In general, specimens encompassed by the synonymy lists are not listed herein.

A number of these fossil plants were discovered late last century by Mines Department geologists and were later figured or listed without accompanying descriptions in the Records, Reports and Publications of the Geological Survey of Victoria; there may have been some doubt about the validity of their publication although Seward (1904) remedied this to some extent. These early names have been accepted by subsequent workers and where possible they have been retained here with the original author as the authority.

Where possible, the authorities for the extant



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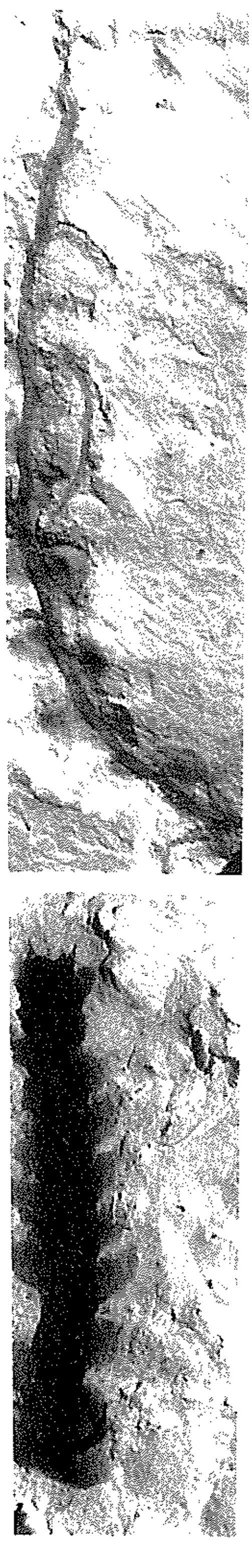

genera and species referred to in this paper have been abbreviated according to the 'Draft Index of Author Abbreviations compiled at the Herbarium, Royal Botanic Gardens, Kew, 1980'. Authorities for fossil genera and species have been given in full, with the exception of A.T. Brongniart, abbreviated herein as Brongn. The classification employed herein follows that of Taylor (1981).

Division HEPATOPHYTA

Order JUNGERMANNIALES

JUNGERMANNIA L. 1753

JUNGERMANNIA? sp. (Fig. 5A–C)

1973 *Thallites* sp. 'b'; Douglas, p.31, pl.8, fig. 4; pl.9, figs 2, 3; text-fig.3,9.

Material. NMVP167310–167324.

Description. Thallus leafy, branched, preserved lengths up to 25mm (total length unknown), stem width 0.3mm. Leaves in two ranks, distant, small, round, approximately 1mm across, arranged distichously to sub-oppositely on the stem, insertion oblique, margins entire, amphigastria absent. Stem branching dichotomous, lateral leafless branches present.

Discussion. Most of the specimens belonging to this taxon are small pieces of sterile thallus preserved as colour stains on the rock surface. None exhibit all of the described characters, but similarities in leaf shape and arrangment allow assignment to one taxon.

In most specimens the leaves are distant and in the few which have some imbricate leaves it is impossible to determine whether their arrangement is succubous or incubous, or even whether the observed surface is dorsal or ventral. The leaves appear to be inserted obliquely and laterally on the stem, and are more or less involute. The leaves toward the base of each branch are smaller than those medially. Rhizoids on the ventral surface of the stem were not observed, but it is improbable that they would have survived in this type of preservation if indeed they had been present. The leafless lateral branches arise directly from the stem, not in the axils of leaves. No sporophytes have been found.

These plants lack the postical leaf lobes but otherwise appear similar to extant *Radula* Dumort. species. Available morphology is consistent with extant *Jungermannia*. The sterile branches with leaves becoming gradually smaller toward the base of the branch are reminiscent of *J. inundata* Hook. F. & Taylor 1844 (*ex icon* Allison & Child, 1975, p. 97), and the branching habit and leafless lateral branches are similar to *J. subulata* Evans 1891 (*ex icon* Inoue, 1974, pl. 49). The rhizoids common on the ventral stem surface in extant species of *Jungermannia* were not observed on the fossil, probably due to poor preservation.

Although standard practice has been to allocate fossil liverworts, particularly pre-Tertiary ones, to extinct genera with Recent affinities (denoted by the suffix -ites, e.g. *Jungermannites* Goeppert), the different usages of such genera have placed some limit on their current usefulness. For example, *Jungermannites* was proposed by Goeppert (1845) as a collective genus for fossil leafy liverworts (which included the anacrogynae), but was restricted by Steere (1946) to include only the fossil members of the acrogynous Jungermanniales. The name itself suggests affinities with *Jungermannia* rather than to the order.

Douglas (1973) described sterile portions of this plant as an unnamed species of *Thallites* Walton and attributed it to the Hepaticae. Additional specimens showing the leafless lateral branches allow comparison with extant *Jungermannia*.

PLAGIOCHILA Dumort. 1835

PLAGIOCHILA? sp. (Fig. 5D,E)

1973 *Thallites* sp. 'a'; Douglas, p.30, pl.8, figs 2, 3; text-fig.3,8.

Material. NMVP167325, 167326.

Description. Thallus leafy, branched, individual branches up to 25mm long. Leaves in two ranks, distant, sub-oppositely arranged, inserted laterally (and possibly obliquely) on the stem. Amphigastria not evident. Stem branching apparently dichotomous, branches elongated distally; leaves becoming reduced distally along the stem, not persisting to the apex. Sporophtyes absent.

Discussion. Poor preservation prevents an adequate description and the considerable size difference between the two available specimens cautions against use of dimensional characters in their taxonomy. One specimen (Fig. 5E) is a

Fig. 5. A–C. *Jungermannia*? sp. A, two pieces of thallus branch, NMVP167310, ×10. B, medial portion of thallus branch, NMVP167317, ×10. C, dichotomizing portion of thallus, with lateral leafless branches showing leaves reduced on distal parts of thallus, NMVP167312, ×5. D,E, *Plagiochila*? sp. D, complete plant with dichotomous thallus branches showing leaves reduced on distal parts of thallus, NMVP167325, ×5. E, medial portion of thallus branch, NMVP167326, ×5.

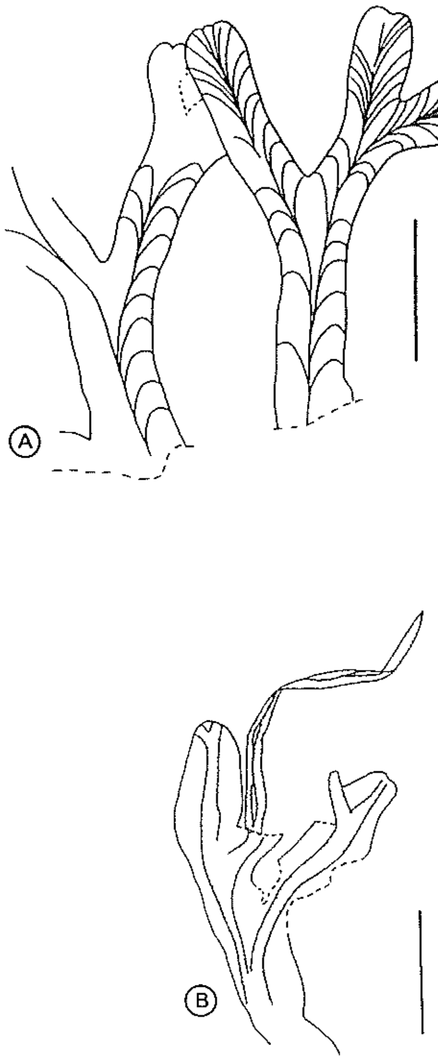

Fig. 6. Dendroceros victoriensis sp. nov. A, dichotomous thallus with arcuate lateral ribs traversing intercostal region, NMVP167331. B, plant with sporophyte, NMVP167333. Scales = 5mm.

portion of thallus 14mm long apparently from a leafy liverwort. The stem is 1.5mm wide and bears two ranks of leaves which are poorly preserved about the margins but were probably more or less rounded and about 1mm across. The other specimen (Fig. 5D) is an almost complete plant with much smaller features and despite unclear imagery gives some indication of the overall habit. It has an almost tufted appearance with once and twice branched stems about 25mm long arising from a common base. The stems are 0.5mm wide and the leaves about 0.5mm across. It is not clear in either of the specimens whether the leaves are free from each other and inserted separately, or whether the stem is alate and the leaf margins are continuous. The stems branch once or twice appearing as equal dichotomies, though one branch may arise as a lateral or postical intercalary shoot. The leaves on the upper portions of the stem are extremely reduced, the distal ends lacking leaves; sporophytes and lateral leafless branches are absent.

These two specimens are separated from the other leafy liverworts by their leaf arrangement and the smaller ratio of leaf size to stem width. Whether or not *Plagiochila*? sp. and *Jungermannia*? sp. are conspecific is in doubt because of the small number of specimens.

The distally elongate stems with reduced leaves are very similar to the gemmiparous shoots of extant members of the Plagiochilaceae, e.g. *Plagiochila, Xenochila* Schuster, (as is the habit). They are also reminiscent of the antheridial shoots of some *Jungermannia* species. Excepting these casual likenesses, the poor state of preservation prevents any other comparisons being made.

Again it is stressed that these specimens may indeed be the same as those previously compared with *Jungermannia*, but they have been maintained here as separate entities to emphasise that they possess some additional and distinctive characters.

JUNGERMANNIALES indet. (Fig. 9A)

Material. NMVP167339.

Description. Plant leafy, 24mm long, stem width 0.5mm. Leaves round, up to 1mm across, sessile, in two ranks, distichous, distant. Lateral spike-like shoots with 3-4 distichous, imbricate, unfolded leaves, arising from the main stem.

Discussion. The sparseness of leaves on a relatively bare stem, casts some doubt as to whether this sole specimen should be considered typical of a species, because few extant leafy liverworts have leaves so distant. The habit, particularly with the leafy

Fig. 7. Dendroceros victoriensis sp. nov. A, dichotomous thallus showing midrib branching into intercostal region to form arcuate lateral ribs, NMVP167331, ×4. B, branching thallus with two sporophytes showing decay of the plant about the base of the sporophytes, MUGD3780, ×3. C, thallus with sporophyte still joined at its apex but dehisced medially by means of longitudinal slits, NMVP167333, ×3. D, dichotomous thallus showing arcuate lateral ribs and the bifurcation of the midrib which initially divides at an acute angle and then diverges at the angle of the thallus dichotomy, NMVP167334, ×3.

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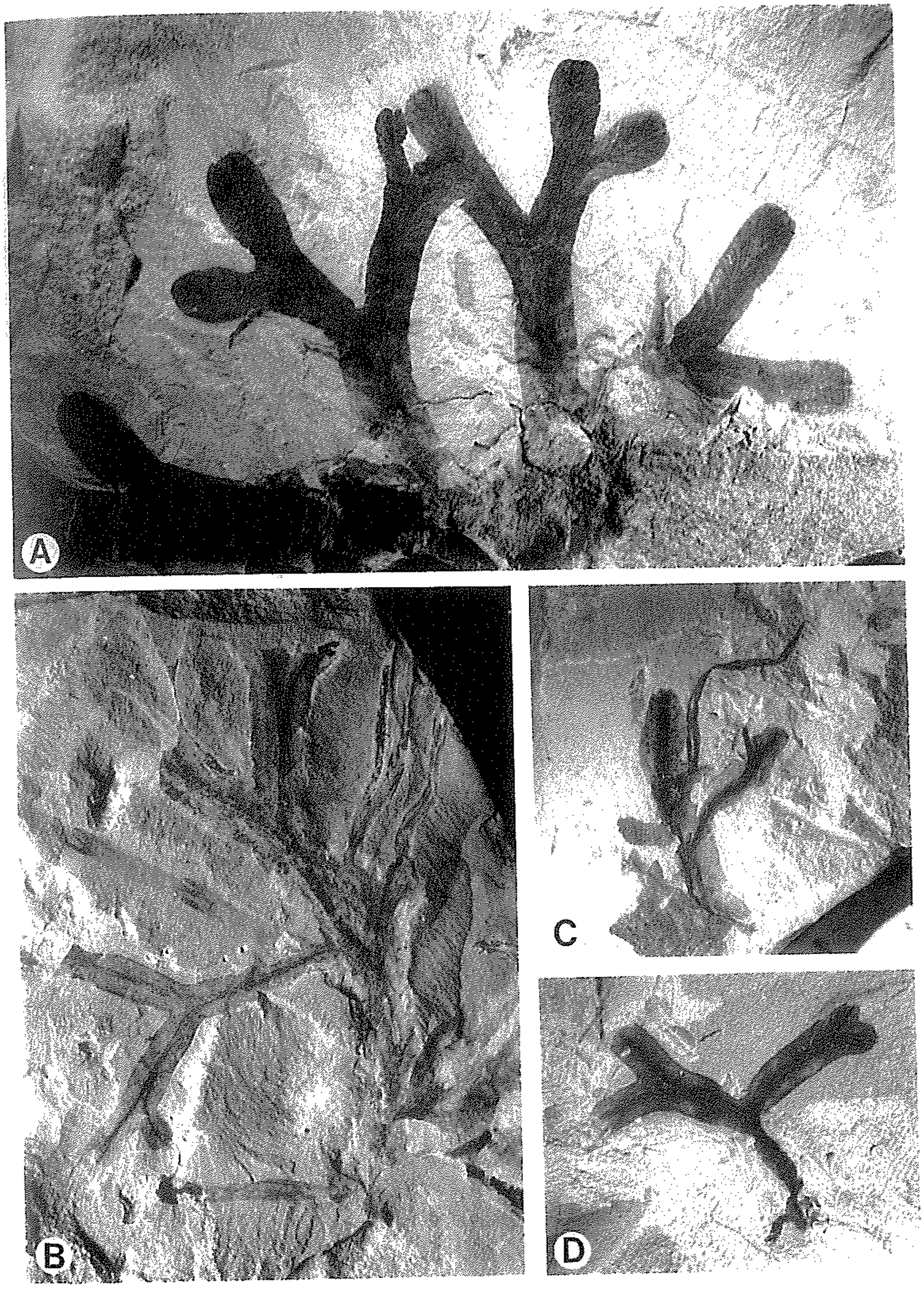

lateral branches, is similar to some species of *Radula*, *Frullania* Raddi, and *Lejeunea* Libert, although amphigastria and postical leaf lobes are not apparent. The apical portion appears to be sheathed in a membraneous structure which is possibly the appressed remains of a perianth. Consideration of only one somewhat unsatisfactory specimen does not allow conclusive relationships to be established.

Order METZGERIALES

Family ANEURACEAE

RICCARDIA Gray 1821

RICCARDIA KOONWARRIENSIS sp. nov. (Fig. 9B,C)

Etymology. Greek *-ensis* a suffix meaning from.

Material. Holotype NMVP167340. Paratypes NMVP167341, 167342.

Diagnosis. Habit thallose, spreading, preserved plants up to 17mm across, irregularly branched. Major thallus branches up to 13mm long by 1mm wide (usually widest near the branch apex) giving rise to smaller lateral branches which may in turn branch again, apices slightly notched. Midrib absent, fertile structures absent, gemmae absent.

Discussion. Although there is no evidence of fertile structures to prove affinity with the Aneuraceae, the habit of this fossil is very similar to extant *Riccardia* species and has been allocated to the family on that basis. The thallus appears to have been prostrate with a few semi-erect branches and its uniform colour indicates, as in extant species, a uniform thallus thickness of several cells. Thallus branch margins are straight and more or less parallel, and apices are rounded to slightly notched or dissected.

Schuster (1964) divided *Riccardia* into three subgenera using two Australian species as types, but a multivariate analysis of Australian and New Guinean *Riccardia* species by Hewson (1970) found Schuster's system unsatisfactory. Unfortunately Hewson's study failed to recognise any discrete features definitive of the resulting groups and most of the characters used, concern structures not present or not measurable in the fossil specimens.

The unavailability of anatomical structure prevents allocation to any extant species of *Riccardia*, but size and habit of the thallus suggest close relationship to several extant species of the genus.

Order ANTHOCEROTALES

Family ANTHOCEROTACEAE

DENDROCEROS Nees 1846

DENDROCEROS VICTORIENSIS sp. nov. (Figs 6,7)

1973 *Hepaticites* sp. 'a'; Douglas, p.28, pl.7, figs 1, 2; text-fig.3,6. (*non* pl.9, fig.1)

Etymology. Greek *-ensis* a suffix meaning from.

Material. Holotype NMVP167333. Paratypes MUGD3780, NMVP167331, 167334. Other specimens examined NMVP167335–167338.

Diagnosis. Habit thallose, prostrate, spreading. Thallus branches more than 35mm long, 2–3mm wide, dichotomizing at least up to three times; initial dichotomy angle of midrib 10–20°, eventual angle of thallus dichotomy 60–90°. Lamina apparently of uniform thickness (probably greater than one cell) or slightly thicker at the midrib, margins entire and parallel. Midrib prominent, up to 0.5mm wide, multiseriate, branching laterally into the lamina for the whole length of the thallus branch forming arcuate ribs which recurve to the lamina margin. Lateral ribs 1.5mm apart on the older portions of the thallus, 0.5mm apart near the branch apices. Midrib terminating diffusely as several crowded arcuate ribs at a rounded, notched apex. Sporophyte approximately 14mm long arising from the costal region of the thallus, slightly proximal to the branch apex (not at a dichotomy).

Discussion. This species can be distinguished by any of three easily recognised features. The first, the arcuate lateral ribs arising from the midrib and persisting to the lamina margins, are most easily seen in the specimens which have preserved a dark colour. In the faded yellow specimens these ribs are less clear, and often not preserved. Similar arcuate ribs in fossil hepatics were noted by Lundblad (1954, 1955) in *Marchantiolites porosus* Lundblad 1954 and *Marchantites hallei* Lundblad 1955, and by Harris (1942, 1961) in *Hepaticites wonnacotti* Harris 1942. Although their significance in these Koonwarra specimens is not clear, Harris (1942) noted that similar ribs are common in the extant Marchantiales, particularly in forms with strongly developed and persistent ventral scales attached along the ribs which are often supplemented by tuberculate rhizoids. No rhizoids or ventral scales could be distinguished in

Fig. 8. Hepaticites undulatus sp. nov. A, complete plant showing its spreading dichotomous habit, NMVP167327, ×2. B, portion of thallus in A enlarged to show paler, presumably less dense areas in intercostal region of thallus, undulate margins and apparent thickness of one cell at margins, NMVP167327, ×6.5. C, apical portions of thallus lacking the paler areas in the intercostal region, NMVP167328, ×2.

S

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sp. nov. (Figs 6,7)

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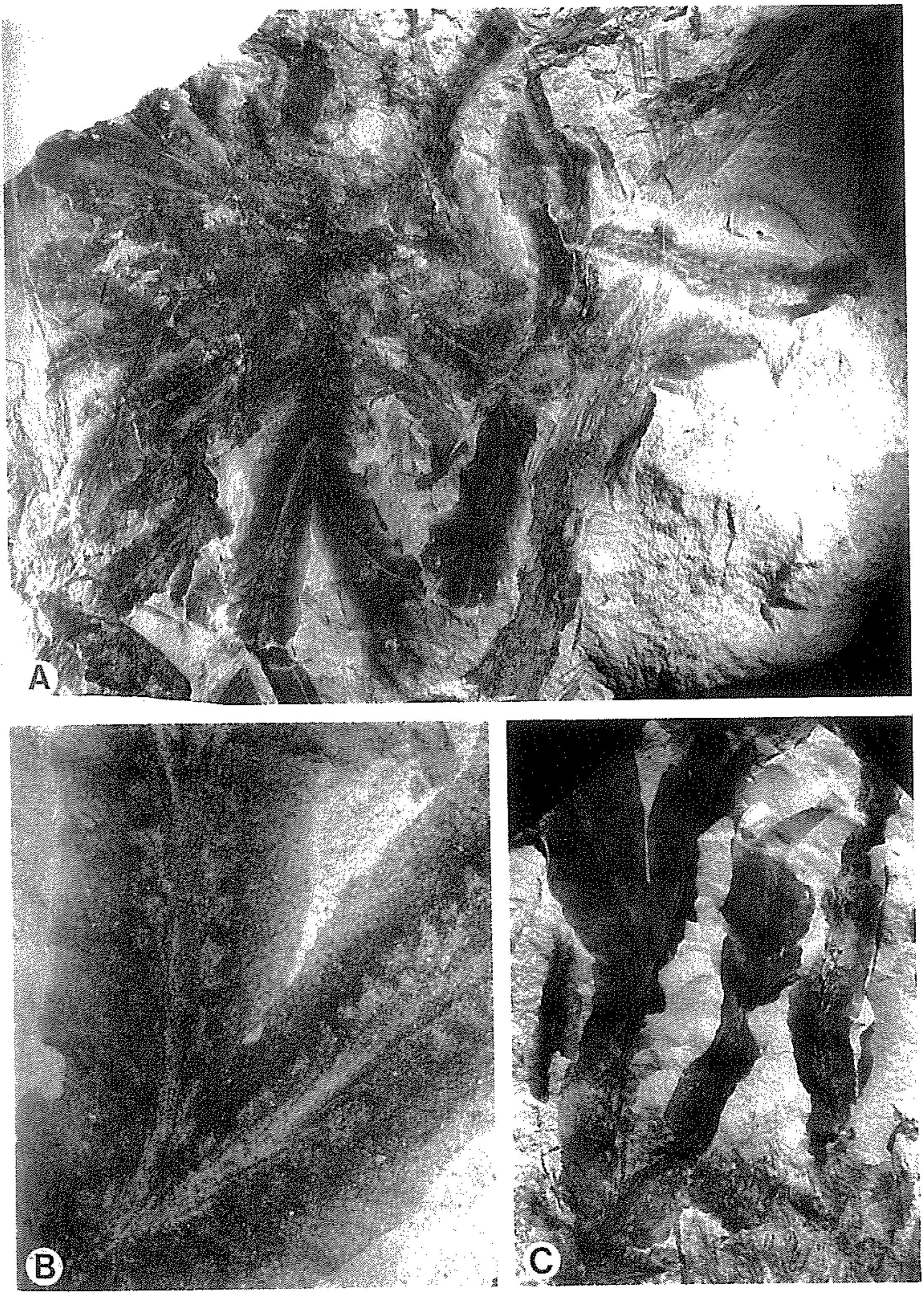

these Koonwarra specimens, and the presence of lateral ribs alone is not sufficient evidence to include this species in the Marchantiales. It is possible but unlikely, that the arcuate ribs are not branches derived from the midrib, but are the impressions of lamellae compressed flat onto the thallus surface similar to those in the liverwort *Petalophyllum* Gottsche. There is also a resemblance to some species of the filmy fern *Trichomanes* L., especially *T. mindorense* Christ 1908 (*ex icon* Copeland, 1933, pl.34, fig.1), which has a similar habit with arcuate venation, but the sporophytes discount any possibility of fern relationships.

The second diagnostic feature, which is obvious in all specimens regardless of preservation, is the nature of the thallus dichotomy and in particular the midrib. The midrib initially divides at 10–20° which is maintained for about 1mm, after which the two 'new' midribs diverge from each other at 60–90°. The angle of the thallus margin in the notch of the dichotomy is uniform.

The third feature is the stranded nature of the sporophytes which appear to arise as a pair of setae. We suggest that these plants belonged to the Anthocerotales and that their sporophytes, which were not the seta/capsule arrangement common to the other hepatics, had dehisced by the time they were preserved. In two specimens (Fig. 7B,C) they are interpreted as dehisced valves which are possibly still joined at their distal ends. Their twisted appearance is consistent with the slits having opened by hygroscopic coiling. Detail of the sporophyte bases is slightly obscure, although they seem to have an involucre which is consistent with the Anthocerotales. In the same two specimens (Fig. 7B,C) the thallus immediately surrounding the sporophyte has decayed, another common feature of the Anthocerotales. Of the extant Anthocerotales, only *Dendroceros* has a defined midrib, but judging from the available literature, no described extant species appears to be so obviously spreading and dichotomous.

Classification is frustrated to some extent by the lack of preserved anatomical structure, but Anthocerotales is suggested on sporophytic characters. Anthocerotalean spores were recorded in Victorian Lower Cretaceous sediments by Dettmann (1963, this memoir).

INCERTI ORDINIS

HEPATICITES Walton 1925

HEPATICITES UNDULATUS sp. nov. (Fig. 8).

Etymology. Latin *undulatus* — undulate: refers to the form of the margin.

Material. Holotype NMVP167327. Paratypes NMVP167328–167330.

Diagnosis. Habit thallose, prostrate, spreading, either a rosette or growing as a cluster of plants. Thallus branches up to 50mm long by 5mm wide, dichotomizing once or twice at 35–45°, apparently several cells thick about the mid-region becoming thinner towards the lamina margins which are probably only one cell thick. Margins entire, slightly undulate. Midrib prominent, 1mm wide, multiseriate, some strands arising from the midrib and entering the lamina but never persisting more than half way to the margin. Midrib terminating diffusely in a notch at the branch apex. Thallus marked by paler, presumably less dense areas 0.5mm × 0.5mm in size, which are arranged oppositely in the intercostal region one row each side of the midrib, located one third of the distance between the midrib and lamina margin, usually about 7–10 per cm, but absent on the distal portions of some thallus branches. Sporophytes not evident.

Discussion. Although *H. undulatus* is reminiscent of extant members of the Marchantiales and the Metzgeriales, it has no sporophytic remains or preserved cellular structure which would indicate to which order it belongs. To prove affiliation with the Marchantiales evidence of air pores, ventral scales, tuberculate rhizoids and gemmae are needed; poor preservation possibly accounts for the lack of the first three and the season of deposition or growth conditions are possible reasons for the absence of gemmae. To ascertain metzgerialean or anthocerotalean affinity sporophytic characters are needed.

The only structures evident in these specimens that may indicate their taxonomic position, are the "less dense" areas in the intercostal region of the thallus. They may represent 1, ventral scales (Marchantiales — although these would be expected to preserve a darker rather than a lighter colour), 2, antheridia — possibly covered by a scale as in some species of *Symphyogyna* Nees & Montagne or *Pallavicinia* Gray (Metzgeriales) or in cavities submerged in the thallus (Anthocerotales); 3, cavities containing colonies of the blue-green alga *Nostoc*, similar to those found

Fig. 9. A, Jungermanniales indet., thallus branch with two different leaf types, and enveloping, membraneous structure located distally on the branch, NMVP167339, ×5. B,C, *Riccardia koonwarriensis* sp. nov. B, spreading thallose plant, NMVP167340, ×5. C, incomplete portion of plant, NMVP167341, ×5. D, *Hepaticites* sp. thallose plant with eroded, undulate margins, NMVP167343, ×5. E, *Thallites* sp. apical portion of thallose branch, NMVP167344, ×5.

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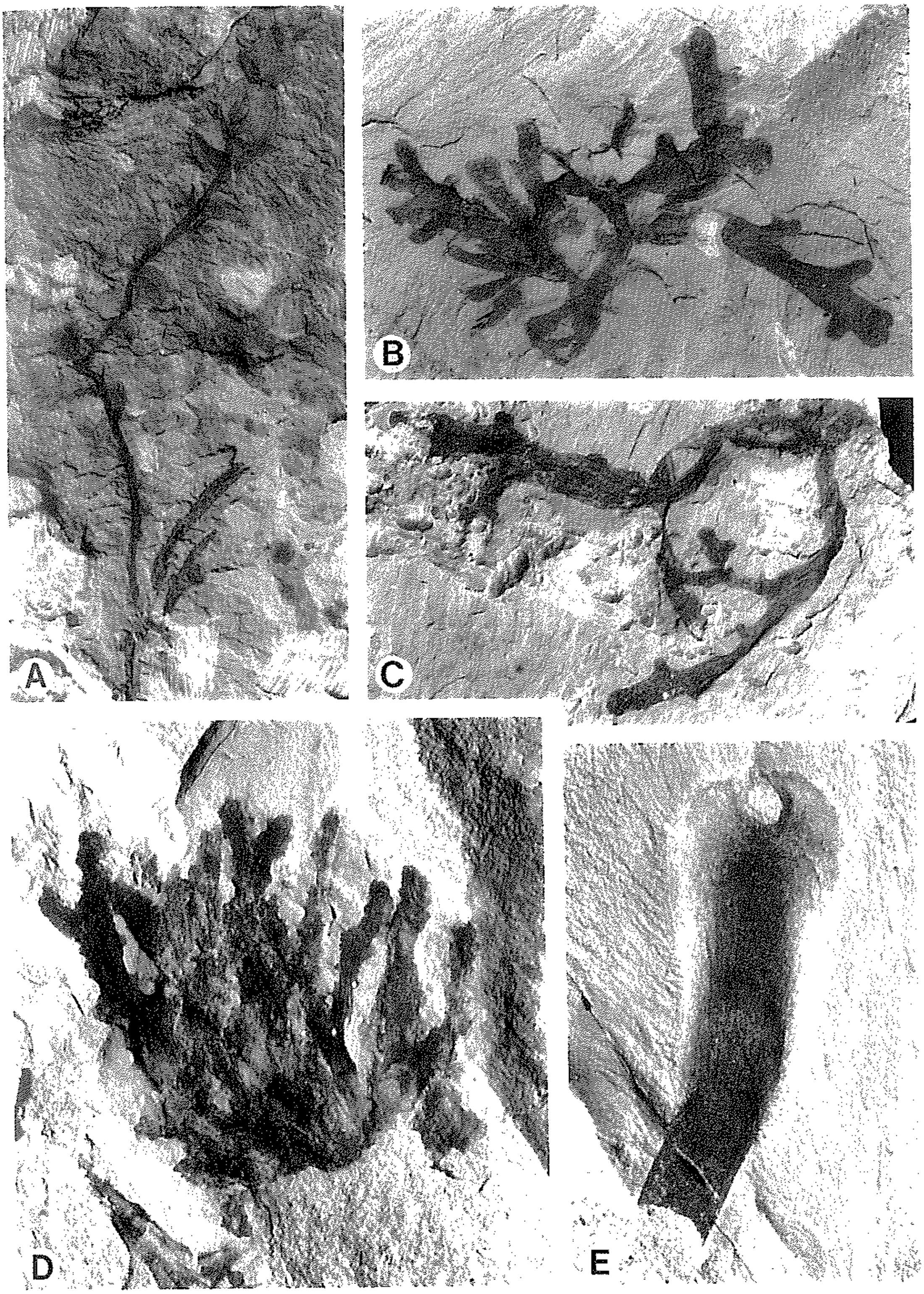

in some species of *Blasia* L. and *Anthoceros* L.; or 4, the submerged sporophytes of *Riccia* L. Their absence from the distal regions of some branches may be due either to vigorous growth or to that part of the thallus being sterile. The discovery of *Riccia*-like spores in the Victorian Lower Cretaceous (Dettmann, 1963, this memoir) further suggests affinity with that genus.

The absence of recognisable sporophytes and the lack of cellular structure prevents taxonomic placement and until specimens with spores and better preservation are found, these plants are best referred to the form-genus *Hepaticites*.

HEPATICITES sp. (Fig. 9D)

Material. NMVP167343.

Description. Plant thallose, spreading. Branches up to 10mm long, 1mm wide (basally), dichotomizing once or twice, lacking a midrib, apparently several cells thick along the centre of the branch and one cell thick about the margins; margins undulate.

Discussion. Due to the ragged edges of the thallus, this specimen appears poorly preserved. The thallus seems to have been more than one cell thick for most of its width, with a narrow, undulate margin (probably only one cell thick). No sporophytic structure is evident and there are no characters which would suggest even an approximate position within the thallose Hepaticae.

THALLITES Walton 1925

THALLITES sp. (Fig. 9E)

Material. NMVP167344, 167345.

Description. Terminal portions of thallus branches 2.5mm wide, probably several cells thick, total length unknown (measured to 15mm), expanding in width along the distal 12mm to a maximum of 5.5mm just proximal to a truncate apex. The expanded regions of the thallus appear to have been a membraneous or very thin wing which has preserved without colour, compared with the dark brown colour of the branch proper which persists almost to the apex. The unexpanded proximal portion of the branch lacks a midrib and seems to have been of uniform thickness.

Discussion. The above measurements were taken from the larger specimen (Fig. 9E). The smaller specimen had a normal branch width of less than 1mm expanding to 2mm just proximal to the apex.

Allocation of these two specimens even to the plant kingdom is somewhat uncertain, but if this is correct they probably belong to either the thallose Hepaticae or algae. Without further evidence their correct, or even approximate, position remains doubtful, and accordingly they are placed in the form-genus *Thallites*.

Division BRYOPHYTA

The few mosses recovered from the Koonwarra Fossil Bed are poorly preserved and it is difficult to determine their correct systematic placement within the Bryophyta. Two quite different types of gametophyte, and two sporophytes (although one possibly belongs to the Anthocerotales) were collected. Both capsules are large (approx. 8mm long) as far as moss capsules are concerned, and one (Sporophyte type 1) shows marked longitudinal striations.

SPOROPHYTE type 1 (Fig. 10B)

Material. NMVP167338.

Description. A capsule 5.7mm long (but may by incomplete basally), 0.5mm wide, longitudinally ribbed.

Discussion. This capsule is preserved amongst a specimen of *Dendroceros victoriensis* and associated with faint leafy remains which are probably moss gametophytes. This casts some doubt on the correct affinity of the capsule. There appears to be a cap-like structure at the apex but it is not sufficiently well preserved to be certain whether it is an operculum or a peristome. The longitudinal striations are similar to those on capsules of several extant mosses (e.g. *Ptychomnion* (Hook.f. & Wilson) Mitten., *Dicranella* (C. Mueller) Schimp., *Mesochaete* Lindb.), but could also indicate lines of dehiscence of a sporophyte belonging to a member of the Anthocerotales. The lack of organic connection makes classification of this specimen impossible.

SPOROPHYTE type 2 (Fig. 10A)

Material. NMVP167346.

Description. Moss sporophyte, seta 11mm long (may be incomplete) by 0.3mm wide, capsule

Fig. 10. A, Sporophyte type 2, moss sporophyte with twisted seta and falcate operculum, NMVP167346, ×10. B, Sporophyte type 1, sporophyte (possibly belonging to the Anthocerotales) with longitidinal striations on capsule, NMVP167338, ×10. C, Gametophyte type 1, moss gametohpyte with small, closely appressed leaves, NMVP167353, ×7. D-F, Gametophyte type 2, D, moss gametophyte, NMVP167352, ×7. E, NMVP167347, ×7. F, branched portion of thallus, NMVP167348, ×7. G, Bryophyta indet., NMVP167354, ×7.

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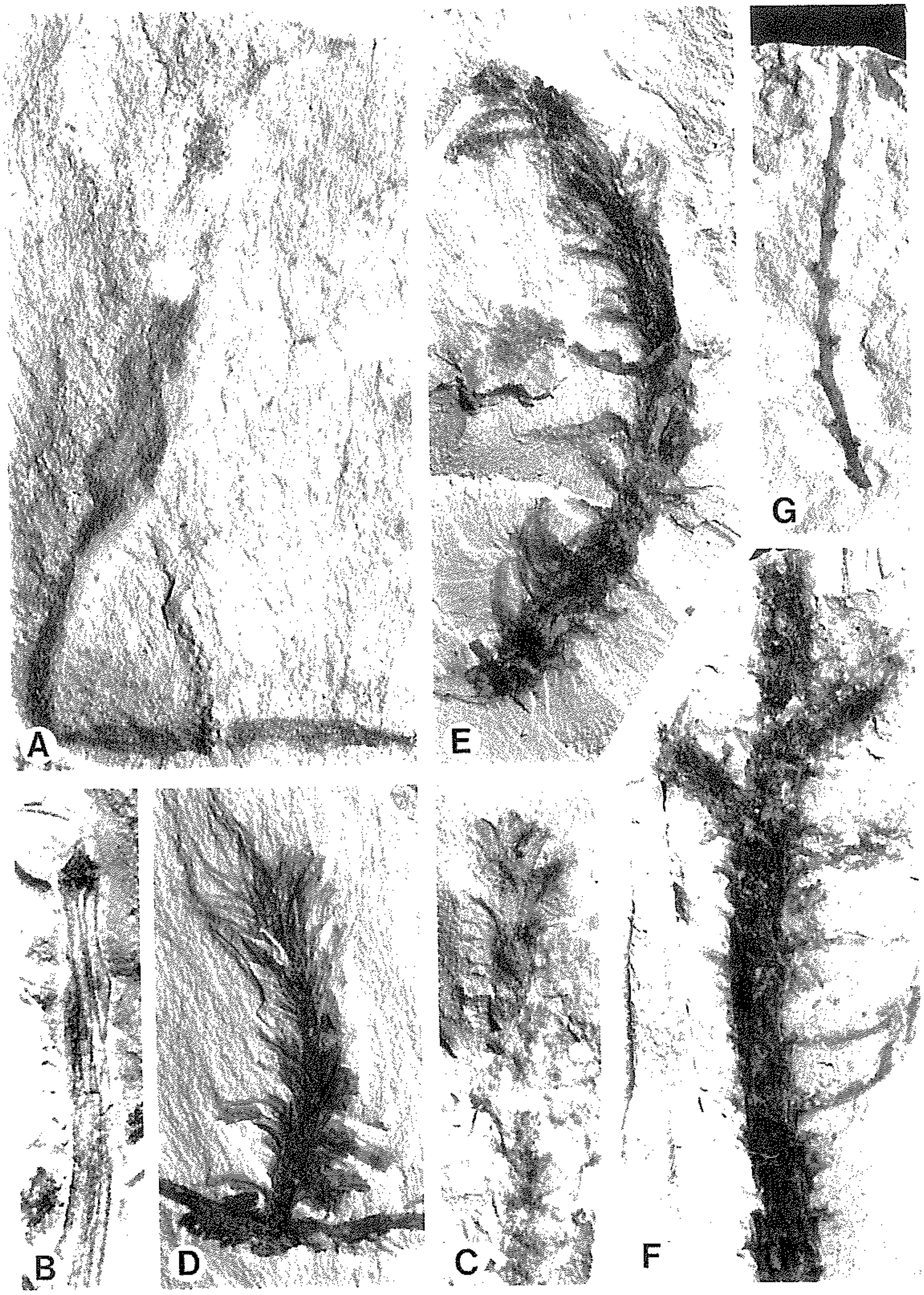

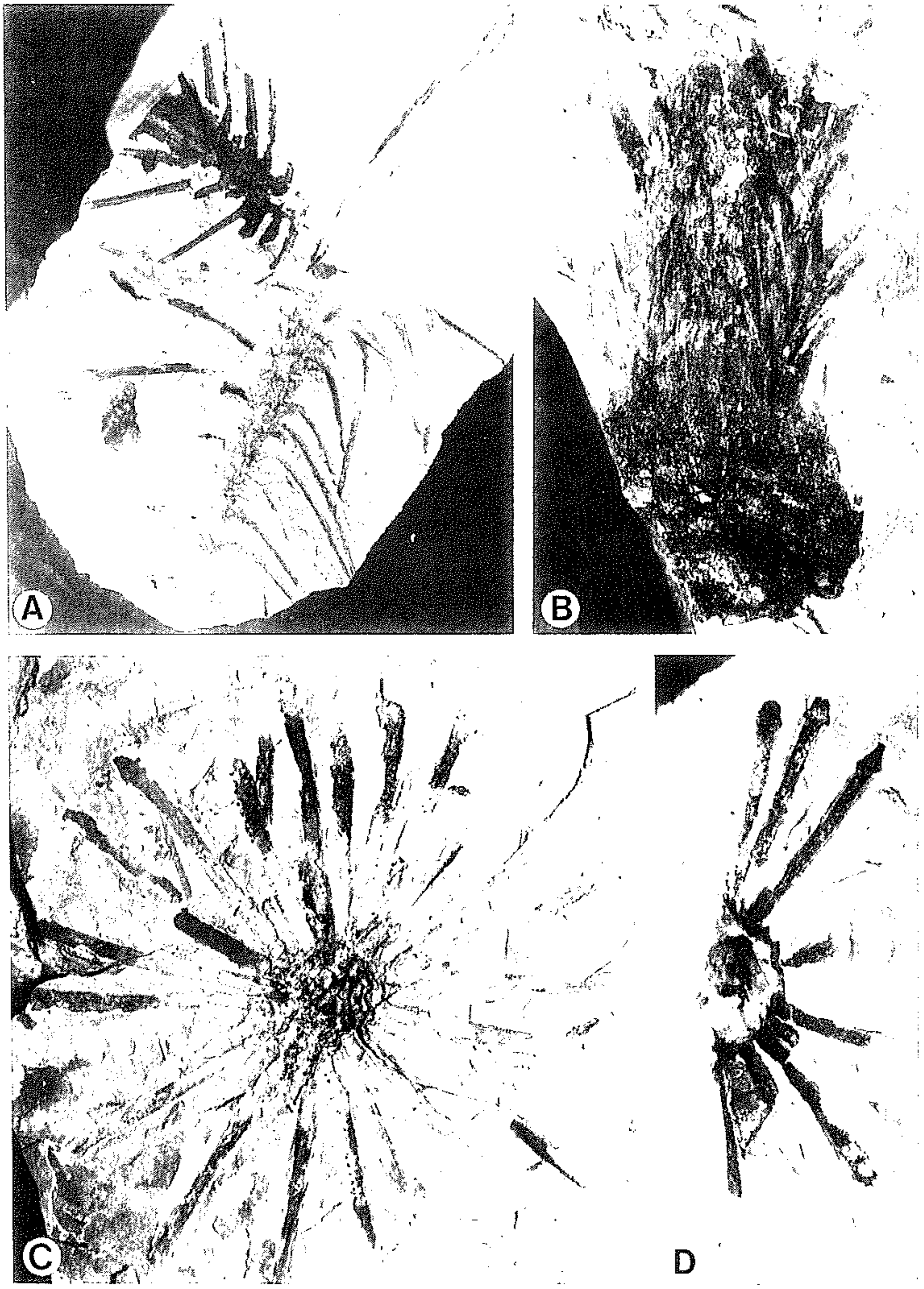
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8.5mm long (base to peristome 6mm, operculum 2.5mm) by 0.8mm wide. Operculum falcate.

Discussion. The imagery of this fossil is faded and does not reveal any surface texture. The seta is twisted several times but whether this is due to hygroscopic coiling (which is a feature of many extant mosses) or is an artifact of preservation is uncertain. Presumably a hygroscopically coiled seta would straighten to some extent when immersed in water (as this one surely has been), but may not uncoil completely.

Because moss taxonomy employs gametophytic characters (e.g. leaf characters — nerve and alar cells) this poorly preserved sporophyte cannot be conclusively placed. However, available characters (shape, size, twisted seta, and curved operculum), allow a comparison with sporophytes of several extant mosses. Amongst those bearing the closest resemblance in the southern Australian flora are species belonging to *Tortula* Hedwig and *Atrichum* P. Beauv. Species of *Rhacomitrium* Brid., *Ditrichum* E. Hampe, and *Barbula* Hedwig have sporophytes with curved opercula and twisted setae which are similar in shape but smaller in size.

GAMETOPHYTE type 1 (Fig. 10C)

Material. NMVP167353.

Description. Plant probably erect, preserved length 12mm, with short, appressed, ovate, leaves.

GAMETOPHYTE type 2 (Fig. 10D–F)

1973 *Thallites* sp. 'c': Douglas, p.32, pl.8, fig. 1, text-fig.3,10.

Material. NMVP167347–167352, 167389.

Description. Habit branched, preserved lengths up to 32mm (total lengths unknown), bearing leaves along its entire length (although they appear to be decayed basally), axis up to 1mm thick, overall plant habit probably dendroid; leaves linear, up to 4mm long by 0.7mm wide with a distinct midrib, acute apices, vein non-excurrent; occasional branches arising from main axis at 45°.

Discussion. As these specimens are only preserved as colour marks on the matrix even their placement in the Bryophyta is not absolutely certain. Many extant moss gametophytes would fossilize in compression with a similar appearance. Dettmann (this memoir) recorded spores similar to those of the extant moss *Sphagnum* L.; the morphology of these megafossils, although lacking anatomical detail, is not inconsistent with such a determination.

BRYOPHYTA indet. (Fig. 10G)

Material. NMVP167354, 167355.

Description. Axis preserved up to 16mm long, 0.5mm thick, with ?two rows (compressed) of small, distichously arranged ?protuberances.

Discussion. Both the nature and affinity of these specimens are uncertain, but they appear similar to the 'droppers' of the extant leafy liverwort *Bazzania* Gray.

Division LYCOPHYTA

Order LYCOPODIALES

Family LYCOPODIACEAE

LYCOPODIUM L. 1753

LYCOPODIUM sp. (Fig. 11A)

Material. NMVP167356.

Description. Plant wholly or partially erect, length of stem preserved 35mm (total length unknown), up to 2.5mm wide. Leaves up to 12mm long, 0.5mm wide, recurving, each containing a single midvein arising at 50° to the stem. Leaf margins straight and parallel, leaf bases appearing to sheath the stem, apices not preserved.

Discussion. This is the only specimen from Koonwarra referrable to the Lycopodiales. Douglas (1973) tentatively recorded some strobili as Lycopodiales cones but for reasons discussed later they are considered to belong to the Coniferales (see *Podostrobus elongatus*).

Although the specimen described here has no structure preserved which would allow definite classification to the Lycopodiales, it is placed in that order on the basis of its gross morphology. As only a small portion of stem is preserved little can be concluded about the habit of the whole plant, but the recurved leaves arising from all sides of the stem suggest an erect habit. The specimen was broken before preservation and the apical part is heavily mineral-stained.

Order ISOETALES

Family ISOETACEAE

Fig. 11. A, *Lycopodium* sp. broken, medial portion of stem with distal part stained dark by mineral accumulation, NMVP167356, ×2. B–D, *Isoetes bulbiformis* sp. nov. B, plant compressed laterally showing the leaves arising distally from the corm, NMVP167357, × 2. C, plant compressed dorsiventrally showing the leaves radiating from the corm (centre), NMVP167358, × 2. D, incomplete portion of plant compressed dorsiventrally showing the flared leaf tips, NMVP167359, × 3.

ISOETES L. 1753

ISOETES BULBIFORMIS sp. nov. (Fig. 11B–D)

1904 Incertae sedis; Seward, p.183, fig.47.
1973 *Isoetes*? sp.; Douglas, p.50, pl.11, figs 1,2, text-fig.5,1 (non pl.12, figs 1,2).
?1973 *Phyllotheca* sp. 'a'; Douglas, p.59, pl.15, figs 1, 2; text-fig. 6,3.

Etymology. Latin *bulbus* — a swelling, and *forma* — shape; refers to corm shape.

Material. Holotype NMVP167357. Paratypes NMVP167358, 167359. Other specimens examined NMVP167360–167362.

Diagnosis. Plant axis up to 35mm in length, giving rise to up to 30 linear, microphyllous leaves. Leaves arising spirally or in several whorls from a basal corm which measures 11mm long by 15mm wide. Leaves up to 23mm long, 1.5mm wide, linear, margins straight and parallel, expanding slightly at the tips, apices acute.

Discussion. Of the six plants collected, five are flattened dorsiventrally suggesting preservation in life position. In these five specimens the leaves radiate from the corm which is represented at the centre as a cast containing carbonaceous remains. The sixth specimen (Fig. 11B) is compressed laterally, showing differentiation into the corm and linear leaves. Roots, leaf vascular traces, and fertile structures are not recognisable. The amount of carbon derived from the corm indicates a substantial structure; the leaves also appear to have been quite solid. The significance of the flared leaf tips is unknown — they may represent the location of sporangia, although this would differ markedly from the basal sporangia of extant *Isoetes* and the medial sporangia of *Stylites* Amstutz.

Comparison of these plants with the Isoetales is based on external similarities, namely the corm and leaves. As there is no evidence of corm dichotomy characteristic of the extant *Stylites*, or vertical ridges on the base of the stem which would allow affiliation with the fossil *Nathorstiana* Richter, it seems these plants compare most closely with *Isoetes*. They share several features with *Isoetes*, most notably the short corm which is wider than it is high.

If preserved in life position, further support is added to their classification in the Isoetales. It would also make them the only plants found which were growing in the water at the Koonwarra site at the time of sediment deposition. If so their size suggests that at least two or three growing seasons elapsed between deluges large enough to bring sufficient detritus to completely bury a living surface layer.

Division SPHENOPHYTA

Order EQUISETALES

PHYLLOTHECA Brongn. 1828

PHYLLOTHECA WONTHAGGIENSIS (Chapman 1914) comb. nov. emend. (Fig. 12)

1914 *Equisetites wonthaggiensis* Chapman, p.317, pl.62, fig.1.
1954a *Equisetites wonthaggiensis* Chapman; Medwell, p.81.
1969 Angiosperm sp. 'b'; Douglas, p.228, pl.42, figs 1, 3; text-fig.4,7.
1973 *Equisetites wonthaggiensis* Chapman; Douglas, p.57, pl.13, figs 1, 2; text-fig.6,1.

Material. Holotype NMVP12893 from Wonthaggi Bore 175, at 650 feet. Other material NMVP167363–167367, 167371–167387 (aerial shoots); NMVP167368, 167388 (rhizomes); NMVP167369 (tubers), NMVP167370 (all three vegetative types closely associated).

Diagnosis. Erect, leafy, aerial shoots arising from a rhizome, total stem lengths unknown (preserved lengths up to 35 mm), 0.5–1.0mm wide. Stems segmented, internodes longitudinally ribbed, up to 10mm long, decreasing in length distally along the shoot, the terminal internode enclosed by the subtending nodal sheath. Two to eight leaves arising from each node (usually 3–4, but with 5–8 at the terminal nodes), united basally into a sheath for one-third to one-half of their length but free from each other distally, sheath 1.0–1.5mm long. Free leaf ends 2.5mm long by 0.6mm wide, linear-elliptical, each with an acute apex, a slightly constricted base, and a prominent, persistent midrib. Stems branching occasionally, lateral shoots arising from the base of the leaf sheath (at the node).

Rhizome (presumably underground) segmented, constricted at the nodes. Internode up to 10mm long by 3mm wide, not longitudinally ribbed but crinkled in appearance. Nodes up to 3mm wide, lacking leafy structures but having a dark coloured band which may be the remnants of scale-like leaves. Tubers and lateral roots situated

Fig. 12. Phyllotheca wonthaggiensis (Chapman) comb. nov. A, aerial shoot showing stippled texture of stem, NMVP167363, ×5.5. B, medial portion of aerial shoot, NMVP167364, ×5.5. C, apical portion of aerial shoot showing elliptical, free leaf ends with prominent midvein, NMVP167365, ×5.5. D, apical portion of aerial shoot, NMVP167366, ×5.5. E, branching aerial shoot showing branch scars, NMVP167367, ×5.5. F, rhizome, NMVP167368, ×1.5. G, rhizome with tubers, NMVP167369, ×2.

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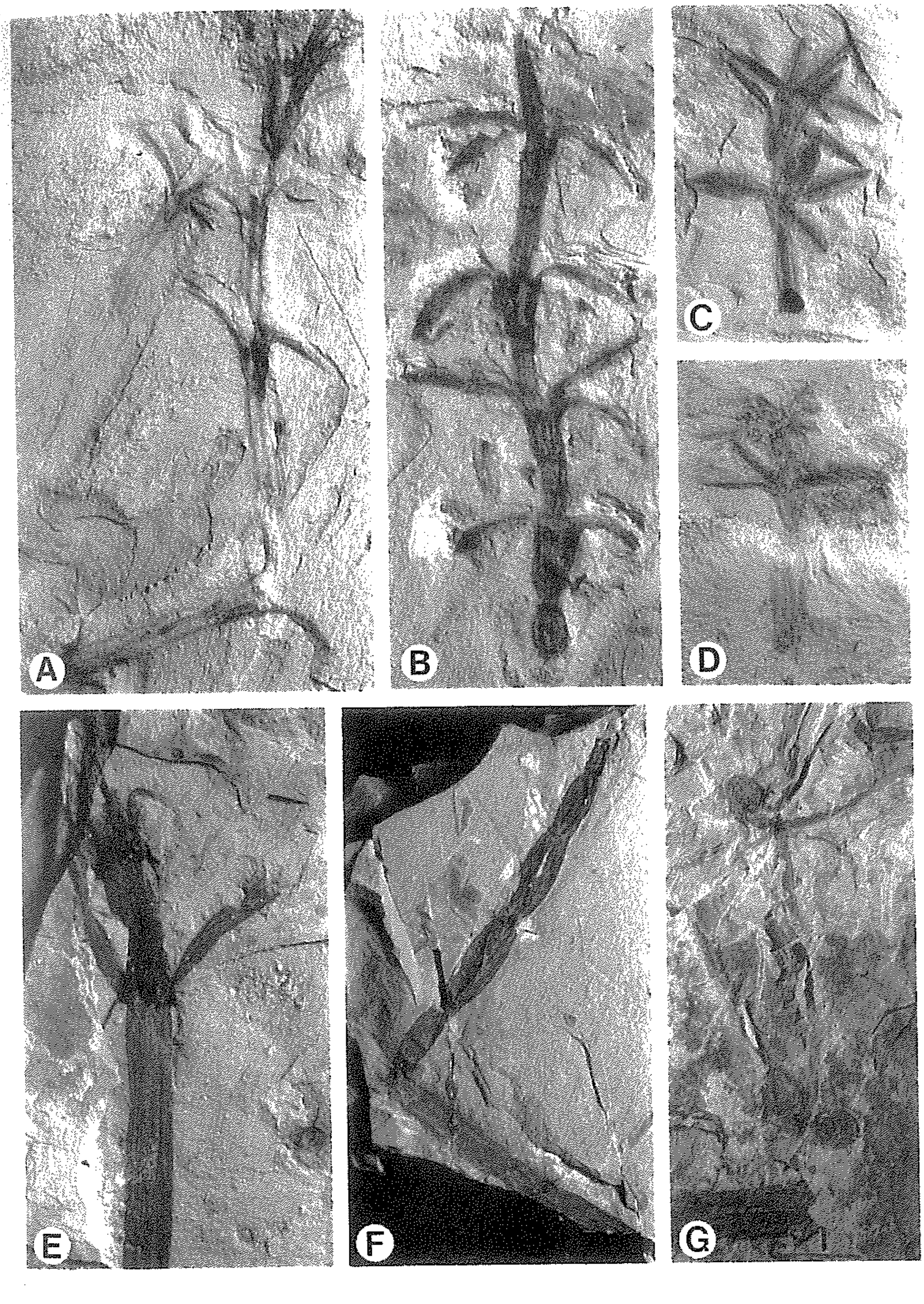

at some nodes of smaller rhizomes. Tubers spherical-oval, 5mm long by 4mm wide.

Discussion. The three vegetative forms (aerial shoots, large rhizomes, small rhizomes with tubers) ascribed to this species have not been found in organic connection but their close association on one specimen (NMVP167370), which is almost devoid of other plant material, strongly suggests they belonged to the same plant. The segmented rhizomes were first described from Wonthaggi bore holes by Chapman (1914) as *Equisetites wonthaggiensis* and similarly listed by Medwell (1954a). Douglas (1973) recorded the three vegetative types; the rhizomes and tubers under Chapman's species *E. wonthaggiensis* and the aerial shoots as an angiosperm of uncertain affiliation (Douglas, 1969).

All three types undoubtedly belong to the Sphenophyta and can be placed with reasonable certainty in the Equisetales, as similar growth habit and morphology is exhibited by the only extant sphenophyte, *Equisetum*. Leaves are not obvious at the nodal constrictions of *P. wonthaggiensis* rhizomes but their colour is sufficiently dark to assume a whorl of reduced scale leaves. The tubers are presumably equivalent to the swollen branches of one internode length which are borne on the rhizomes of extant *Equisetum* species and which provide capacity for vegetative propagation. In *P. wonthaggiensis* they are located on slender, noded but not constricted, secondary branches from the larger, constricted rhizomes. Rhizoids arise from the nodes of both the thick and slender rhizome types and are associated with the tubers. Noded aerial shoots are preserved up to 35mm long and although incomplete, their delicate nature suggests a small plant unlikely to have exceeded 100mm in height. Ribbed internodes, which are longest toward the base of the plant, are often preserved with a stippled texture (also observed in several of the *Equisetum* specimens described below) which may be attributable to a siliceous epidermis. Leaves arise in a whorl at each node and are initially fused into a leaf sheath which is appressed to the stem, but are free from each other distally and diverge from the stem for at least half of their length. The prominent midrib is a continuation of an internode vascular trace. Lateral branches are preserved arising in pairs at occasional nodes, although the presence of leaf scars suggests a possible whorl of branches. None of the shoots or branches had remains of cones or fertile structures.

The aerial shoots of *P. wonthaggiensis*, while similar in habit to *Equisetum*, have leaves which differ from the reduced, pointed teeth of the leaf sheaths of the extant members of the genus. The size of their free ends (compared to the length of the fused sheath), their shape, and the prominence of the single vein resembles the leaf whorls of some species of *Annularia* Sternberg, a Palaeozoic Calamitales. *Phyllotheca*, recorded from both the Palaeozoic and Mesozoic, has free leaves arising from a fused sheath, and it is this feature on which the assignment of the Koonwarra material is based. Townrow (1955) noted that most post-Palaeozoic *Phyllotheca* species could, with equal justification, be placed in *Equisetum* and considered the former genus to be a less developed but close relative of *Equisetum* which had retained branched sporangiophores. Fertile remains were not found at Koonwarra. The sterile stems are placed here in *Phyllotheca* on the basis of leaf characters, but their probable close relationship to *Equisetum* is emphasised. Saksena (1954) reconstructed two Permian species of *Phyllotheca*, one from India and the other from the Newcastle Series, eastern Australia; they had nodal sheaths with prominent free leaf ends located distally on the shoot, while the basal nodal sheaths had only pointed vestigial leaf tips. This raises the question of the relationship between these small Koonwarra shoots and the larger equisetaceous stems found in the same strata which have the characteristic *Equisetum* leaf sheaths. Although the possibility that they belong to one taxon does remain, there is no evidence of organic attachment or even close association to warrant species aggregation. For the time being, a separate description enables a more accurate assessment of the combinations of characters they possess and the ways in which they differ.

Family EQUISETACEAE

EQUISETUM L. 1753

EQUISETUM sp. 1 (Fig. 13C–H)

Material. NMVP167396–167409.

Description. Stems erect, complete lengths unknown but preserved lengths of up to 30mm

Fig. 13. A,B, *Equisetum* sp. 2. A, portion of aerial shoot showing internodes decreasing in length distally along the shoot, NMVP167390, ×5. B, portion of aerial shoot showing awn-like extensions of the leaves in the two most basal nodal sheaths, NMVP167391, ×7. C–H, *Equisetum* sp. 1. C, portion of stem with a nodal sheath which has broken in two (distally) showing stippled texture of nodal sheath, NMVP167396, ×3. D, portion of stem which has frayed at a broken end, NMVP167397, ×3. E, portion of stem which has frayed at a broken end, NMVP167398, ×5. F, portion of stem, NMVP167399, ×3. G, nodal sheath, NMVP167400, ×5. H, portion of stem with branch scars and ?injury marks, NMVP167406, ×5.

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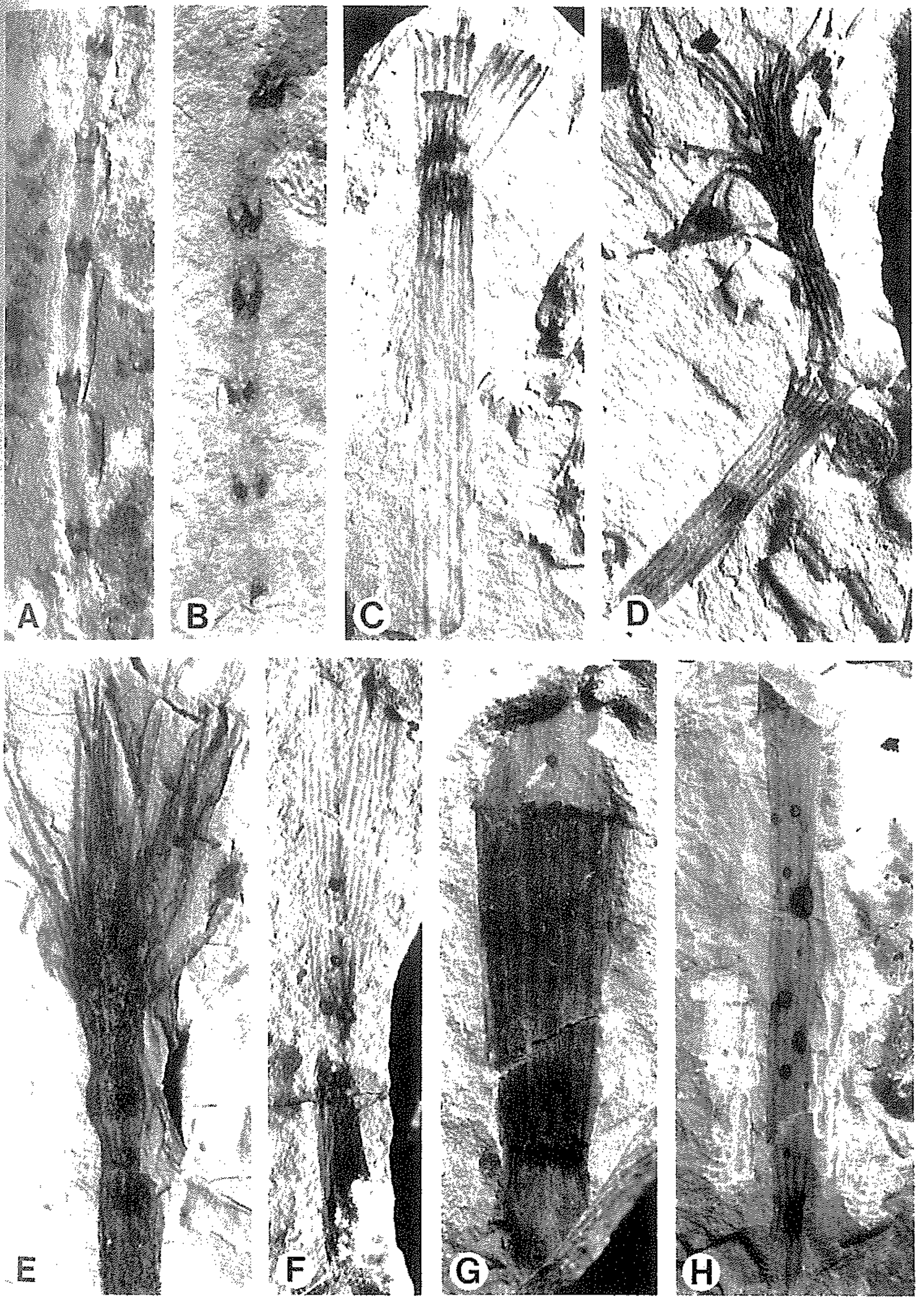

represent only small portions of the shoot, up to 3mm wide, segmented into a node/internode habit. Internodes longitudinally ribbed (up to 10 ridges counted). Leaves equal in number to internode ridges, arising in a whorl from each node, fused into a leaf sheath with only the apex of each leaf free. Leaf sheaths 5–11mm long, closely appressed to the stem.

Discussion. The possibility that all the equisetaceous specimens from Koonwarra belong to the same species was considered in the discussion of *Phyllotheca wonthaggiensis* (above). One of the most marked likenesses is the stippled texture of some stems and leaf sheaths which may be due to a siliceous epidermis. None of the stems had branches attached but scars at the base of some leaf sheaths indicate the position of abscissed lateral shoots. The leaves are fused into a sheath for their entire length (excepting the tips) and remain appressed to the stem. Several of the specimens (Fig. 13D,E) have tufted apices which appear leafy, but this is only where the broken stem has frayed. No fertile specimens were found.

Although only small portions of stem are preserved, there is little doubt that they belong to *Equisetum*, but as subdivision of the genus is based on stomatal characters further taxonomic assignment is not possible for this material. They resemble several Mesozoic and extant species of *Equisetum*, (e.g. *E. laterale* Phillips 1829 and *E. bryanii* Gould 1968 from the Mesozoic of southeastern Queensland (Gould, 1968), and *E. laevigatum* A. Braun 1865 (extant)).

EQUISETUM sp. 2 (Fig. 13A,B)

1969 Sphenopsid? stem; Douglas, pl. 42, fig. 2.
1973 *Equisetites* sp. 'b'; Douglas, p. 59, pl. 14, fig. 8

Material. NMVP167390–167395.

Description. Aerial shoots, preserved lengths up to 57mm (complete lengths unknown), 0.7mm wide, segmented into a node/internode habit. Internodes not noticeably ribbed, up to 10mm long basally, decreasing in length distally along the stem to about 1.5mm long near the apex. Leaves arising in a whorl of six from each node, fused basally into a sheath for two-thirds to three-quarters of their length, the acute apices remaining free but closely appressed to the stem, leaf length usually less than 1mm. Stem branching not evident, fertile structures not present.

Discussion. These stems which exhibit some variation are the smallest representatives of the Equisetales collected at Koonwarra and differ from *Phyllotheca wonthaggiensis* by having short, acute, appressed, free leaf tips. It is possible that they are actually lateral branches that have been shed from the nodes of the previously described *Equisetum* sp. 1; similar whorls of lateral branches are common in extant *Equisetum* species.

Division PTERIDOPHYTA

Class FILICOPSIDA

Order FILICALES

SPHENOPTERIS (Brongn. 1822) Sternberg 1825

SPHENOPTERIS WARRAGULENSIS McCoy 1892 (Fig. 14)

1890 *Sphenopteris warragulensis* McCoy; Murray, p. 18.
1892 *Sphenopteris warragulensis* McCoy; McCoy *in* Stirling, p.11, figs 6,8.
1892 *Sphenopteris ampla* McCoy; McCoy *in* Stirling, p.11, figs 7,9.
1892 *Sphenopteris crassinervis* McCoy; McCoy *in* Stirling, p.13.
1900 *Sphenopteris ampla* McCoy; Stirling, p.4, pl.3, figs 1,5. (non pl.3, figs 2,6).
1900 *Sphenopteris warragulensis* McCoy; Stirling, p.4, pl.4, figs 1–6.
1900 *Sphenopteris crassinervis* McCoy; Stirling, p.4, pl.3, figs 3,7.
1900 *Sphenopteris fosteri* Stirling, p.4, pl.3, fig.17.
1904 *Sphenopteris ampla* McCoy; Seward, p.165, figs 10–16.
1954a *Sphenopteris hislopi* Oldham & Morris; Medwell, p.91.
1973 *Sphenopteris warragulensis* McCoy; Douglas, p.73, pl.20, figs 1, 2; text-figs 7,6–9.

Material. Neotype NMVP21341, Jeetho Valley, designated Douglas (1973). Other material NMVP167410–167412, 167424–167440 from NMVPL425 and NMVP167413–167423 from NMVPL426.

Description. Fronds bipinnate (at least), preserved lengths up to 145mm (complete fronds unknown). Rachis 1.5mm wide, lacking a lamina wing.

Pinnae sub-oppositely arranged, inserted laterally or slightly dorsally on rachis, attachment

Fig. 14. Sphenopteris warragulensis McCoy. A, sterile pinna, NMVP167411, ×1. B, sterile frond, NMVP167410, ×0.8. C, sterile pinna, NMVP167412, ×1. D, partially fertile pinna from Cape Horn, NMVP167413, ×1.3. E, fertile pinna from Cape Horn, NMVP167414, ×1.3. F, sorus from Cape Horn showing protruding sporangia, NMVP167415, ×10.

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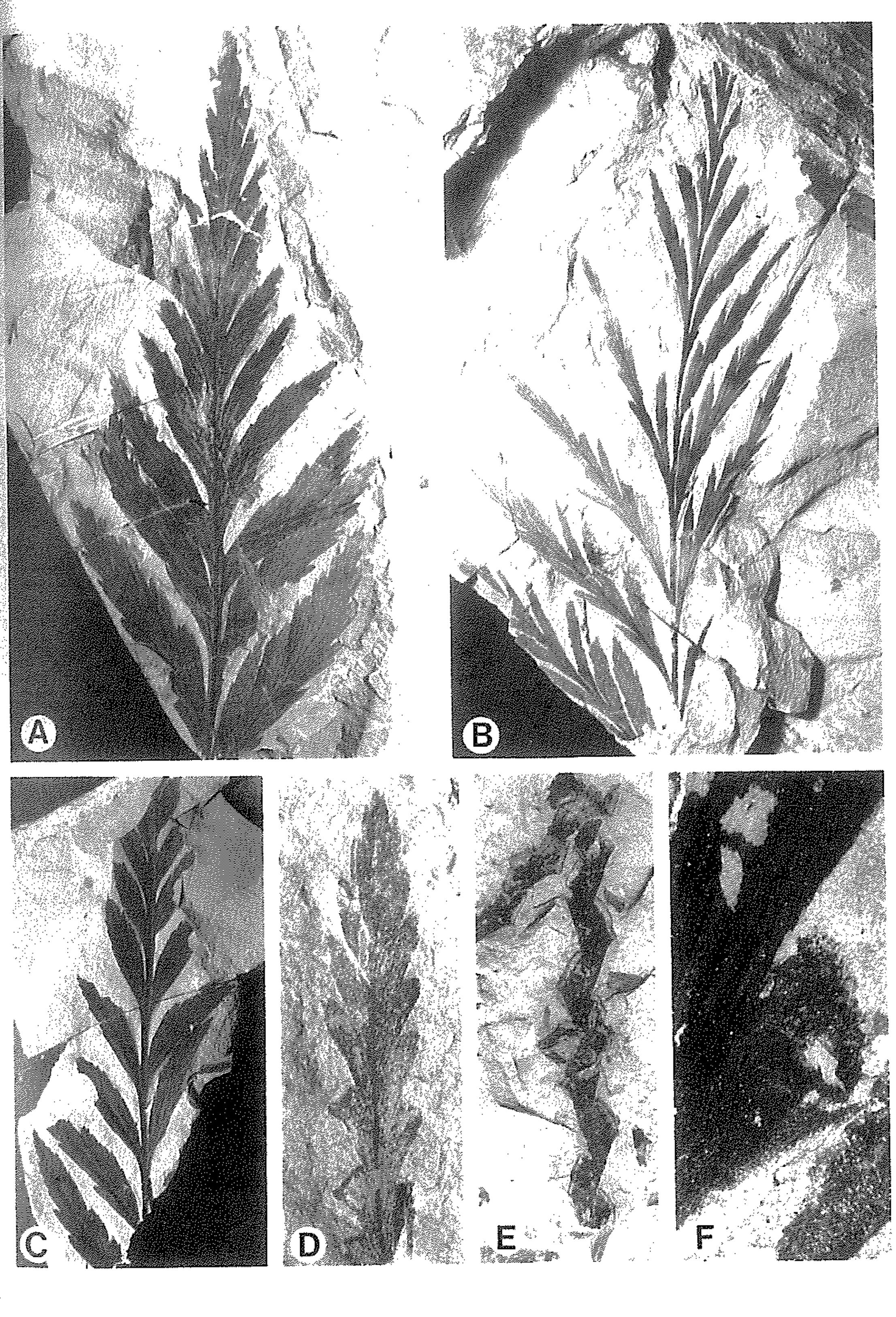


sub-petiolate, diverging from rachis at 40°. Pinna size and shape varying along frond; basal pinnae well defined (margins incised almost to the rachilla), becoming reduced distally along the rachis (margins entire, rachilla ill-defined), the terminal few pinnae reduced to segments resembling pinnules. Larger pinnae measuring up to 130mm long by 50mm wide.

Pinnules opposite to distichous, inserted laterally on the rachilla, attachment adnate by a slightly constricted base. Venation sphenopteroid, one vein only entering each pinnule from the rachilla. Midvein persistent for two-thirds to three-quarters of pinnule (fading into terminal branching), giving rise to up to eleven, more or less parallel, secondary veins which emerge at an acute angle (less than 30°) and dichotomize once or twice before reaching the margin. Initial secondary vein katadromic. Pinnule margins serrate, and in larger pinnules incised, each veinlet ending at the tip of a serration, each group of veinlets derived from the same secondary vein being contained within successive incisions. Pinnules increasingly reduced distally along the rachilla, the larger pinnules measuring up to 50mm long by 11mm wide.

Fertile pinnules reduced in length. Sori marginal or submarginal, broad, linear to crescent-shaped, one per pinnule, containing numerous leptosporangia, spore type unknown.

Discussion. These fragmentary specimens show great variation, and while this may partly reflect the growth habit of the plant, it is also almost certainly a reflection of the small pieces of foliage which have been preserved. For example, the pinnae toward the base of the frond are well-defined, as are the pinnules toward the base of each pinna, but toward the apex of the frond the pinnae are reduced to the extent that the frond becomes pinnatifid rather than pinnate, and eventually grades into segments which can more or less be referred to as pinnules. Thus, the distal portion of the frond is morphologically inseparable from a well-defined basal pinna. Similarly, the pinnules become reduced distally along the pinna, of which the distal portion is inseparable from a well-defined basal pinnule. This similarity of parts also applies to the rachilla and venation, the rachilla fading distally into terminal branching similar to pinnule venation.

Most pieces of this foliage type are pinnae or small sections of frond bearing only a few incomplete pinnae, making it difficult to determine with any certainty which part of a frond it represents, or whether the range of characters exhibited by the specimens is due to intraspecific variation or the range of growth form on very similar fronds. Nearly all the variation at Koonwarra is in the degree of dissection of pinnule margins, size and shape of pinnules, spacing of pinnules along the rachilla (and pinnae along the rachis), and the width of the lamina wing along the rachilla - variable characters which in extant ferns show a similar range along a single frond.

Although no fertile *S. warragulensis* foliage was found at Koonwarra, material from Cape Horn (near Cape Otway) in the Otway Group allows some interpretation of the fertile condition of this species. The broad sori which occupy most of the margin of the reduced pinnules make this species easily recognisable in the fertile condition. Pinnule length may be decreased by as much as two-thirds, appearing distally truncated; the sorus forms along the truncation. Sorus shape varies along the pinna, basal pinnules (which in the sterile foliage would have been the longest) having slightly curved convex sori, distal pinnules having straight sori, and medial pinnules having sori which grade between the two. In most specimens sori are orientated perpendicular to the pinnule axis. The extreme pinnule reduction makes the sphenopteroid venation almost unrecognisable; the basal sori receive several vein endings, while distal ones often terminate a single vein.

Although details of the sorus are unknown, its habit and position are reminiscent of several extant genera e.g., *Lindsaea* Dryander *ex* J.E. Smith, *Adiantum* L., *Ochropteris* J. Smith and *Cheilanthes* Sw. of the Adiantaceae, and *Histiopteris* (J.G. Agardh) J. Smith of the Dennstaedtiaceae. The protrusion of mature sporangia distally from the sorus (Fig. 14F) seems to exclude the possibility of a strongly recurved sorus characteristic of *Adiantum* and *Ochropteris*, while the apparent absence of an indusium (although it is unlikely that it would be evident even if preserved), leaves some doubt about affiliation with the lindsaeoid and dennstaedtiaceous ferns. The truncate apices of fertile pinnules and the absence of sporangia at the edge of the immature sori suggest the lamina may be slightly recurved to protect the developing sporangia as in *Cheilanthes*. Some fertile pinnae have sterile apical pinnules but others have a continuous fertile region around the margin of the apex and several most distal segments in a similar manner to *Cheilanthes tenuifolia* (Burm. f. 1768) Sw. 1806, and *Lindsaea trichomanoides* Dryander 1797.

At Cape Horn sterile and fertile *S. warragulensis* foliage occurs with fertile foliage referred to as *Adiantites lindsayoides* by Seward (1904) and Douglas (1973). Until now no sterile foliage has been attributed to *A. lindsayoides*, although characters discussed below in consideration of that species show it to be the fronds allocated previously to *Sphenopteris mccoyi* (Seward 1904) Douglas 1973. *Adiantites lindsayoides* also has one continuous marginal sorus per pinnule and is easily confused with *S. warragulensis* when fragmentary. It can be distinguished from *S. warragulensis* by the shape of its pinnule margins (and thus the sori) which are usually semi-circular but tend to an obtuse shape in some specimens. Although occasional basal pinnules of *S. warragulensis* have slightly curved sori, they do not approach the shape or regularity of *Adiantites lindsayoides*. Veins in *A. lindsayoides* are more prominent, numerous, and spreading than in *S. warragulensis* which has condensed, sub-parallel venation.

Taxonomy of *Sphenopteris* foliage is particularly confused. *Sphenopteris* (Brongn.) Sternberg has been widely used (and abused) for sterile foliage of unknown affinity (either fern or seed fern) showing the characteristic sphenopteroid pinnule venation. *Sphenopteris*, therefore, should be used as a form-genus for foliage of which the fertile form is either unknown, or provides insufficient evidence for allocation to a natural taxon.

Maithy (1972), after examining several types of foliage from the Indian Lower Gondwanas previously allocated to *Sphenopteris*, concluded that although their venation was sphenopteroid, the pinnules did not meet Brongniart's other criteria of a cuneate base onto a naked rachilla, but were adnate and decurrent on an alate rachilla. Establishment of *Neomariopteris* by Maithy (1972) to accommodate this foliage type, seems superfluous; division of a form-genus into several of the same rank serves only to complicate taxonomy without clarifying natural groupings. Although *S. warragulensis* has the features quoted by Maithy (1972) for *Neomariopteris* we prefer to use *Sphenopteris*. As noted above in *S. warragulensis*, the pinnule attachment and the extent to which they are decurrent varies along the same frond. In this treatment of the Koonwarra fern flora all foliage of uncertain phylogenetic relationship which has pinnules supplied by one vein, either straight or flexuose, and exhibits katadromic sphenopteroid venation, has been included in the form-genus *Sphenopteris* regardless of the mode of pinnule attachment.

Sphenopteris warragulensis sterile foliage was first figured by McCoy in Murray (1890), the fertile condition being later illustrated in Stirling (1892). Douglas (1973) designated NMVP21341 (Stirling, 1892, fig. 6) as the holotype (actually a neotype) but citing this piece of fertile foliage as 'holotype' was unfortunate, first because the species is included in a form-genus for sterile fronds, and secondly because the first specimens illustrated (McCoy in Murray, 1890) were portions of sterile frond. Also illustrated by McCoy (in Stirling, 1892) are two pieces of sterile pinnae considered by him to be a different species *S. ampla* McCoy 1892, but which in the light of the numerous specimens collected this century are best interpreted as distal portions of *S. warragulensis* fronds. Stirling (1900) erected a further species *S. fosteri*, which together with *S. crassinervis* McCoy 1892, and *S. ampla* belongs to *S. warragulensis*.

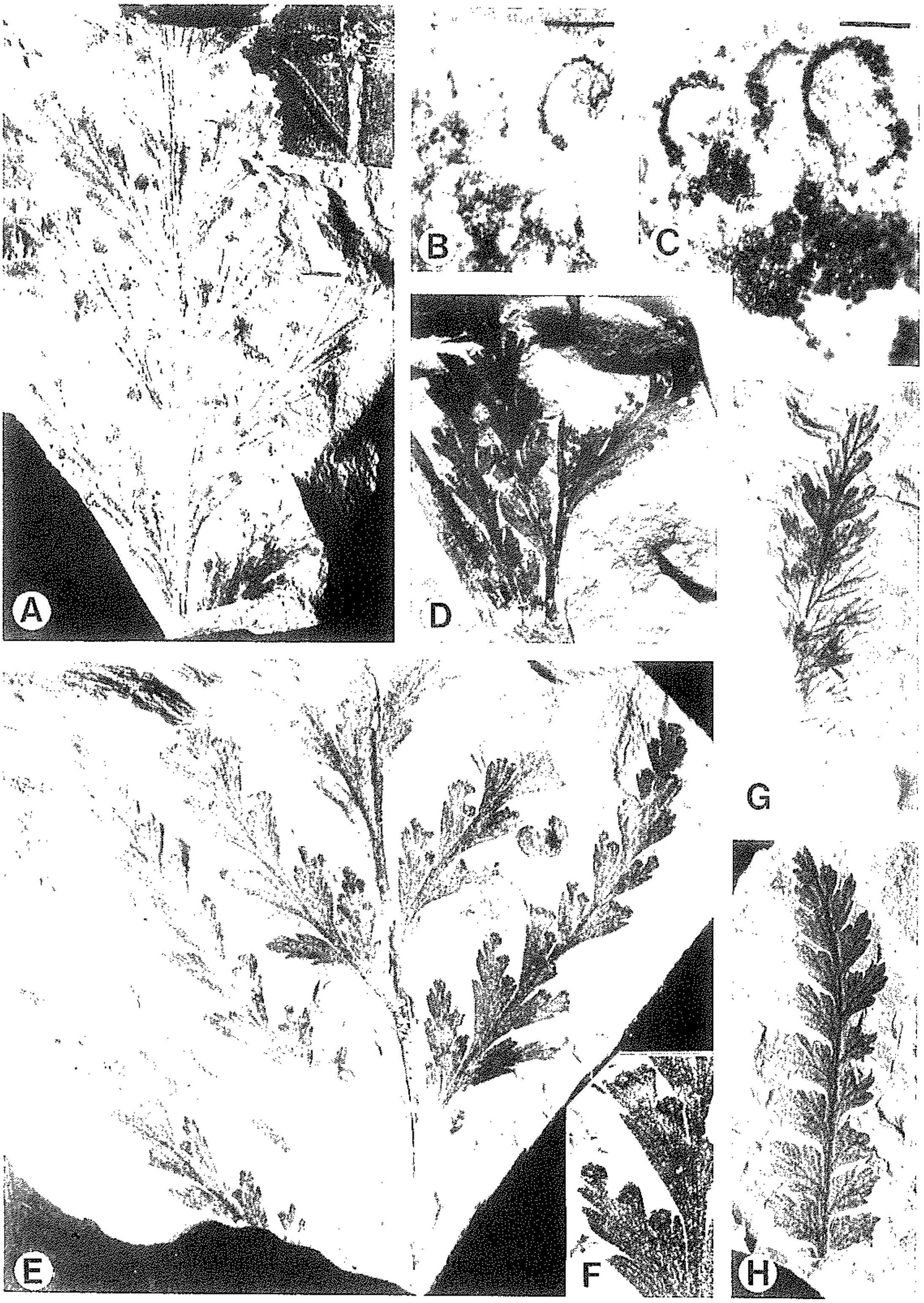
Seward (1904) noted the resemblance of Victorian *Sphenopteris* specimens to *S. hislopi* from the Rajmahal Hills of India, but refrained from including them in that species. Medwell (1954a), however, showed no such hesitation and transferred the Victorian Lower Cretaceous species previously described as *Sphenopteris* to *S. hislopi*. Douglas (1973) preferred the local name *S. warragulensis* for Medwell's aggregate, but excluded *S. travisi* which he compared closely to *Coniopteris hymenophylloides* from the Yorkshire Jurassic. Douglas noted the significance of the fertile foliage of *S. warragulensis* but, as little could be determined from the soral regions, decided against removing the species from the form-genus.

Douglas (1973, pl. 20, fig. 1) also included under *S. warragulensis* a fertile fern frond from Whitelaw (Korumburra Group) which, although showing sphenopteroid venation similar to sterile *S. warragulensis*, differs from Cape Horn foliage by having pinnules (or distal pinnae) which are only slightly reduced, and secondary veins which are terminated by individual sori. The abundance of the 'reduced' pinnae with broad sori at Cape Horn and Jeetho Valley (see Douglas, 1973, pp. 73-75) suggests that they represent the common fertile form, and that the Whitelaw specimen (Fig. 15A–C) may be atypical.

There is a marked similarity between these *S. warragulensis* specimens and *S. hislopi* from India, but as *S. hislopi* fertile foliage is unknown, and the published illustrations (Oldham & Morris, 1863; Surange, 1966, p. 115, fig. 73) are unsatisfactory for accurate comparison, specific separation is maintained here. Another similar fossil fern frond is *S. erecta* (Tenison-Woods) Walkom 1919 from the Lower Cretaceous of Queensland (Walkom, 1919). Although fertile foliage suggests similarities with some extant ferns noted above, numerous transfer preparations failed to reveal any sorus detail useful for classification. Until it is more completely known we follow Douglas (1973) and retain *S. warragulensis*.

SPHENOPTERIS TRAVISI Stirling 1900 (Fig. 15D–H)

1900 *Sphenopteris travisi* Stirling, p.4, pl.13, figs 18,19.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1904 *Coniopteris hymenophylloides* Brogniart var. *australica* Seward, p.162, figs 5,7–9.
1954a *Coniopteris hymenophylloides* Brongniart var. *australica* Seward; Medwell, p.85.
1973 *Coniopteris* cf. *C. hymenophylloides* Brongniart; Douglas, p.83, pl.24, figs 1–3; pl.25, figs 1–6; text-figs 7,19, 7,20, 7,22, 7,23. (non pl.39, fig.2; pl.42, fig.1; text-fig.7,21).

Material. Lectotype (designated herein) NMVP21353 from Korumburra. Other specimens NMVP167442–167451 from NMVPL425, NMVP14192–14194, 14196 from Jumbunna, NMVP14195 from Outtrim, NMVP110687 from Cape Paterson.

Description. Frond bipinnate (at least) preserved lengths up to 50mm (complete frond unknown), width up to 55mm. Rachis 0.8mm wide, lacking a lamina wing.

Pinnae arranged distichously to subdistichously, inserted laterally or slightly dorsally on the rachis, attachment sessile. Basal pinnae up to 50mm long by 12mm wide, pinna size decreasing distally along rachis, the several most distal pinnae being so reduced that they resemble pinnules. Pinnae diverging from rachis at 40–45°.

Pinnules distichously arranged, inserted laterally on the rachilla, attachment adnate by a slightly narrowed base. Venation sphenopteroid, one vein only entering each pinnule from the rachilla; midvein poorly defined, persistent for half pinnule length, branching laterally into lamina. Secondary veins arising from midvein at 45°, sometimes branching (often twice) before reaching the pinnule margins, initial secondary vein katadromic. Pinnule margins incised, each veinlet ending at a serration, each group of veinlets arising from the same secondary vein contained within successive incisions. Basiscopic margin decurrent, continuing along rachilla as a lamina wing to the acroscopic margin of the subtending pinnule. Basal pinnules 7mm by 3mm, decreasing in size distally along the rachilla, up to sixteen pinnules per pinna.

Fertile frond with similar pinnules only slightly reduced about the margins, with little change to pinnule shape. Sori spherical, 0.7mm diameter, marginal, each sorus terminating a secondary vein. Sporangia 250–300μm diameter, leptosporangiate, annulus more or less vertical; spores trilete (Douglas, 1973).

Discussion. *Sphenopteris travisi* sterile foliage is somewhat similar to that of *S. warragulensis* in overall shape and venation, but is distinguished by its smaller size, more delicate appearance and its fertile foliage. In most previously reported fertile specimens the pinnules are completely fertile, i.e. each secondary vein is terminated by a sorus, but in the fertile frond from Koonwarra (Fig. 15E,F) only the segments of the acroscopic margins of some pinnules are fertile. Douglas (1973, pl. 25) illustrated a specimen from Cape Paterson (Korumburra Group) with sporangia approximately 250μm in diameter and apparently leptosporangiate, the annulus oriented more or less vertically and with trilete spores.

A sterile pinna belonging to this species was figured by Stirling (1900) as *S. travisi* but was not described. Seward (1904) gave the first description (which included fertile foliage) and identified the plants as a variety (*australica*) of *Coniopteris hymenophylloides* from the Yorkshire Jurassic. This classification was subsequently used by Chapman (1908, 1909) and Medwell (1954a). Douglas (1973) accepted assignment to *Coniopteris* but was doubtful of the specific assignment suggesting comparison with *C. hymenophylloides*.

Fertile material of *S. travisi* allows the inclusion of the taxon in the leptosporangiate ferns, but does not show sufficient soral or sporangial detail to allow family placement and may only be compared with extant ferns on the basis of similarities in shape and habit. The sterile foliage is similar to some of the less dissected members of the Hymenophyllaceae (e.g. *Hymenophyllum laminatum* Copeland 1911) and the development of the sori at the vein endings is not unlike *Hymenophyllum* as a whole, although there is no evidence of elongated receptacles protruding from the sori. Copeland's (1937) drawings of *Hymenophyllum* however, show an anadromic pinnule arrangement while branching in *S. travisi* is strictly katadromic. The apparent uniformity of anadromic branching in *Hymenophyllum* supports Harris's (1961) use of the branching pattern as a significant, if only secondary, taxonomic character of fossil fern foliage. Other possibilities are affiliation with the Dennstaedtiaceae (e.g., *Dennstaedtia davallioides* (R. Br. 1810) T. Moore 1858 and *Dicksonia* L'Hér. and the dicksonioid line of the family Cyathaceae (Dicksonioideae = Dicksoniaceae *sensu* Harris, 1961).

Fig. 15. A–C, Atypical *Sphenopteris warragulensis* McCoy specimen from Whitelaw. A, portion of fertile pinna, NMVP167441, ×2. B, sporangium from A. C, sporangia from A. scale bars = 100μm. D–H, *Sphenopteris travisi* Stirling. D, partially fertile portion of frond from Cape Paterson, NMVP110687, ×2. E, partially fertile portion of frond, NMVP167442, ×2. F, fertile pinnule of E enlarged, NMVP167442. G, sterile pinna, NMVP167443, ×2. H, sterile pinna, NMVP167444, ×2.

Harris (1961), in his treatment of Yorkshire Jurassic ferns, divided *C. hymenophylloides* (*sensu* Seward 1900) into several species. The Victorian *S. travisi* lacks the filiform lobe extensions of the basal pinnule on each pinna of *C. hymenophylloides sensu* Harris 1961, as well as differing in the degree of fertile pinnule reduction. *Sphenopteris travisi* bears greater resemblance to *C. bella* Harris 1961 (= *Coniopteris hymenophylloides sensu* Seward). While comparison with the Yorkshire Jurassic *Coniopteris* species must be noted, the inability to conclusively place this species in the Dicksonioideae (i.e. *Coniopteris*) suggests the most appropriate taxonomic placement at present is *Sphenopteris*.

SPHENOPTERIS sp. (Fig. 16A)

?1969 *cf. Stenopteris williamsonis* (Brongn.) Harris; Douglas, p.45, pl.13, fig.3, text-fig.1,43.
1973 Fern-like foliage sp. 'a'; Douglas, p.98, pl.45, text-fig.7,47.

Material. NMVP167452.

Description. Frond tripinnate (at least), preserved length 5.7mm (complete length unknown), up to 70mm wide. Rachis 0.7mm wide lacking a lamina wing.

Pinnae arranged oppositely to slightly sub-oppositely, inserted laterally or slightly dorsally on the rachis, attachment petiolate (excepting the few most distal reduced pinnae which are sessile). Basal pinnae 37mm long by 20mm wide, pinna size decreasing distally along the rachis, the several most distal pinnae being so reduced they resemble pinnules. Rachilla up to 0.5mm wide, mostly free of lamina wing but becoming alate distally as pinnules become reduced. Pinnae diverging from rachis at 70°.

Pinnules arranged oppositely to sub-oppositely, inserted laterally on rachilla. Basal pinnules petiolate (petiole length up to 2mm, decreasing distally along pinna) grading distally to sessile, and finally adnate, pinnules. Venation sphenopteroid, a single vein entering each pinnule from the rachilla. Midvein straight, persistent for most of pinnule length, branching laterally into lamina. Secondary veins sub-opposite, arising from midvein at 45°, branching once or twice before reaching the lamina margin. Initial secondary vein katadromic. Margins incised, each veinlet terminating at a serration, each group of veinlets arising from the same secondary vein contained between successive incisions. Segments of basal pinnules so dissected that they in turn resemble small pinnules. Basiscopic margins decurrent only in distal adnate pinnules, continuing as a lamina wing to the acroscopic margin of the subtending pinnule. Basal pinnules 13mm long by 9mm wide, decreasing in size and degree of dissection distally along the rachilla. Up to 14 pinnules per pinna. Fertile foliage unknown.

Discussion. The high degree of dissection of the basal pinnules has led to segments which are similar to pinnules, giving the frond a tripinnate form. The reduction of pinnae distally along the rachis, pinnules along the pinnae, and segments along the pinnules, is the same growth habit as mentioned above for *S. warragulensis*. The marked tendency of the pinnules to become pinnate themselves is the most obvious difference between this species and *S. travisi* in which all of the pinnules are simple. *Sphenopteris* sp. has oppositely arranged, petiolate pinnae and pinnules, compared to the distichously arranged sessile pinnae and adnate pinnules of *S. travisi*. As well as these differences, the midvein of *Sphenopteris* sp. is straighter and more persistent than that of *S. travisi*. It must be noted that the terminal portions of *Sphenopteris* sp. and *S. travisi* pinnae are inseparable, and that small pieces of frond or isolated pinnules cannot be identified with certainty. The absence of fertile foliage prevents a more definitive classification.

GLEICHENITES Goeppert 1836

GLEICHENITES NANOPINNATUS (Douglas 1973) comb. nov. (Fig. 16B-F)

1973 *Coniopteris nanopinnata* Douglas, p.87, pl.29, figs 1-3; pl.30, fig.1; text-figs 7,26, 7,27.
1973 *Coniopteris* sp. 'b'; Douglas, p.89, pl.30 figs 2, 3; text-fig.7,29.

Material. Holotype (by original designation) NMVP167456 from Balook, NMVPL430. Other material MUGD3793, NMVP24146-24147 from NMVPL425, NMVP167454, 167455 from Balook, NMVPL430, NMVP167457 from Skenes Creek Road, NMVP15695 associated with *Cladophlebis* from the shore platform at Inverloch.

Description. Frond tripinnate (at least), preserved lengths up to 40mm (complete fronds unknown),

Fig. 16. A, *Sphenopteris* sp. portion of sterile frond, NMVP167452, ×1. B-F, *Gleichenites nanopinnatus* (Douglas) comb. nov. B, portion of sterile frond showing the 'zig-zag' branching pattern, MUGD3793, ×1.5. C, sterile pinna, NMVP21417, ×4. D, portion of fertile frond from Balook showing the 'zig-zag' branching pattern, NMVP167454, ×4. E, portion of fertile frond from Balook, NMVP167456, ×2. F, fertile pinnules from Skene's Creek Road, NMVP167457, ×6.

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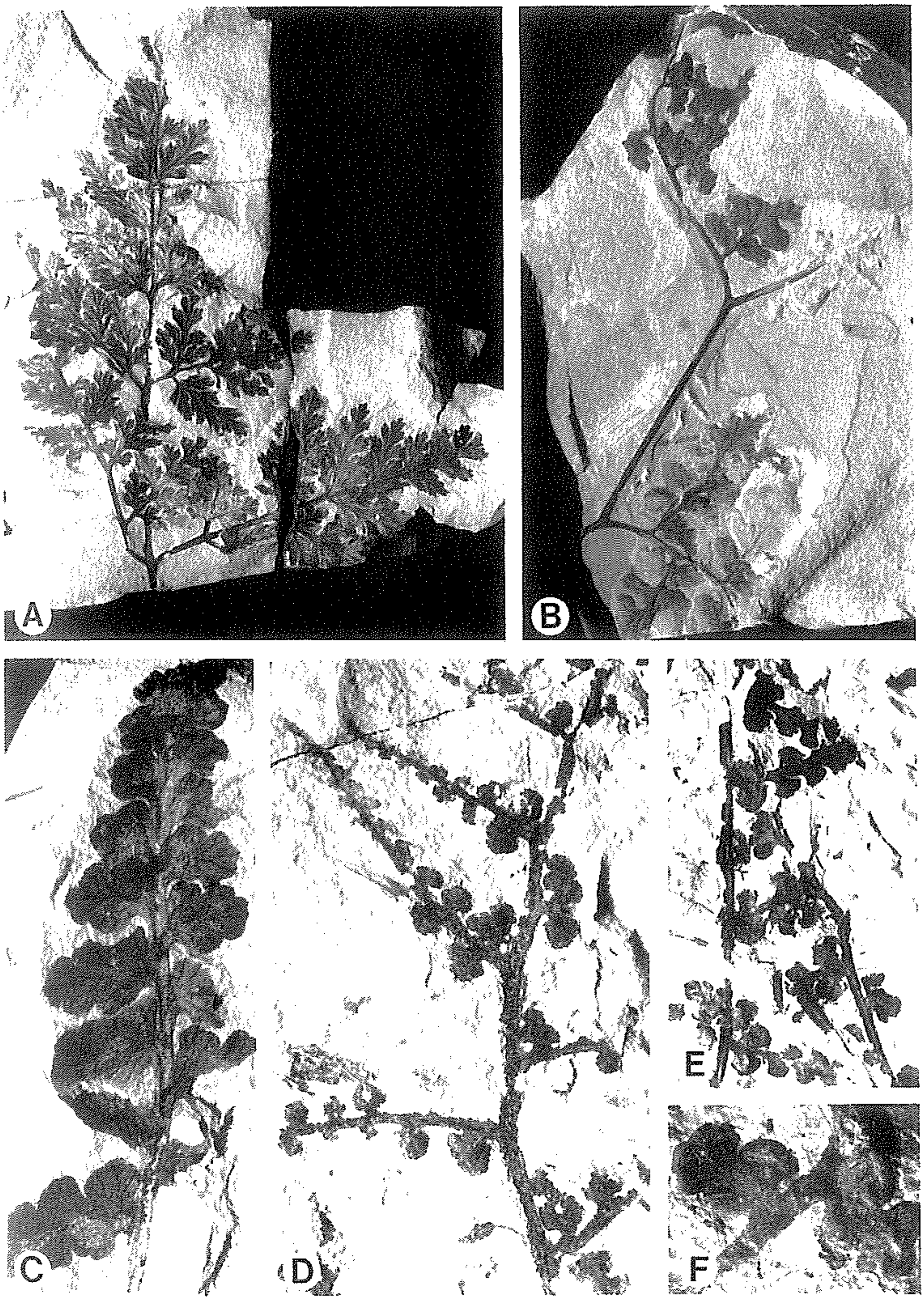

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50mm wide. Rachis 0.7mm wide, free of lamina wing. Frond branching apparently by successively over-topped dichotomies giving a sympodial appearance, the branch diverging away from the frond axis becoming pinnate and limited in growth and the other branch continuing as the rachis. Angle of dichotomy 80–90°.

Pinnae in two ranks, distichously arranged, arising laterally from the rachis one per dichotomy, attachment petiolate. Rachilla lacking a lamina wing.

Pinnules up to 35mm long by 30mm wide, distichously arranged, inserted laterally on rachilla, attachment sub-petiolate to sessile, the most basal pinnule on each pinna arising on the acroscopic side of the rachilla (anadromic). One vein only entering each pinnule from the rachilla at 90°; midvein flexuose, not persistent or prominent, branching laterally into the lamina. Secondary veins sometimes branching once before reaching the pinnule margin, initial secondary vein anadromic. Margins dissected into rounded lobate segments, each secondary vein and its derived veinlets supplying one lobe, margins not noticeably serrated at veinlet endings. Basal pinnules deeply dissected into segments resembling pinnules. Fertile pinnules similar but with the lobe margins apparently inrolled to protect submarginal sori.

Discussion. This fern is distinguished from associated foliage types by its method of frond branching, the anadromic pinnule arrangment and venation, and its rounded lobate pinnules, and can be recognised even as small fragments. The 'zig-zag' frond branching is probably regular, but absence of the apical portion makes it impossible to determine whether growth is sympodial, by bifurcation of a monopodial axis, or a series of successively over-topped unequal dichotomies. This branching pattern is unique among known Victorian Early Cretaceous ferns, and bears some resemblance to extant members of the Gleicheniaceae. Branching in the Gleicheniaceae however, is not by true dichotomies, as growth of the main axis is arrested and it remains as a dormant bud in the angle of the two primary laterals, and pinnules are often associated with the branching; these features appear to be absent in this fossil species. The pinnules are similar in shape and venation to the juvenile foliage of some species of *Gleichenia* (e.g. *G. linearis* (Burm. f. 1768) C.B. Clarke 1880; *ex icon* Bower, 1926, fig. 473). Its overall appearance is also strikingly similar to *Adiantopsis dichotoma* (Cav.) T. Moore 1857 (= *Cheilanthes dichotoma* Sw. 1806; *ex icon* Hooker, 1858, Tab. CIIB) and to a lesser extent *Adiantum feei* T. Moore 1857; (*ex icon* Bower, 1928, fig. 633H); both these species have a pseudosympodial branching pattern.

The fertile foliage described by Douglas (1973) as *Coniopteris nanopinnata* from several Victorian Lower Cretaceous (Zone C) localities is similar to the Koonwarra sterile foliage in most respects, namely, the distichous and anadromic pinna and pinnule arrangement, the orientation of the pinnules perpendicular to the rachilla, and the overall pinnule appearance. The 'zig-zag' branching is not as definite, although this could be due to the fact that the most complete specimen appears to be an apical portion of frond, the 'zig-zag' habit possibly developing later by over-topping. The 'zig-zag' habit may also be lost with the reduction from sterile to fertile fronds. These fertile pinnules are slightly reduced, having ?broad sori located submarginally one per lobe (or one per pinnule on the more reduced, distal portions of the pinnae). The swollen appearance of the fertile pinnule margins suggests an inrolled margin similar to that in *Cheilanthes, Adiantum* and a few species of *Gleichenia* (e.g. *G. circinata* Sw. 1800).

There is little doubt that the fronds from Koonwarra and those described as *Coniopteris nanopinnata* by Douglas (1973) are the sterile and fertile forms of the same species. Although its systematic position is still uncertain, the branching pattern and venation of this fern warrant its removal from *Coniopteris* Brongn. and generic separation from the other Koonwarra ferns. Available evidence is insufficient to allow inclusion of this species in an extant family or genus, although its gross morphology suggests an affinity with the Gleicheniaceae. On this basis it has been assigned here to the form-genus *Gleichenites*.

ADIANTITES Goeppert 1836

ADIANTITES LINDSAYOIDES Seward 1904 emend. (Figs 21A–C, 22A,B).

1900	*Sphenopteris ampla* McCoy; Stirling, pl.3, figs 2,6.
1904	*Adiantites lindsayoides* Seward, p.162, figs 5,5a.
1904	*Thinnfeldia mccoyi* Seward, p.174, fig.28.
1910	*Adiantites lindsayoides* Seward; Seward, p.376, fig.279B.

Fig. 17. Onychiopsis paradoxus Bose & Dev. A, portion of fertile frond from Cape Horn, NMVP167458, ×2. B, partially fertile portion of pinna from Cape Horn showing the basal pinnule with several lobes in a manner similar to the sphenopteroid ferns, but distal pinnules reduced to a lamina flange subtending the fructification, NMVP167460, ×3. C, portion of fertile pinna with damaged pinnules, NMVP167462, ×6. D, fertile pinna from Cape Horn, NMVP167459, ×4.

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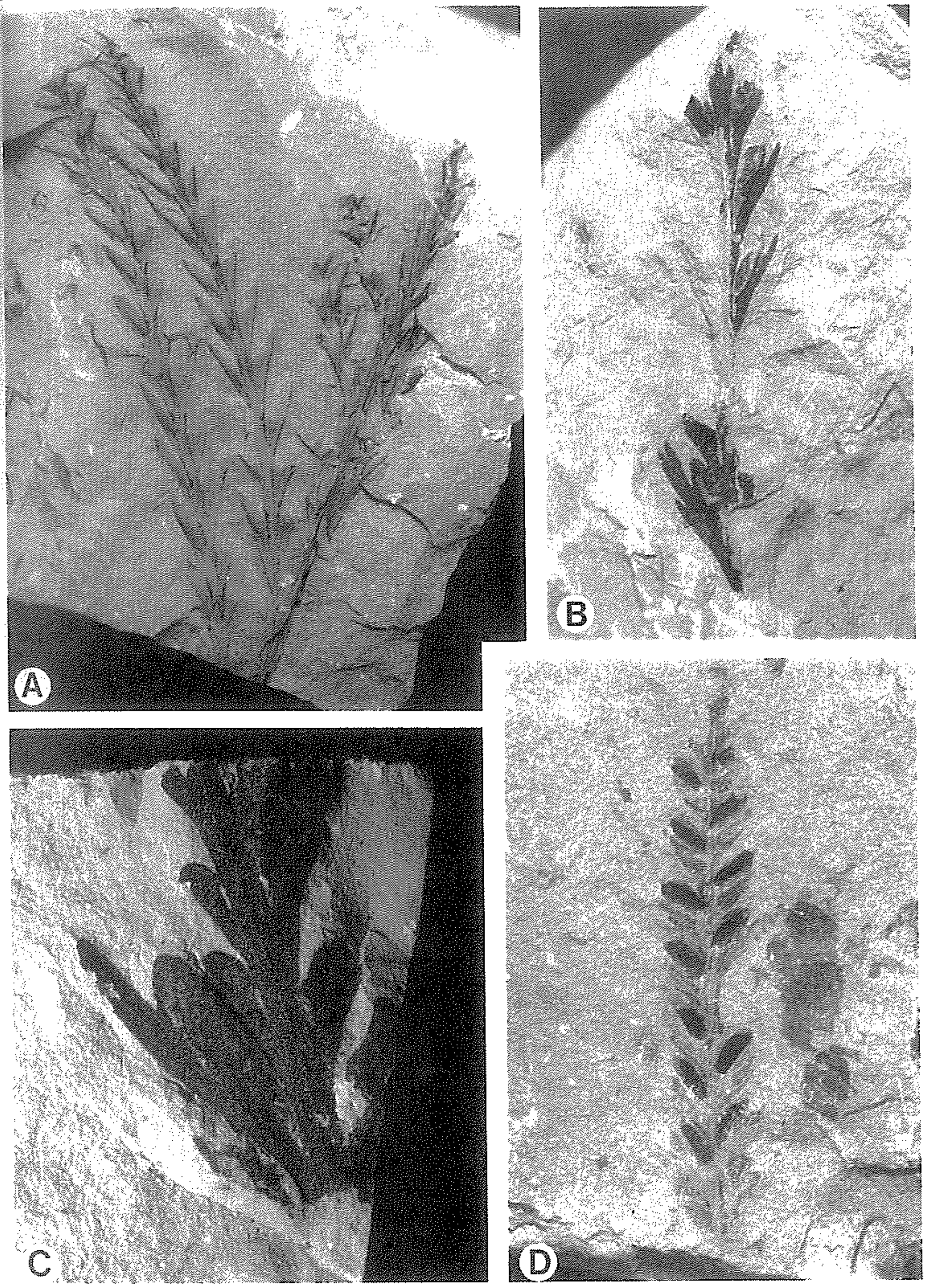

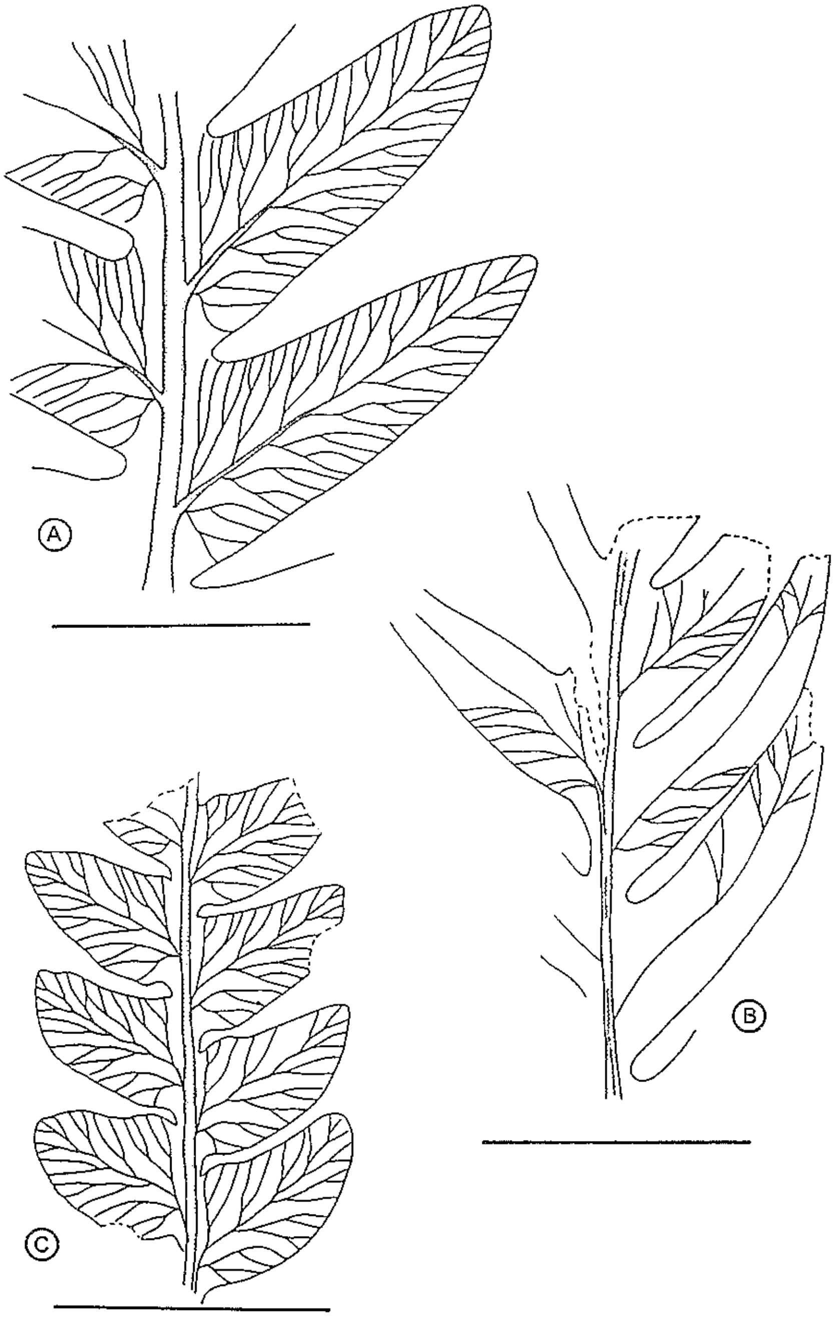

Fig. 18. A, *Cladophlebis* sp. cf. *C. oblonga* Halle NMVP167465. B, *Cladophlebis biformis* sp. nov. NMVP167463. C, *Cladophlebis* sp. NMVP167467. Scales = 10mm.

Fig. 19. A,B, *Cladophlebis biformis* sp. nov. A, medial portion of pinna, NMVP167463, ×2. B, apical portion of frond from Inverloch showing the gradation of pinnules from pinnate to alate distally along the rachis, MUGD3618, ×2. C, *Cladophlebis* sp. cf. *C. oblonga* Halle, medial portion of pinna, NMVP167465, × 2. D, *Cladophlebis* sp., pinna, NMVP167467, ×2.

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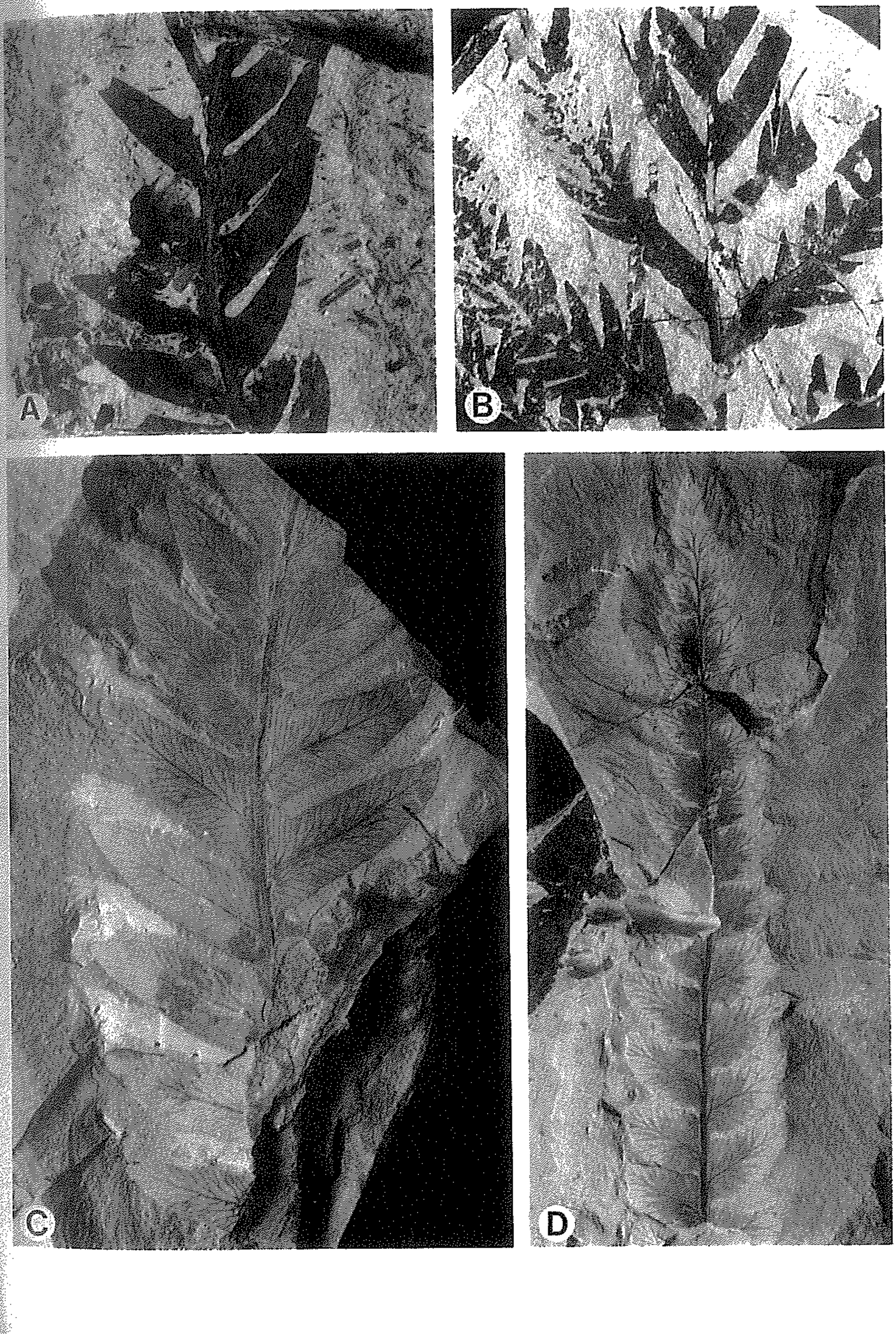

1954a *Adiantites lindsayoides* Seward; Medwell, p.86.
1954a *Thinnfeldia mccoyi* Seward; Medwell, p.94.
1973 *Sphenopteris mccoyi* (Seward) Douglas, p.75, pl.21; pl.23, fig.1; pl.46, fig.2; text-figs 7,10, 7,11.
1973 *Adiantites lindsayoides* Seward; Douglas, p.90, pl.31; text-figs 7,30–7,34.

Material. Holotype (by monotypy) NMVP14192A, B from Jumbunna. Other material NMVP167470, 167471, 167473–167484 all from NMVPL425; MUGD3594 (MUGD3595 counterpart) from shore platform at Inverloch; NMVP167485, 167691–167696 (sporangia) from Cape Horn, NMVPL426.

Emended diagnosis. Frond bipinnate (at least), preserved lengths up to 150mm (complete fronds unknown). Rachis 4mm wide, robust, lacking a lamina wing, but bearing one zwischenfiedern (a pinnule which arises directly from the rachis) between successive pinnae on each side of the rachis. Zwischenfiedern inserted laterally on the rachis, adnately attached, and similar to pinnules in size, shape and venation.

Pinnae distichously arranged, inserted slightly dorsally on the rachis up to 80mm apart (Douglas, 1973), attachment sub-petiolate, lamina dissected almost to the rachilla resulting in a pinnate shape. Rachilla up to 2mm wide.

Pinnules up to 20mm long by 10mm wide, distichously arranged, inserted laterally on rachilla, attachment adnate. Margins serrate, the tip of each serration terminating a veinlet. Basiscopic margin slightly decurrent, continuing to the acroscopic margin of the subtending pinnule. Two veins enter each pinnule from the rachilla. The most prominent vein arises from the rachilla at 30–40°, entering the pinnule about the midpoint of the base, and is persistent for about one-fifth of the pinnule length, dichotomizing several times before reaching the margins. These secondary veins and derived veinlets terminate along the acroscopic margin and the distal one-third of the basiscopic margin. The branching of this vein is anadromic. The other vein enters the basiscopic half of the pinnule and dichotomizes once or twice before reaching the proximal two-thirds of the basiscopic margin. None of the veinlets arising from this vein are particularly prominent.

Fertile pinnules smaller than sterile pinnules but similar in shape and venation, with a continuous sorus (or many contiguous sori) forming around the pinnule margin. Zwischenfiedern similarly fertile. Sorus details unknown. Leptosporangia approximately 250μm diameter, annulus more or less vertical. Spores trilete, 40–50μm equatorial diameter.

Discussion. This species may be identified by the finely serrate broad pinnules (or if fertile the continuous marginal sori), the characteristic venation, and, where preserved, the zwischenfiedern. Size appears to be the only major variation in this species. Specimens from Koonwarra are all about the same size but are considerably smaller than the limits given by Douglas (1973, p. 76). Pinnae of the Koonwarra specimens were probably about 80mm long (preserved up to 65mm) by 20mm wide and are spaced about 40mm apart on the main rachis. Pinnules are 20mm long with a basal attachment of 13mm, and there were probably 6 or 7 along each side of the rachilla (5 preserved).

Stirling (1900, pl. 3, figs 2,6) included in *Sphenopteris ampla* (now *S. warragulensis*) a sterile specimen (NMVP1985) which is quite faded and, like most of the specimens figured around the turn of the century, is covered by a thick layer of varnish which further reduces its clarity. Although venation is not obvious, pinnule shape suggests it belongs to *A. lindsayoides*. Seward (1904, p. 174) separated this sterile foliage type from *Sphenopteris* and placed it in *Thinnfeldia* Ettingshausen. Medwell (1954a) followed Seward with *T. mccoyi* but incorrectly described the venation as alethopteroid. Douglas (1973) suggested that Seward had not intentionally implied pteridosperm affiliation by using *Thinnfeldia*, and considering the fronds to belong to a fern, transferred them to *Sphenopteris*.

The sterile foliage, however, does not conform with Brongniart's (1828) definition or with emended criteria adopted for *Sphenopteris* in describing this flora (see above). *Adiantites lindsayoides* has two veins entering each pinnule, neither of which is persistent enough to exhibit sphenopteroid branching. The venation is similar to the Carboniferous seed fern *Lescuropteris* Schimper (*ex icon* Taylor, 1981, p. 384).

Until now fertile and sterile foliages of this plant have been regarded as separate species. The fertile form was described by Seward (1904) as *A. lindsayoides* and similarly recorded by Medwell (1954a) and Douglas (1973). Douglas (1973) noted that fragments of the two types could be confused, but discounted the possibility of affiliation because of the larger dimensions of sterile *S. mccoyi* specimens available to him. Koonwarra material

Fig. 20. Aculea bifida Douglas. A, fertile frond, NMVP167530, × 1. B, fertile frond, NMVP167531, × 2. C, sterile frond, NMVP167536, × 2. D, sterile frond, NMVP167533, × 1.

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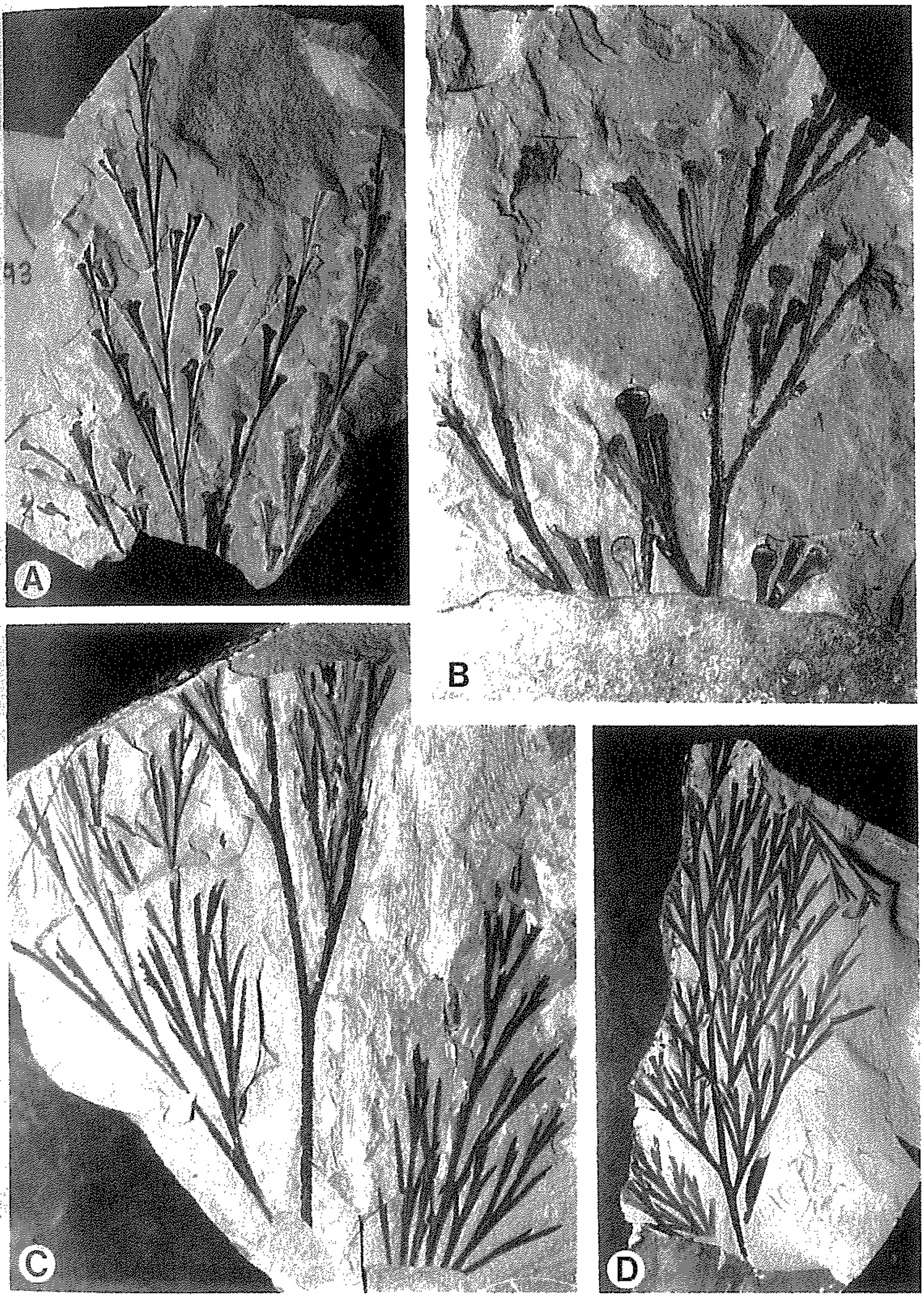

includes several sterile pieces of foliage with smaller pinnules than those Douglas had observed, and although no fertile material is available from there, examination of previously collected specimens ascribed to *A. linsayoides* has enabled comparisons to be made.

The similarities noted here are most easily seen in NMVP167470 (Fig. 22A) and MUGD3595 (Fig. 21A), although all the dimensions of the former specimen are about twice those of the latter. Overall habit of the fronds is identical (i.e. shape and arrangment of pinnae and pinnules), but two critical common features are the venation pattern, in which two veins enter each pinnule and the presence of zwischenfiedern located on the rachis between successive pinnae. Supporting these facts is the common co-fossilization of the two foliage types at other localities. As noted above, the fertile foliage is easily confused with fertile *S. warragulensis* when fragmentary material of the two species is preserved together.

Although detail of the sorus is incompletely known, some comparison can be made with extant groups within the leptosporangiate ferns. The tendency of much of the soral region to be detached with the counterpart (presumably the portion of the sorus in the immediate vicinity of the sporangia) leaving a gap between the majority of the pinnule lamina and the thin edge of the pinnule margin, suggests that development or at least placement of the sporangia is sub-marginal. General appearance of the fertile fronds is reminiscent of extant *Lindsaea* spp. and also of *Histiopteris incisa* (Thunb. 1800) J. Smith 1875 (Dennstaedtiaceae). The margins do not appear to be recurved in the manner of *Adiantum*. The sporangia (Fig. 21B,C) are similar in size and appearance to those of *Lindsaea*, having a more or less vertical annulus of about 12–14 cells with the stomium located several cells away from the insertion of the stalk. Dettmann (1981) allied the spore-type *Cyathidites* to the Cyathaceae. This species is retained as *A. lindsayoides* although there is insufficient evidence available to indicate certain affinity with any extant fern family.

INCERTAE ORDINIS

ONYCHIOPSIS Yokoyama 1889

ONYCHIOPSIS PARADOXUS Bose & Dev 1961 (Fig. 17)

1961 *Onychiopsis paradoxus* Bose & Dev, p.57, pl.1, figs 1–9; pl.2, figs 10–20; text-figs 1–3.
1966 *Onychiopsis paradoxus* Bose & Dev; Surange, p.125, figs 81–83, 84C.
?1973 cf.*Stachypteris* sp.; Douglas, p.97, pl.44, fig.1; text-figs 7,45, 7,46.

Material. Holotype (by original designation) Birbal Sahni Institute for Palaeobotany 31616 from Early Cretaceous Jabalpur Series in India. Other material NMVP167462 from NMVPL425; NMVP167458–167461 from Cape Horn, NMVPL426.

Description. Fronds bipinnate (at least), preserved lengths up to 50mm (complete fronds unknown). Rachis 0.7mm wide, without a lamina wing.

Pinnae up to 50mm long, arranged distichously, inserted laterally or slightly dorsally on the rachis, attachment sub-petiolate, diverging from rachis at 40°. Pinnules up to 8mm long by 2mm wide, distichously arranged, broadly attached by the constricted base (more distal pinnules almost petiolate), inserted laterally on rachilla, diverging at a 40° angle. Most pinnules fertile. Fructification elliptical, up to 6mm long by 1mm wide, orientated along pinnule axis. In most fertile pinnules the lamina is reduced to a wing on the basiscopic margin of the fructification (or the fructification covers most of the pinnule lamina), although the lamina of occasional basal pinnules is not as reduced showing dissected margins and sphenopteroid venation. It is unclear whether the fructifications are marginal, or located on the lamina surface but displaced toward the acroscopic margin. Completely sterile foliage is unknown.

Discussion. One small piece of foliage was found at Koonwarra; the description is based mainly on material collected near Cape Horn (Otway Group). Sterile foliage, as indicated by the less reduced basal pinnules on fronds that are otherwise fertile, is sphenopteroid with pinnule margins dissected about the vein endings. Fertile foliage, instead of having one small sorus at each vein ending (as in *S. travisi*) or a broad fructification terminating each pinnule (as in *S. warragulensis, A. lindsayoides*), has one large elliptical sorus forming on or near the acroscopic margin of reduced pinnules. The Koonwarra specimen shows only seven pinnules, three of which appear damaged or aborted. The lack of similar pinnae on Cape Horn specimens makes dimorphism an unlikely explanation.

Two pieces of similar, if not identical, foliage from Boola Boola Forest Beds (Zone B) were compared by Douglas (1973) to *Stachypteris* Pomel. Affinity of one of these Zone B specimens with the pinnules from Koonwarra and Cape Horn is slightly uncertain due to its prominent lamina (Douglas, 1973, pl. 44, fig.1; text-fig. 7,45), but the other closely resembles the pinnules from Cape Horn (Douglas, 1973, text-fig. 7,46).

The Koonwarra and Cape Horn specimens are, as far as can be determined, identical to *O. paradoxus* from the Jabalpur Stage in India. The

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basal pinnules of the Indian fronds show sphenopteroid venation, and the lamina of the distal pinnules is reduced to a basiscopic wing of the elliptical fructification. Bose & Dev (1961) did not observe sporangia (only spore masses were recovered), and suggested that spore dehiscence probably occurred via a longitudinal slit on the fructification surface. No longitudinal slits were observed in the Cape Horn fertile structures, and maceration failed to reveal evidence of sporangia or spores.

The inability to extract sporangia from fertile pinnules of *O. paradoxus* from India, led Bose & Dev (1961) to conclude the structures were exannulate monosporangiate fructifications. Similar observations were made by Tattersall (1961) on English Jurassic specimens of *O. psilotoides* Stokes & Webb 1824 (= *O. mantelli* (Brongn. 1828) Seward 1894). If their interpretations that these ferns lack leptosporangia are correct then resemblance to *Onychium* Kaulf. is superficial, and these plants do not have the implied relationship to the Adiantaceae.

CLADOPHLEBIS Brongn. 1849

CLADOPHLEBIS BIFORMIS sp. nov. (Figs 18B, 19A,B)

1892	*Alethopteris* (*Pecopteris*) *australis* Morris; Stirling, p.11.
1900	*Alethopteris australis* Morris; Stirling, p.3, pl.2, figs 3,3a.
1904	*Cladophlebis denticulata* Brongniart var. *australis*; Seward, p.171, figs 25–27.
1954a	*Cladophlebis australis* (Morris) Seward; Medwell, p.84. partime
1973	*Cladophlebis australis* (Morris) Seward; Douglas, p.68, pl.17, figs 1–4; text-figs 7,2, 7,3. (non pl.16; pl.18, figs 2, 3; text-fig.7,1).

Etymology. Latin *bi-* — two and *forma* — shape; referring to two types of pinnae.

Material. Holotype MUGD3618 from the shore platform at Inverloch. Paratype NMVP167463 from NMVPL425. Other material MUGD3617, 3619, 3620 from NMVPL425 and NMVP15695 from the shore platform at Iverloch.

Diagnosis. Frond bipinnate (at least, complete fronds unknown). Rachis lacking a lamina wing.

Pinnae distichously arranged, inserted laterally on rachis, attachment adnate. Basal pinnae well defined, dissected into pinnules; pinnae becoming reduced distally along the rachis, the terminal few pinnae resembling pinnules.

Pinnules distichously arranged, inserted laterally on rachilla, attachment adnate, falcate in shape, widest at base (up to 10mm) tapering uniformly to an acute apex. Margins entire, acroscopic margin slightly concave, basiscopic margin straight for half pinnule length then curving distally to the pinnule apex. Pinnule margins neither decurrent nor surcurrent, but continuous with subtending and succeeding pinnules. Basal and medial pinnules largest (up to 30mm long) usually well defined, pinnules decreasing in size distally along the pinna which is terminated by an elongate pinnule as large as the well defined medial and basal pinnules. The several most basal pairs of pinnules on the distal pinnae (which have almost graded into pinnule-like segments) are reduced to form a broad alate wing on each side of the rachilla. Pinnule venation pecopteroid, with a single vein entering each pinnule from the rachilla at 45°; midvein straight, persisting almost to pinnule apex. Secondary veins diverging from midvein at 45°, dichotomizing once or twice before reaching the lamina margin.

Discussion. The systematic treatment of 'cladophleboid' sterile foliage presents considerable problems. 'Cladophleboid' foliage types are abundant in Mesozoic floras world-wide, with *Cladophlebis denticulata* Brongn. 1849 from the European Jurassic being generally accepted as the yardstick for comparison. Morris (1845) first used *Pecopteris australis* for Triassic specimens collected by Strzelecki in the Jerusalem Basin, Tasmania, which he considered different to *C. denticulata*. McCoy (1874) described the first Victorian 'cladophleboid' material from Bellarine and assigned it to *C. australis*. Stirling (1892) considered the specimens better placed in *Alethopteris* Sternberg; Seward (1904) used the Yorkshire Jurassic name *C. denticulata* but retained *australis* Morris as the variety. Walkom (1917, 1919a, 1919b, 1921) attributed specimens from the Mesozoic of New South Wales and Queensland to *C. australis* (Morris) Walkom maintaining that *C. denticulata* was distinct and different. It is uncertain whether the Victorian specimens are conspecific with those considered by Walkom. Medwell (1954a) and Douglas (1973) both used Walkom's determination *C. australis* for what can be loosely termed the "aggregate" of the Victorian material. Although a complete treatment of Australian Mesozoic *Cladophlebis* fronds is beyond the scope of this work, an attempt has been made to elucidate the 'components' of the Victorian *C. australis* (*sensu* Douglas, 1973). It has been divided into two species which both differ from *C. australis* (*sensu* Morris).

The only specimen of *C. biformis* available from Koonwarra (Fig. 19A) is a small medial portion of pinna fossilized in one of the coarser sandstone layers. Although the venation is poorly preserved and the basal and apical parts of the pinna are missing, it is sufficient for comparison with two similar pieces of frond, MUGD3617 and MUDG3618 (Fig. 19B) from the shore platform at Inverloch. All three specimens were illustrated by Douglas (1973, pl. 17, figs 1,2,4) as *C. australis*. They differ from *C. australis* (*sensu* McCoy 1874) in that the pinnae are terminated by an elongate odd pinnule, and the gradual reduction of pinnae distally along the rachis occurs by reduction of their basal pinnules. This leads to pinnae which are pinnate distally but broadly alate basally, and a gradation of pinnae ranging from completely pinnate to completely alate. Pinnules of *C. australis* (*sensu* Morris) grade distally to a diminished terminal pinnule and persist basally even on the distal pinnae.

CLADOPHLEBIS sp. cf. C. OBLONGA Halle 1913 (Figs 18A, 19C)

1874	*Pecopteris australis* Morris; McCoy, p.16, pl.14, figs 3,3a.
1890	*Pecopteris australis* Morris; Feistmantel, p.109, pl.27, figs 3,3a.
1954a	*Cladophlebis australis* (Morris) Seward; Medwell, p.84.
1973	*Cladophlebis australis* (Morris) Seward; Douglas, p.68, pl.16: pl.18, figs 2, 3; text-fig.7,1. (non pl.17, figs 1-4; text-figs 7,2, 7,3).

Material. NMVP167465, 167466 from NMVPL425; NMVP12205 from Bellarine; NMVP165738 from Boola Boola Forest, NMVPL429 and NMVP165830 from Whitelaw, NMVPL427.

Description. Fronds bipinnate (at least), preserved lengths up to 200mm (complete fronds unknown). Rachis narrow, up to 2mm wide, without lamina wing.

Pinnae up to 100mm long by 30mm wide, distichously arranged, inserted laterally or slightly dorsally on rachis, attachment sub-petiolate (Douglas, 1973, text-fig. 7,1). Basal pinnae largest, pinnae decreasing in size (mainly length) distally along the rachis but with only a minor reduction of the pinnate habit.

Pinnules up to 20mm long by 7mm wide, distichously arranged, inserted laterally on rachilla, adnate. Pinnules widest at point of attachment, narrowing toward the apex. Margins entire, more or less straight and sub-parallel for most of pinnule length, curving distally toward a pointed (but sometimes rounded) apex. Margins neither decurrent nor surcurrent, but continuous with the subtending and succeeding pinnules. Venation pecopteroid, one vein only entering each pinnule from the rachilla, resulting in a pinna/pinnule angle of 50–80°. Midvein straight, persistent for most of pinnule, bearing up to 15 secondary veins. Secondary veins distichously arranged, diverging from midvein at 45°, dichotomizing once or twice before reaching the pinnule margin. Initial secondary vein katadromic, arising close to the midvein-rachilla junction. Pinnule secondary veins arising only from midvein, no veinlets entering the lamina wing from the rachilla as in *Alethopteris* type pinnules.

Discussion. McCoy's original specimen from Bellarine, the two specimens from Koonwarra and those specimens of *C. australis* of Douglas (1973) not already assigned above to *C. biformis* appear to belong to a separate taxon, and do not differ sufficiently from each other to warrant further specific division. These are different from the specimen *C. (P.) australis* of Morris (1845) which has some constriction of both acroscopic and basiscopic margins at the pinnule base, a character which is absent in both species described above. The Victorian fronds more closely resemble *C. oblonga* Halle from the ?Jurassic of Hope Bay, Grahamland, Antarctica. Halle (1913) noted similarities in venation between *C. oblonga* and *C. australis*, but separated them on the basis of pinnule shape, *C. oblonga* having straight, oblong pinnules with more or less rounded apices, as opposed to the narrow, noticeably falcate pinnules of *C. australis*.

CLADOPHLEBIS sp. (Figs 18C, 19D)

Material. NMVP167467.

Description. Frond pinnate (at least), preserved pinna 55mm long (total length unknown), 12mm wide. Pinnae dissected almost to rachilla resulting in pinnate form.

Pinnules up to 7mm long by 4mm wide, distichously arranged, inserted laterally on the rachilla, attachment adnate, pinnule shape hastate. Margins entire — acroscopic margin straight, occasionally slightly concave, constricted slightly at point of attachment to the rachilla but expanding into a small auricle; basiscopic margin convex, curved distally to a blunt but not rounded apex, constricted slightly at the pinnule base and decurrent to the acroscopic margin of the subtending pinnule. Pinnules widest at the auricle just above the basal constriction. Venation pecopteroid, one vein only entering each pinnule, at first diverging very acutely from the rachilla but immediately recurving into the pinnule resulting in a pinna/pinnule angle of about 50°. Midvein flexuose, persistent for two-thirds of pinnule length after which it fades into terminal veinlets. Up to seven secondary veins diverging from the midvein at 45°, distichously arranged, dichotomizing once or twice before reaching the

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margin. Initial secondary vein katadromic, arising very close to the junction of the midvein and the rachilla.

Discussion. This specimen differs from the two previous species by its smaller feathery appearance, flexuose pinnule midvein, slightly constricted auriculate pinnule base, and squatter hastate pinnule shape. It is possibly a portion of pinna from a bipinnate frond with a similar habit to that of the other two Koonwarra *Cladophlebis* species, but without more complete portions of plant little else can be said about its morphology or affinities. In many respects its external morphology compares closely with *Cladophlebis* sp. 'a' of Douglas (1973, text-fig.7,4).

ACULEA Douglas 1973

ACULEA BIFIDA Douglas 1973 (Fig. 20)

1892	Unnamed; Stirling, pl.1, fig.5.
1904	*Sphenopteris* sp.; Seward, p.167, fig.17.
1909	*Stenopteris* sp.; Chapman, p.109, pl.13, fig.3.
1909	*Stenopteris elongata* Carruthers; Chapman, p.109, pl.13, fig.4.
1973	*Aculea bifida* Douglas, p.93, pl.35; pl.36, fig.1; text-figs 7,37, 7,38.

Material. Holotype (by original designation) NMVP165730 from Boola Boola Forest, NMVPL429. Other material NMVP167530–167551.

Description. Fronds up to 100mm long, deeply dissected, consisting of narrow linear segments up to 1.5mm wide (usually about 1mm) which each contain only a midvein. Branching pattern anadromic, lateral branches arising from the main axis, distichously arranged, similarly branching into segments. Segment margins entire, parallel, angle of branching acute (10–20°), segment apices acute. Branching often irregular.

Fertile segments slightly reduced in length, terminated by a sorus giving the apices a swollen appearance and the lamina possibly extending to form an enveloping involucre. On most fertile foliage all, or nearly all, of the frond segments are fertile. Occasionally essentially sterile foliage bears one or a few sori.

Discussion. In this particularly finely dissected fern it is difficult to delineate between pinnae and pinnules. The main axis is determined only by its central position in the more or less bisymmetrical fronds; there is no strongly defined rachis or rachilla. At any one position on the frond, be it main axis or ultimate segment, the plant consists only of the straight longitudinal midvein and up to 1.5mm width of lamina. The lamina and midvein branch together, the margins remaining entire, straight, and parallel.

Sterile foliage of this type was figured by Stirling (1892), and by Seward (1904) who considered it a species of *Sphenopteris* Brongn. It differs from the other Victorian *Sphenopteris* fronds by having an anadromic branching pattern (Harris (1961) considered katadromic v. anadromic an important taxonomic character). Chapman (1909) described two specimens as different species of *Stenopteris* Saporta, but the subseqent discovery of fertile foliage suggests affiliation with the ferns (not pteridosperms). Douglas (1973) noted the previous assignment to *Sphenopteris* and the similarities in frond habit to his *Sphenopteris* sp. 'e' and *Sphenopteris* sp. 'f', but erected *Aculea* on the basis of fertile specimens.

Although few species of the extant ferns are as dissected as these fossils, the branching pattern and the sorus position resemble several extant taxa (e.g. some *Davallia* Smith species like *D. schimperi* Hook. 1846 (*ex icon* Hooker 1846, p. 169, Tab. LA) and some filmy ferns like *Hymenophyllum australe* Willd. 1810). Unfortunately peels of soral regions failed to elucidate any involucral or sporangial details. Assignment to a family of the Pteridophyta must await more satisfactorily preserved sporangial detail.

MARSILEALES ? indet. (Fig. 21D,E)

Material. NMVP167525, 167526.

Description. Stem with leaves attached, length preserved 27mm. Stem 1.3mm thick, longitudinally ribbed. Leaves petiolate, petiole 10mm long by 0.8mm wide, continuous with leaf lamina. Lamina ?obovate, 8mm long (at least), 10mm wide, margins cleft. Venation spreading, one vein entering the leaf from the petiole and branching into the lamina. Leafy parts arising from a pubescent rhizome.

Discussion. Of these two small specimens only one leaf is sufficiently expanded to show the shape and venation (Fig. 21D). The distal margin of this leaf is broken and compressed onto the lamina obscuring the cleft dissection. Venation is branched and spreading, originating from a single vascular trace which enters the lamina from the petiole; there is no evidence of reticulate secondary venation. The longitudinal ridges on the stem probably represent 'corners' of an axis that was angular in transverse section in a manner similar to the stipes of many species of ferns. This, together with the pubescent rhizome (Fig. 21E), suggests that these plants were ferns. Preserved close to the leaf petiole of NMVP167525 (Fig. 21D), but not conclusively attached, is a dark coloured structure approximately 3mm in diameter. If this structure does belong to the plant it may be a sporocarp, the plant itself resembling the extant water ferns of the Marsileales. Dettmann (1963) recorded, from the Victorian Lower Cretaceous, megaspores (*Pyrobolospora* Hughes) and microspores (*Crybelosporites* Dettmann) which appear similar to those of the extant Marsileales.

A leaf of similar size and shape, and also from Koonwarra, was illustrated by Douglas (1973, pl.33, fig.3, text-fig.7,44) as a species of *Hausmannia* Dunker (Dipteridaceae). His specimen was not available for examination for this study, but from the figures and description (which illustrate a reticulate network of secondary veins) the more recently discovered leaves compared here with the Marsileales are interpreted as a different taxon.

Division PTERIDOPHYTA?/ PTERIDOSPERMOPHYTA?

PHYLLOPTEROIDES Medwell 1954

PHYLLOPTEROIDES LANCEOLATA (Walkom 1919) Medwell 1954 (Fig. 22C–E)

1919a *Phyllopteris lanceolata* Walkom, p.23, pl.3, figs 1–3.
1954b *Phyllopteroides lanceolata* (Walkom) Medwell, p.19, pl.2, fig.1.
?1954b *Phyllopteroides expansa* (Walkom) Medwell, p.19.
1969 *Phyllopteroides lanceolata* (Walkom) Medwell; Douglas, p.67, pl.1, figs 5, 6; text-figs 1,76, 1,77.

Material. Holotype (by monotypy) Geological Survey of Queensland No. F1a from the Lower Cretaceous Burrum Series in Queensland. Other material NMVP167486–167491 from NMVPL425.

Description. Leaves simple, 15–60mm by 7–20mm wide, elliptical to oval (occasionally with a slightly truncate base), arranged distichously to sub-oppositely along a narrow stem 0.5–1.0mm wide, inserted laterally or slightly dorsally, attachment sessile to sub-petiolate, divergence angle 45–50°. Petiole continuing into leaf as midvein, persistent almost to leaf apex. Secondary veins arising from midvein at 45°, oppositely arranged, dichotomizing once or twice (usually twice) before reaching the margin, up to seven pairs of secondary veins per 15mm of midvein. Margins serrated (serration tips corresponding to veinlet endings), occasionally slightly more incised at limits of veinlet groups derived from the same secondary vein.

Discussion. One Koonwarra specimen consists of leaves attached to a stem, others are unattached leaves which are oval rather than elliptical and smaller than those illustrated by Douglas (1969, pl. 15, fig. 3); the largest one from Koonwarra measures 21mm by 10mm. However, venation, attachment, and arrangement are similar. The consistency of these latter characters in the small number of Koonwarra leaves available, suggests that they are best placed in the same species.

Medwell (1954b) described *P. lanceolata* from Killara Bluff (Zone D), and all Douglas's specimens came from Boola Boola Forest (Zone B). The Koonwarra leaves are the first record of *Phyllopteroides* type leaves from Zone C sediments. An apparently closely related leaf *P. dentata* Medwell 1954 is common in Zone D beds of western Victoria and differs from *P. lanceolata* by having crowded secondary veins which usually dichotomize only once between the midvein and the strongly serrate margin. The Koonwarra leaves, apart from being smaller, show characters intermediate between these Zone B and Zone D *Phyllopteroides* foliage types, which may reflect the stratigraphic position of Koonwarra between the Boola Boola Forest Zone B and western Victorian Zone D localities.

Inclusion of *Phyllopteroides* in 'pteridosperms and unknowns' (Douglas, 1969) was not meant to imply definite seedfern affiliation and indeed, no fructifications definitely attributable to this species have been found. The foliage is similar to several extant ferns (e.g. *Pellaea* Link, *Danaea* Smith and *Todea* Willd.) and it is possible that *P. lanceolata* belongs to the Pteridophyta.

THINNFELDIA Ettingshausen 1852

THINNFELDIA sp. cf. T. INDICA Feistmantel 1876 (Fig. 23)

Material. NMVP167492–167501.

Description. Fronds pinnate, preserved lengths up to 70mm (total lengths unknown). Rachis 2.5mm

Fig. 21. A–C, *Adiantites lindsayoides* Seward. A, portion of fertile frond from Cape Paterson showing zwischenfiedern fertile in a manner similar to the pinnules, MUGD3595, ×2. B, sporangium from Cape Horn isolated in the sediment but closely associated with fertile *Adiantites lindsayoides* fronds, NMVP167693, scale = 100 μm (similar sporangia were seen protruding from *A. lindsayoides* sori). C, sporangium (from Cape Horn), NMVP167692, scale = 100 μm. D,E, Marsileales ? indet. D, portion of leafy shoot showing the margin of the large leaf compressed back onto the lamina obscuring the incised nature of the leaf edge, and darkly coloured structure at the base of the petiole NMVP167525, ×4. E, portion of leafy shoot arising from a pubescent rhizome, NMVP167526, ×4.

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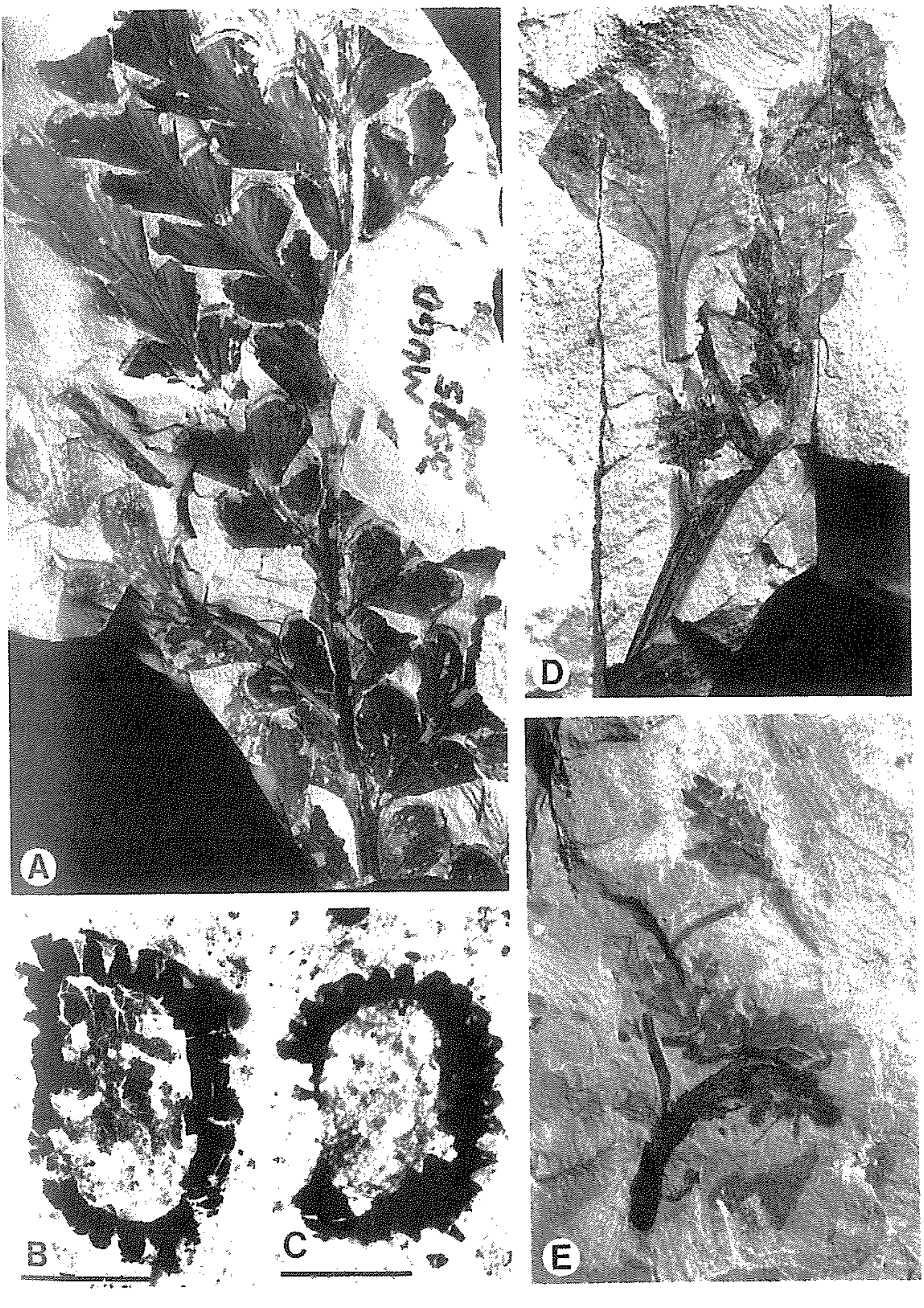

wide, lacking a lamina wing. Pinnae up to 40mm long by 13mm wide, oppositely arranged, inserted laterally or slightly dorsally on the rachis, attachment sessile to sub-petiolate. Distal pinnae lanceolate, sometimes recurved to be slightly falcate, varying in size from 40mm × 13mm to 21mm × 8mm, margins entire to slightly undulate, acroscopic margin convex, basiscopic margin concave, apices bluntly acute. Proximal pinnae smaller, 20mm × 11mm, obovate, slightly recurved, margins undulate to lobate, apices obtuse. Pinna venation neuropteroid, one vein entering each pinna and persisting for about half the pinna length. Secondary veins arched, diverging from the midvein at 20°, dichotomizing several times and persisting to the pinna margins. Secondary veins and veinlets crowded.

Discussion. The fronds are once pinnate and exhibit two different pinna types. Distal pinnae are lanceolate-falcate, with entire margins which taper to acute apices, and a sessile basal attachment which is slightly decurrent. Pinnae more central on the frond are obovate with sub-petiolate attachment and obtuse apices; their margins are lobed but not enough to warrant pinnate status. The two pinna types are not exhibited by any one specimen, but the trend from entire to undulate margins can be seen in one Koonwarra specimen (Fig. 23C). The gradation from one pinnule type to the other does not seem to be equivalent to the reduction of apical parts exhibited by the 'sphenopteroid' and 'cladophleboid' ferns already discussed, and may represent a transition from young to mature foliage.

Pieces of frond bearing some resemblance to this species were described by Douglas (1969) from older Lower Cretaceous Zone B sediments at Boola Boola Forest and Zone C sediments at Jumbunna. He noted a number of similarities to *Thinnfeldia chunakalensis* Sah & Dev 1957 from the Rajmahal Hills, and provisionally placed the fronds in that species. Apical portions of the Koonwarra fronds are similar to those from Boola Boola Forest in shape and arrangement, but have a more crowded secondary venation. Proximal pinnae, however, differ considerably from Douglas' specimens, being obovate rather than linear, and having truncate bases and less dissected margins. They show a much closer resemblance to *T. talbragarensis* from the Jurassic of New South Wales and *T. indica* from the Jurassic of the Rajmahal Hills, India. Walkom (1921) described a similar range of entire, rhombic to undulate, oblong pinnae for *T. talbragarensis*, illustrating specimens similar to both Koonwarra types. The *T. indica* specimens figured by Zeba-Bano *et al.* (1979) resemble the distal lanceolate pinnae from Koonwarra (Fig. 23A,C). While fronds from Koonwarra are not identical with any of the three species they are compared with above, the similarities in pinna form and variation suggest a close affinity. Taking into account the different ages it would not be unreasonable to consider them time related variants of a single taxon.

Without fertile foliage it is impossible to determine whether this taxon is a fern or seedfern. Its placement in *Thinnfeldia* is based on frond similarities to the three species noted above, particularly *T. indica*, and is not intended to imply definite pteridosperm affinity.

INCERTAE SEDIS

Order PENTOXYLALES

TAENIOPTERIS Brongn. 1828

TAENIOPTERIS DAINTREEI McCoy 1874 (Fig. 24)

1860 *Taeniopteris daintreei* McCoy, p.97.

1874 *Taeniopteris daintreei* McCoy, p.15, pl.14, figs 1,1a,2.

1878 *Taeniopteris daintreei* McCoy; Etheridge, p.100.

1890 *Taeniopteris daintreei* McCoy; Feistmantel, p.114, pl.27, figs 4,5.

1892 *Taeniopteris daintreei* McCoy; McCoy *in* Stirling, p.12, pl.2, figs 11,12.

1898 *Angiopteridium spathulatum* McClelland; Dun, p.390.

1900 *Taeniopteris carruthersi* Tenison-Woods; Stirling, p.13, pl.1, figs 1,1a,2.

1900 *Taeniopteris daintreei* McCoy; Stirling, p.13, pl.1, fig.5b; pl.2, figs 4,7,7a; pl.2a, figs 1,1a,2.

1904 *Taeniopteris daintreei* McCoy; Seward, p.168, figs 18-22.

1904 *Taeniopteris daintreei*McCoy var. *major*; Seward, p.171, figs 25-27.

1908 *Taeniopteris spatulata* McClelland; Chapman, p.215, pl.36, figs 1,2.

1908 *Taeniopteris spatulata* McClelland var. *carruthersi* Tenison-Woods; Chapman, p.215, pl.37, figs 1,2.

1908 *Taeniopteris spatulata* McClelland var. *daintreei* McCoy; Chapman, p.216, pl.37, fig.3.

Fig. 22. A,B, *Adiantites lindsayoides* Seward. A, portion of sterile frond showing the zwischenfiedern (pinnules arising directly from the rachis between successive pinnae). NMVP167470, × 1.3. B, sterile pinna with two veins entering each pinnule from the rachilla, NMVP167471, ×2.5. C-E, *Phyllopteroides lanceolata* (Walkom) Medwell. C, portion of sterile frond, NMVP167486, ×2.5. D, isolated leaf, NMVP167487, ×3.5. E, isolated leaf, NMVP167488, ×3.5.

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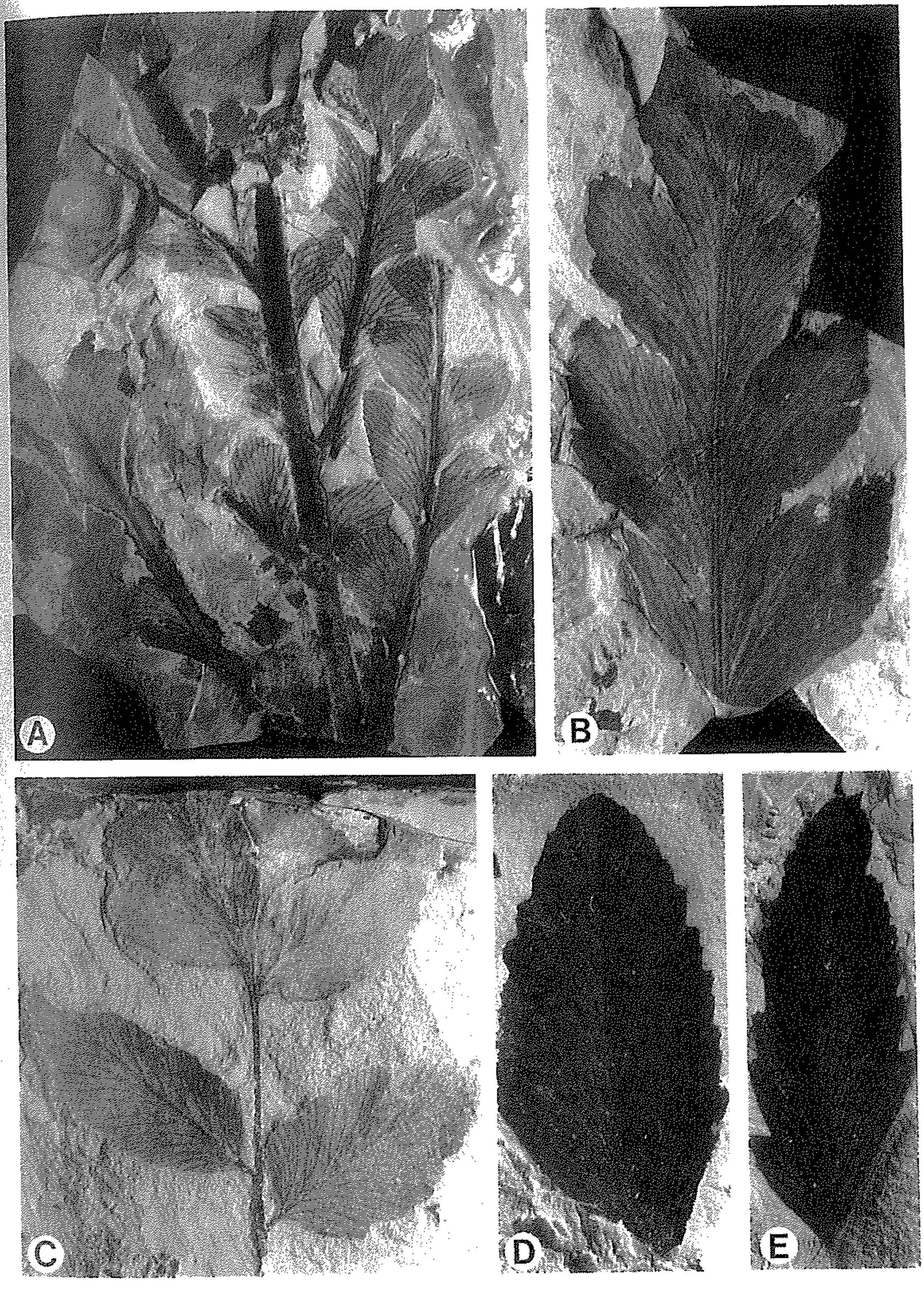

1909	*Taeniopteris spatulata* var. *crenata* McClelland; Chapman, p.109, pl.14, figs 5,6; pl.15, fig.8.
1954a	*Taeniopteris spatulata* Oldham & Morris; Medwell, p.86, fig.11.
1954a	*Taeniopteris crenata* McClelland; Medwell, p.89.
1969	*Taeniopteris daintreei* McCoy; Douglas, p.53, pl.17, figs 3, 4; pl.18, fig.3; text-figs 1,1, 1,51-1,55, 1,65.
1985	*Taeniopteris daintreei* McCoy; Drinnan & Chambers, p.90, figs 1-4.

Material. Lectotype (designated Drinnan & Chambers, 1985) NMVP12270 from the shore platform at Cape Paterson, NMVPL428. Other material NMVP167502-167513 from NMVPL425.

Description. Leaves petiolate, simple, linear, variable in size and shape, ranging from 100mm × 10mm to 300mm × 30mm, arrangement on shoot or stem uncertain. Petiole variable in length, up to half the length of the leaf lamina, 1-2mm wide, continuing into the leaf as a prominent midvein persisting to the leaf apex. Secondary veins parallel, arising from the midvein at 90° (slightly more acute toward base and apex), most dichotomizing once or twice before reaching the margin. Secondary vein density 15-30 per 10mm of lamina measured midway between the midvein and leaf margin. Leaf margins entire, usually straight and parallel but occasionally undulate, tapering gradually to an acute base, and terminating distally at an acute to obtuse apex.

Discussion. Taeniopteris daintreei was the most abundant plant species collected from Koonwarra and was well represented in all layers of the deposits. As noted in the description, this species exhibits wide variation in leaf form. Although leaves with most combinations of characters have been found, the larger, wider leaves usually have margins that tend to be undulate, apices which are obtuse to almost truncate, and densely arranged secondary veins which arise at right angles to the midvein. The secondary veins often divide at or very close to the midvein giving them a tuning fork appearance. Narrower leaves tend to have straight margins, acute apices, and secondary veins which are more sparsely arranged, are not as strictly perpendicular to the midvein, and divide at any distance between the midvein and leaf margin. Leaves of intermediate size exhibit intermediate characters.

Drinnan & Chambers (1985) provided a more detailed account and ascribed *T. daintreei* to the extinct gymnospermous Order Pentoxylales, based on the association in the Victorian Lower Cretaceous of these leaves with the pentoxylalean female cones, *Carnoconites cranwellii* (at Apollo Bay) and pollen organs, *Sahnia laxiphora* (Koonwarra Fossil Bed and Whitelaw). Significantly, in all other definite reports of Pentoxylales fertile organs (e.g. Sahni, 1948; Vishnu-Mittre, 1953, 1957; Harris, 1962; White, 1981) the reproductive structures are co-fossilized with *Taeniopteris* type leaves.

SAHNIA Vishnu-Mittre 1953

SAHNIA LAXIPHORA Drinnan & Chambers 1985 (Fig. 25)

1969	Fertile Organ Bearing Microsporangia; Douglas, p.240, pl.45, figs 1, 2; pl.46, figs 1, 6; pl.48, fig.1; pl.51, fig.1; text-figs 5.2-5.6.
1985	*Sahnia laxiphora* Drinnan & Chambers, p.97, figs 9,10.

Material. Holotype (by original designation) NMVP167524 from Whitelaw, NMVPL427. Other material NMVP167521-167523 from NMVPL425.

Description. Microsporangiate structures consisting of more than 30 sporophylls arising from the surface of a conical receptacle. Receptacle up to 25mm long by 7mm wide (at base), tapering gradually to an obtuse apex. Sporophylls up to 12mm long, 0.5mm diameter, each bearing numerous sporangia (more than 20) along its distal half. Sporangia oval-spherical, 1.0mm by 0.7mm, shortly stalked, arrangement uncertain. None of the specimens show seed bearing parts, involucral leaves or bracts, or attachment to a stem or shoot.

Discussion. One Koonwarra specimen (Fig. 25C) is compressed laterally showing sporophylls attached to an elongate axis. The other two are compressed dorsiventrally showing the sporophylls radiating from all sides of the receptacle. The holotype (Fig. 25D) is preserved obliquely, but apparently with a much shorter axis than that compressed laterally (Fig. 25C). Although an elongate axis is not obvious in the three latter specimens, their preservation indicates a receptable of substantial structure. While it is possible that one specimen with its elongate

Fig. 23. Thinnfeldia sp. cf. *T. indica* Feistmantel. A, portion of sterile frond with recurved lanceolate leaves, NMVP167492, ×1.3. B, portion of sterile frond showing pinnules with undulate to slightly lobed margins, NMVP167493, ×1.3. C, apical portion of sterile frond, with a slight gradation of pinnules from entire to undulate margins proximally along the rachis, NMVP167494, ×1.3. D, sterile frond, NMVP167495, ×1.3.

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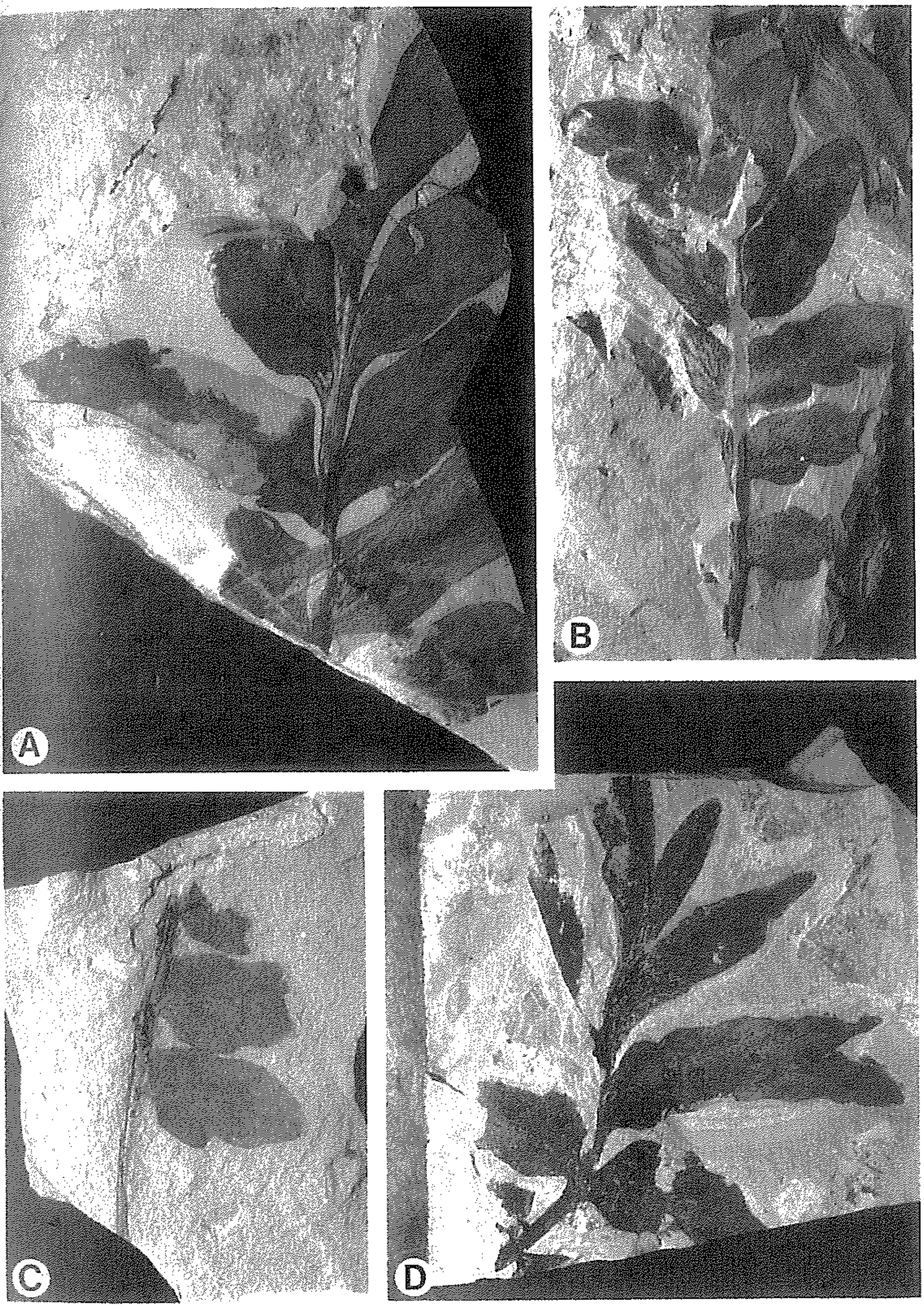

receptacle (Fig. 25C) may represent a different taxon to the others, there are too few specimens to be certain.

Without any organic connection or close association with leaves it is impossible to determine the exact affinities of any fossilized reproductive organs, but these specimens are almost certainly pollen bearing organs of a pentoxylalean plant, bearing leaves of the species *Taeniopteris daintreei* (Drinnan & Chambers, 1985). They bear a striking resemblance to *S. nipaniensis*, the pentoxylalean male fructification from Jurassic sediments in the Rajmahal Hills, India, the type area of the order.

A more detailed consideration of *Sahnia laxiphora* is provided by Drinnan & Chambers (1985) in their paper on Lower Cretaceous Pentoxylales of Victoria.

Division GINKGOPHYTA

Order GINKGOALES

Family GINKGOACEAE

GINKGO L. 1771

Seward (1919, p. 12) erected *Ginkgoites* for ginkgoalean leaves which, due to the lack of associated reproductive organs, did not show sufficient affinity to the only extant species *Ginkgo biloba* to justify assignment to the same genus. Florin (1936, p. 105) assigned to *Ginkgo* fossil leaves having epidermal or other anatomical characters of systematic importance resembling leaves of *G. biloba*. Florin emended *Ginkgoites* Seward to encompass leaves in which epidermal or other anatomically important characters were either unknown or differed significantly in one or more apsects from *G. biloba*. Florin redefined *Baiera* Braun as deeply dissected leaves with narrow linear segments, each segment having not more than four veins.

The different applications of the name *Ginkgoites* by Seward (1919) and Florin (1936) leads to generic separation without an adequate basis for morphological distinction. This inconsistency prompted Harris & Millington (1974) to discard *Ginkgoites* in favour of *Ginkgo*. Harris & Millington noted the overlap between *Ginkgo* and *Baiera sensu* Florin which occurs due to intraspecific variation, but considered few leaves intermediate in that respect and retained *Baiera* as taxonomically useful.

Following Harris & Millington (1974), and taking into consideration the presence at Koonwarra of male strobili which, based on external morphological features, are very similar to those of *G. biloba*, the Victorian Early Cretaceous leaves previously ascribed to *Ginkgoites australis* (McCoy 1892) Florin 1936 are here transferred to *Ginkgo australis* (McCoy 1892) comb. nov.

GINKGO AUSTRALIS (McCoy 1892) comb. nov. (Figs 26, 28A–E)

1892 *Baiera australis* McCoy *in* Stirling, p.12, pl.1, fig.2.
1892 *Baiera subgracilis* McCoy *in* Stirling, p.12, pl.2, fig.13.
1892 *Baiera robusta* McCoy *in* Stirling, p.12.
1899 *Baiera* sp.; Dun, p.161.
1900 *Baiera subgracilis* McCoy; Stirling p.5, pl.1, figs 4–7.
1900 *Baiera robusta* McCoy; Stirling, p.5.
1900 *Baiera australis* McCoy; Stirling, p.5, pl.1, figs 3,3a.
1901 *Baiera subgracilis* McCoy; Etheridge *in* Stirling, p.9.
1901 *Baiera bidens* Tenison-Woods; Etheridge *in* Stirling, p.9.
1902 *Baiera subgracilis* McCoy; Etheridge, p.6.
1904 *Ginkgo* sp.; Seward, p.177, pl.17, fig.35.
1904 *Baiera australis* McCoy; Seward, p.177, pl.18, figs 36,37.
?1904 *Baiera deliculata* Seward, p.178, fig.38.
1936 *Ginkgoites australis* (McCoy) Florin, p.106.
1954a *Ginkgoites australis* (McCoy) Florin; Medwell, p.96.
1954a *Ginkgoites antarcticus* (Saporta) Seward; Medwell, p.97.
?1954a *Baiera deliculata* Seward; Medwell, p.97.
1965 *Ginkgoites australis* (McCoy) Florin; Douglas, p.20, figs 3–5,7,11–18.
1969 *Ginkgoites australis* (McCoy) Florin; Douglas, p.191, pl.36, figs 1–3, 5, 6; pl.37, figs 1–4; pl.38, figs 1–3, 5; text-figs 3,1–3,16, 3,36.
?1969 *Baiera deliculata*Seward; Douglas, p.201, pl.35, fig.9; pl.36, fig.7.

Material. Holotype (by monotypy) NMVP110685 from Burne's Creek, SE Victoria. Other material NMVP167552–167574 from NMVPL425.

Fig. 24. Taeniopteris daintreei McCoy. A, almost complete leaf showing leaf lamina tapering gradually to the leaf base, NMVP167502, ×1. B, basal portion of leaf lamina with entire margins, NMVP167503, ×1.5. C, medial portion of leaf with crenate margins, NMVP167504, ×1.5. D, apical portion of leaf with broadly pointed apex, NMVP167505, ×1.5. E, medial portion of leaf showing sparsely arranged secondary veins which often dichotomize at any distance between the midvein and the lamina margin, NMVP167506, ×2. F, apical portion of leaf with obtuse apex and dense secondary veins which usually dichotomize very close to the midvein, NMVP167507, ×2. G, apical portion of leaf with acute apex, NMVP167508, ×2. H, apical portion of leaf, NMVP167509, ×2.

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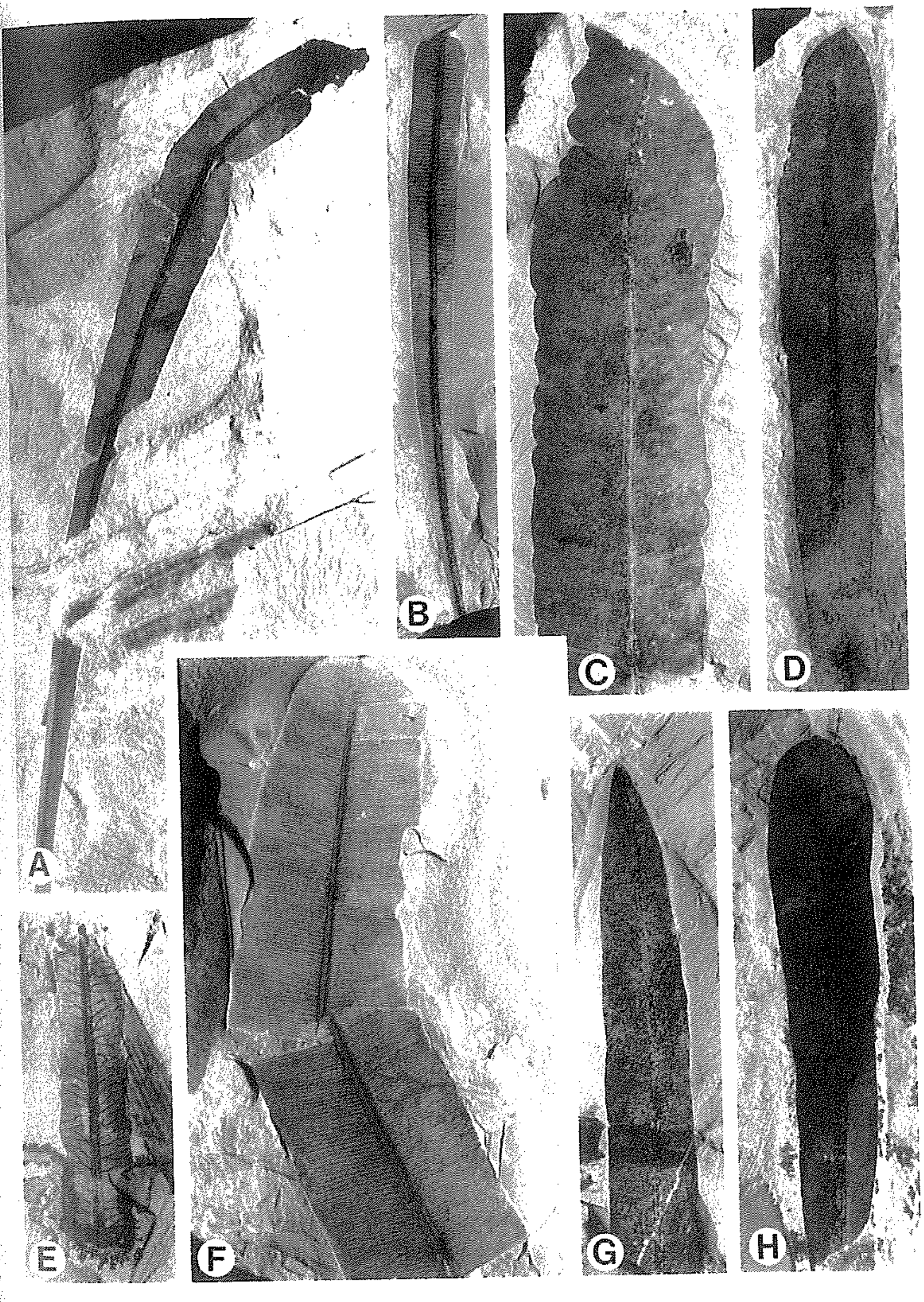

Description. Leaf simple, petiolate, lamina radius 8mm to 90mm, petiole length up to 1.5 times the lamina length and 2mm in diameter. Lamina fan-shaped, digitate, deeply dissected, basal angle 45° to 180°. Major dissection bipartite along the center of the leaf to the lamina base. Subsequent segments dissected to varying degrees, the number of ultimate segments ranging from two to sixteen. Leaves symmetrical about the petiolar axis. Segments spatulate, 2mm to 5mm wide, margins straight, parallel for most of segment length, tapering to an acute base (if persistent to the petiole) and terminating at an obtuse apex. Venation parallel, veins dichotomizing at an acute angle several times between the lamina base and segment ends. Leaves borne closely on a ?short shoot.

Although not preserved on Koonwarra specimens, Douglas (1965, 1969) described the cuticle from a bore at Port Campbell, the main features being a hypostomatic leaf divided into vein (elongate cells) and intervein (polygonal cells) areas. The normal epidermal cells each have one short, hollow papilla, and the 4-7 subsidiary cells per haplocheilic stomata each have a longer, thinner papilla.

Discussion. Together with *Taeniopteris daintreei* and *Sphenopteris warragulensis*, leaves of *G. australis* are the most abundant and most variable elements of the Koonwarra flora. Presuming *G. australis* had a deciduous habit similar to the extant *G. biloba*, it may be assumed that most of the unattached leaves were shed in a senescent state and represent mature rather than developing foliage. Only one specimen has leaves attached to a stem (Fig. 28E) and this appears to have been a short shoot similar to those of living *G. biloba*. The leaves tend to occur in definite layers within the bedding planes which strengthens the evidence for seasonal abscission. Excepting a couple of leaves which are divided into only two linear segments, the majority of leaves are variably incised and segmented. All have the bipartite dissection to the lamina base and at least one other dissection of each of the subsequent lamina halves, giving a minimum of four spatulate segments. In most cases the four quarter segments are also incised, but not as deeply into the lamina. The subsequent eight segments are often dissected again (even more shallowly) producing leaves with a maximum of sixteen ultimate segments.

Ginkgo australis leaves are among the more common fossils in the Korumburra Group and the older sediments of the Otway Group, and are excellent guide fossils for Zone C (Douglas, 1969). Belonging to such an abundant and widespread species they were among the first Victorian Lower Cretaceous plants described. McCoy (in Stirling, 1892), apparently after examining only a small collection, assigned these leaves to three species of *Baiera*. He considered them closely related to English Jurassic specimens and thus further supporting an Oolitic age for the Victorian sediments. The specimen illustrated by McCoy (in Stirling, 1892, pl. 1, fig. 2), until recently thought to be lost (Douglas, 1965), was located by Dr P.A. Jell in the Museum of Victoria Collection. Subsequent to the illustration by McCoy (which was reversed) the specimen has broken in two along the fracture evident in the illustration. Also re-discovered is another specimen, NMVP110686, from the type locality with a style of label that indicates it was almost certainly available to McCoy at the time of his original determination. McCoy's classification was followed by Stirling (1900), Etheridge (1902) and Seward (1904). Seward included a specimen from Cape Otway as *B. deliculata* which is possibly distinct. Florin (1936), listed under the '*Ginkgo*-like-but-cuticle-unknown' genus *Ginkgoites*, the species *G. australis* but made no reference to McCoy's other species *B. robusta* or *B. subgracilis* either as transferred to *Ginkgoites* or retained in *Baiera*, but presumably he considered the three species identical. Medwell (1954a) followed Florin's usage of *G. australis*, except for one specimen she assigned to *G. antarcticus* (Saporta) Seward 1919. This specimen is however, almost certainly a portion of a *Ginkgo australis* leaf. The leaves from Koonwarra exhibit the range of variation noted by Douglas (1969) which includes (at one extreme) the delicate dissection of *Baiera deliculata*.

Leaves of *G. australis* are similar to those of Mesozoic ginkgoaleans. On external morphology they are almost identical to *G. huttoni* (Sternberg 1833) Heer 1876, *Ginkgo* sp. cf. *G. sibirica* Heer 1876 and *G. longifolius* (Phillips 1829) Harris 1974 as described by Harris & Millington (1974) from the Yorkshire Jurassic, but differ in cuticle characters concerning papillae and trichomes. *Ginkgo rajmahalensis* from the Jurassic of northeastern India falls well within the range of variation of leaf size and shape exhibited by *G.*

Fig. 25. *Sahnia laxiphora* Drinnan & Chambers. A, microsporangiate structure compressed dorsiventrally, showing sporangiophores radiating from a central axis, NMVP167521, × 3. B, microsporangiate structure compressed dorsiventrally, NMVP167522, × 3. C, microsporangiate sturcture compressed laterally showing elongated axis, NMVP167523, ×3. D, microsporangiate structure from Whitelaw compressed slightly obliquely, showing sporangia located on the distal portions of the sporangiophores, NMVP167524, ×3.

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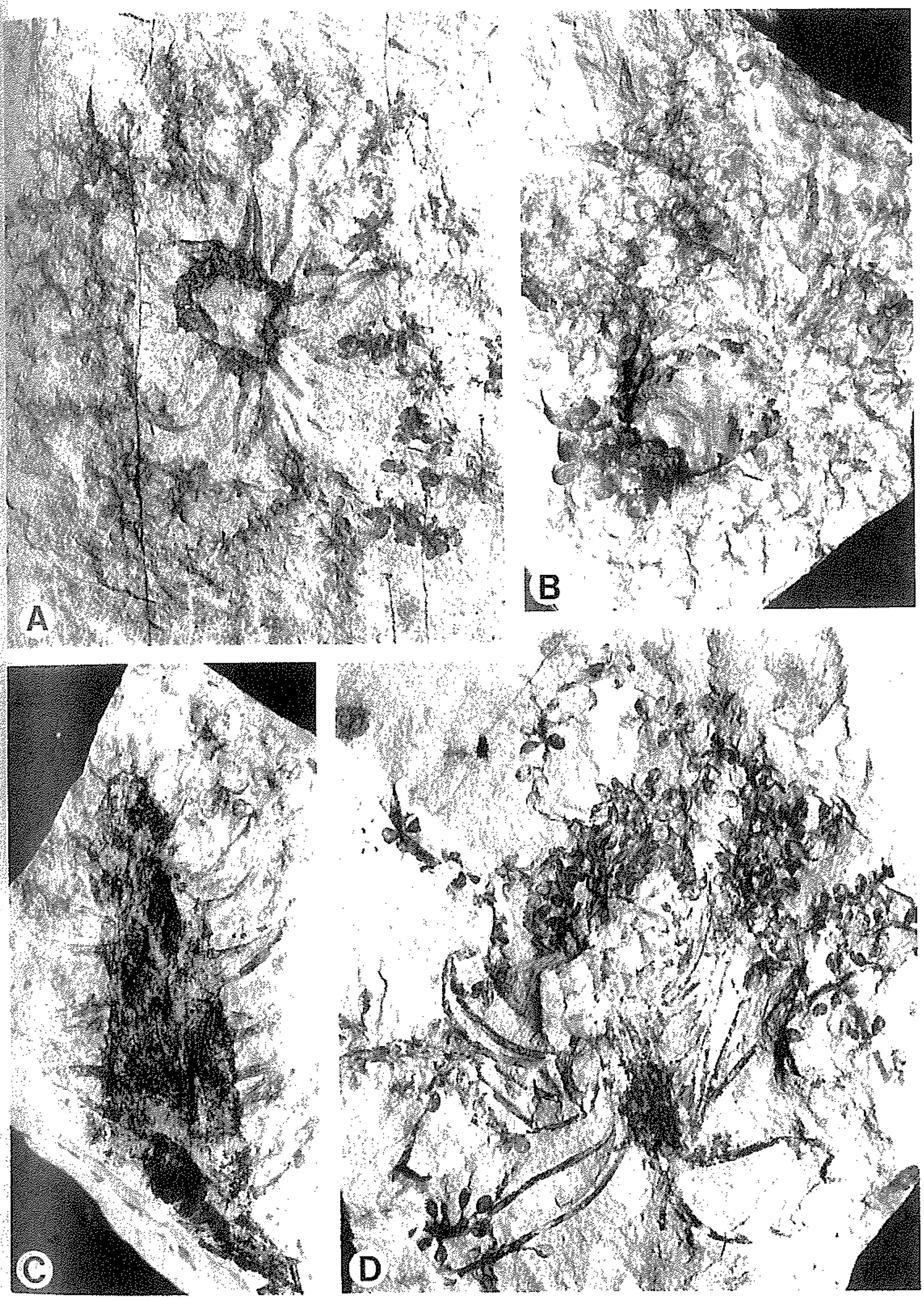


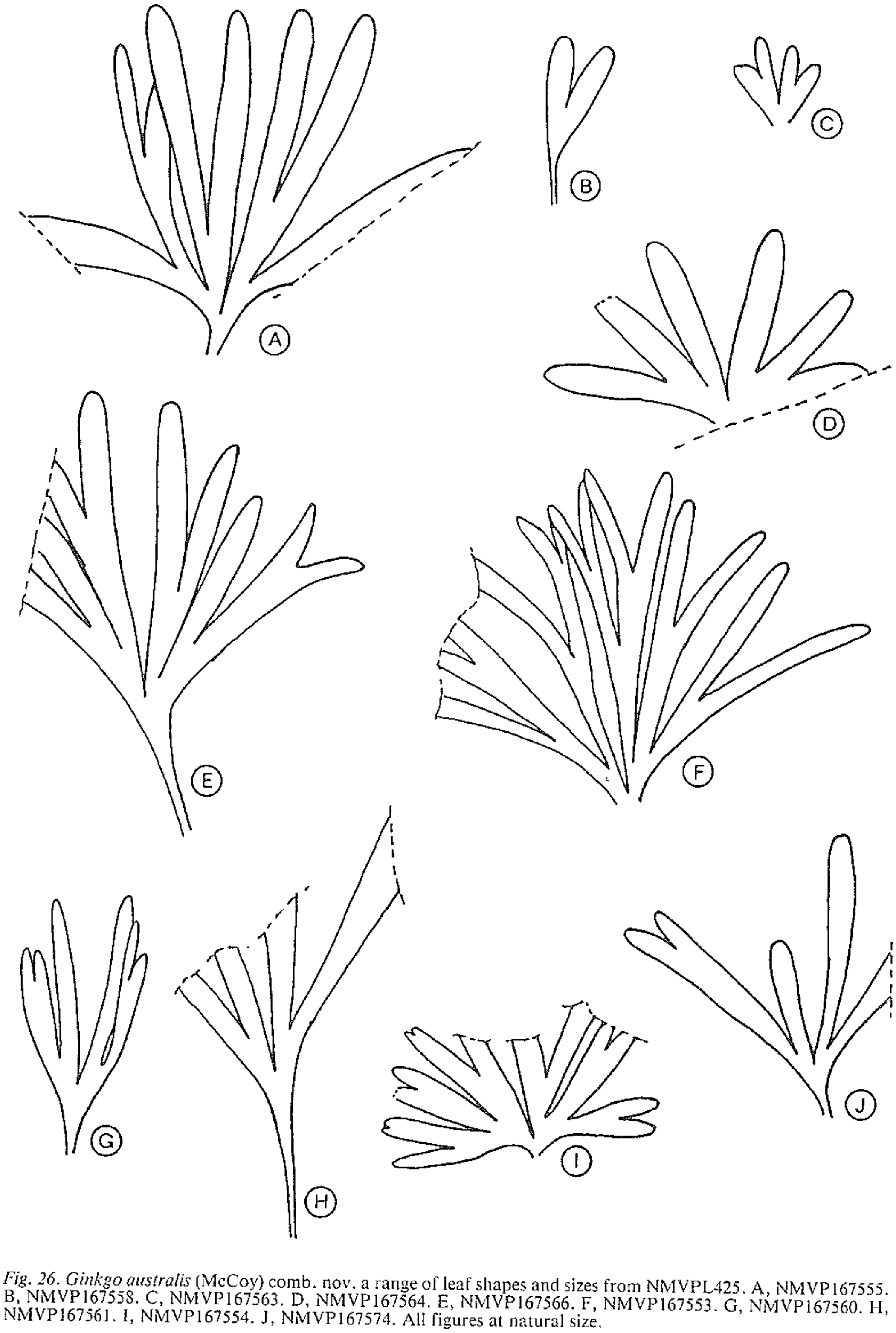


Fig. 26. Ginkgo australis (McCoy) comb. nov. a range of leaf shapes and sizes from NMVPL425. A, NMVP167555. B, NMVP167558. C, NMVP167563. D, NMVP167564. E, NMVP167566. F, NMVP167553. G, NMVP167560. H, NMVP167561. I, NMVP167554. J, NMVP167574. All figures at natural size.

5. A, NMVP167555.
3, NMVP167560. H,

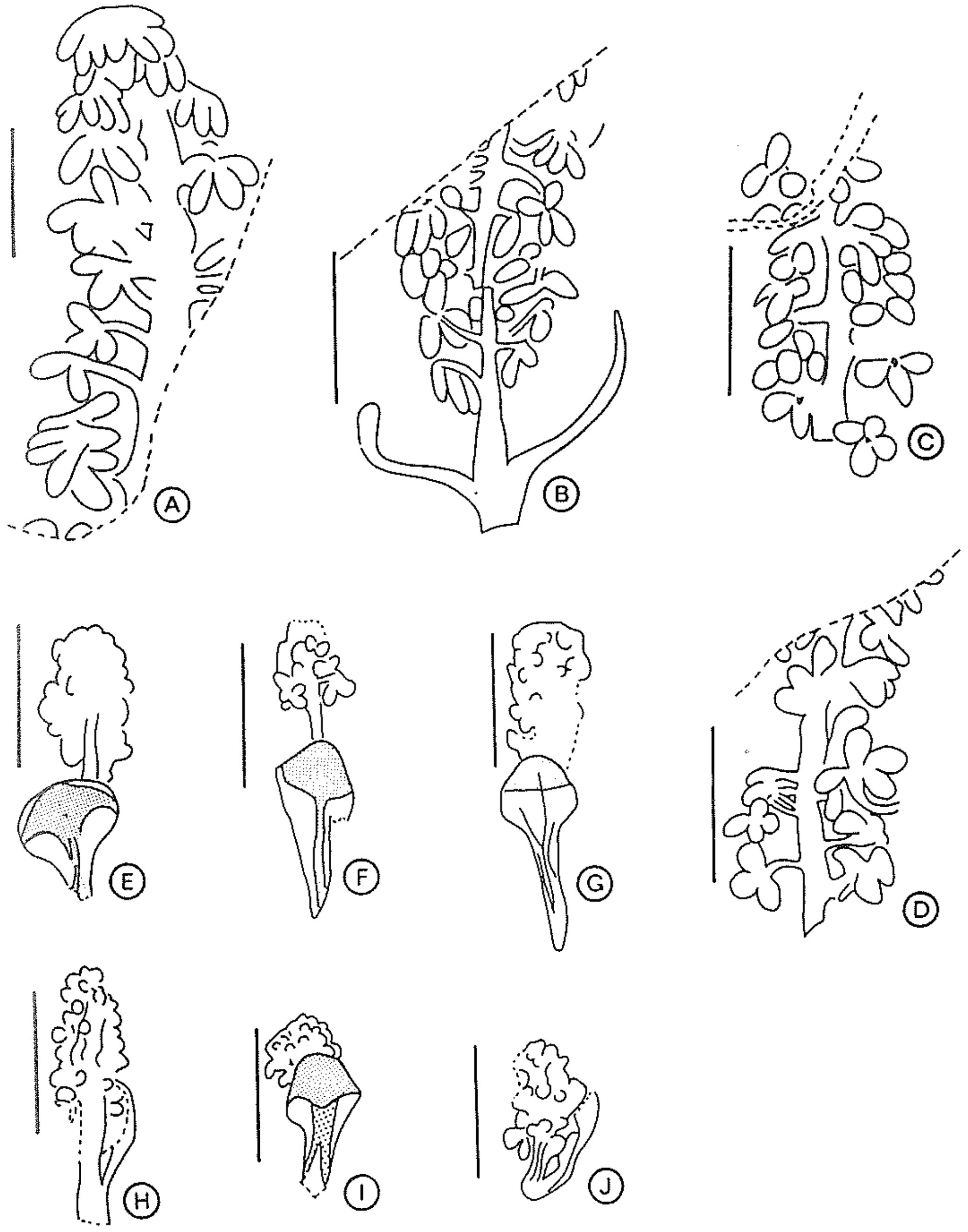
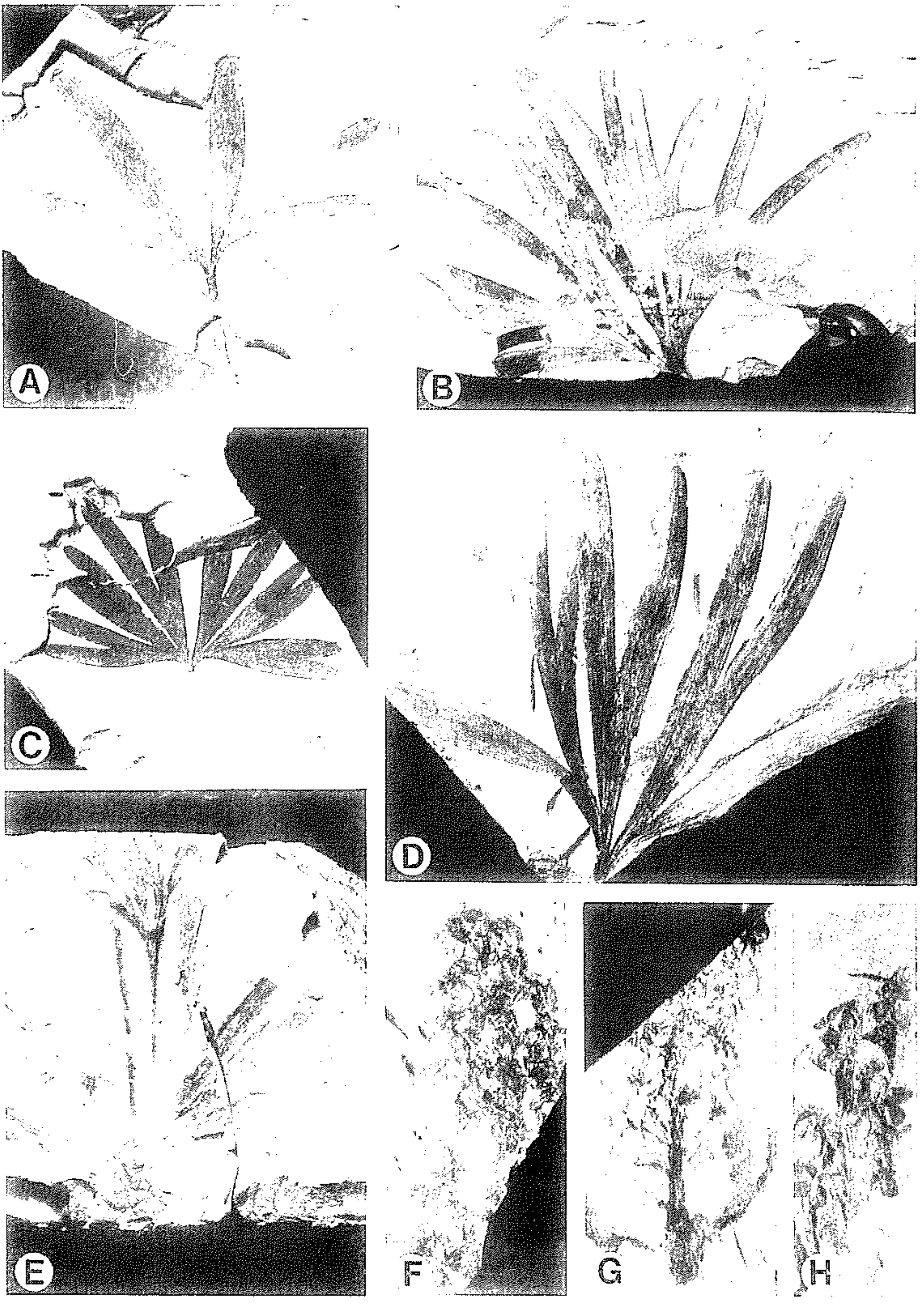


Fig. 27. A–D, *Ginkgo* male strobilus. A, NMVP167575. B, NMVP167576. C, NMVP167577A. D, NMVP167577B, counterpart of C. E–J, *Ginkgo* male strobilus (immature). E, NMVP167527. F, NMVP167528. G, NMVP167697. H, NMVP167529. I, NMVP167698. J, NMVP167528. Scales = 5mm.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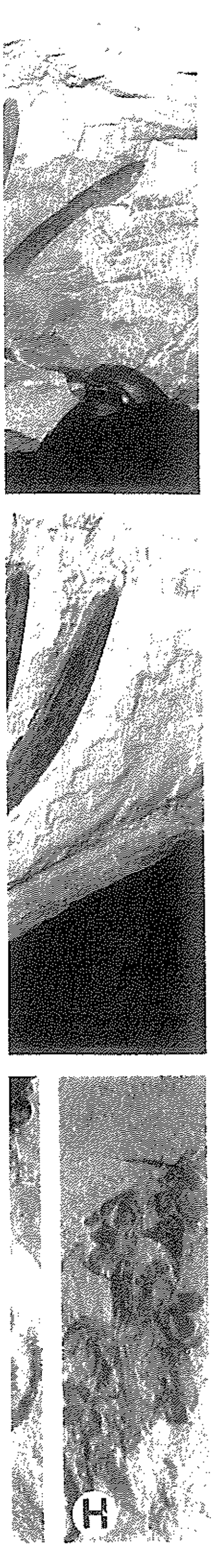

australis; its cuticle is unknown. *Ginkgoites tigrensis* Archangelsky 1965 from the Ticó flora, Argentina (Archangelsky, 1965) differs from *Ginkgo australis* on cuticular characters only, and *Ginkgoites ticoensis* Archangelsky 1965 (also from the Ticó flora), although slightly smaller than the average *Ginkgo australis* leaf, has a very similar shape and general cuticle anatomy.

It is probable that the Cretaceous Gondwana species *G. australis, Ginkgoites ticoensis* and *G. tigrensis* and perhaps even the Jurassic *Ginkgo rajmahalensis* are closely related, possibly conspecific. The apparent cuticular differences are only slight and are based on characters that are capable of showing a wide variation. Harris & Millington (1974) noted a number of characters in *G. huttoni* which varied independently from each other, amongst which were the cuticular features — frequently and length of trichomes, development of papillae on epidermal cells of both upper and lower lamina surfaces and on subsidiary cells, and stomatal density (upper surfaces 1-50 per mm², lower surface 50-90 per mm². Cuticle variation to this extent and the wide range of leaf shapes and sizes in Mesozoic ginkgoaleans make specific separation possible only when there is little or no overlap in these characters. Consequently separation of *Ginkgo australis, Ginkgoites ticoensis* and *G. tigrensis* lacks a satisfactory taxonomic basis. Southeastern Australia, northeastern India and southern South America have been interpreted as having been situated along a similar latitude as part of the Gondwana supercontinent during the Early Cretaceous so the close affinities of these species would not be surprising.

GINKGO MALE STROBILUS (Figs 27A-D, 28F-H)

Material. NMVP167575-167578.

Description. Strobili, 30mm × 8-10mm. Main axis 1mm thick bearing more than fifteen lateral microsporophylls. Each sporophyll bearing several (two, three or four) sporangia distally, sporangia oval-elliptical, 1mm × 0.7mm, sessile, surface texture wrinkled. Arrangement of sporophylls uncertain but they do become more crowded distally along the axis. Sporangia on the basal sporophylls largest and presumably the most mature. Strobili subtended by ?two ?unequal bracts. Attachment to shoot not evident.

Discussion. These strobili are almost identical to the male catkins of *G. biloba*. Size of all elements of the cone are very similar, as is the tendency for denser distribution of sporophylls distally along the axis. In *G. biloba* the group of catkins on each short shoot is subtended by unequal leafy bracts, two of which can be seen still attached to the fossil strobilus (Figs 27B, 28G). The only difference between these fossil cones and those of living *G. biloba* is the larger number of sporangia per sporophyll, but even this may be due to preservation of sporangia which had already dehisced. If this was the case each half of a dehisced sporangium would appear identical to one immature sporangium. Because the co-occurring *G. australis* is the only ginkgoalean leaf type in Zone C strata of Victoria it is highly probable that these strobili are the pollen organs of that species.

GINKGO MALE STROBILUS (immature) (Figs 27E-J, 36A-C)

Material. NMVP167527-167529, 167697, 167698.

Description. Isolated strobili (probably pollen bearing), 10mm × 3.5mm, each subtended by a bract. Each strobilus consisting of an axis bearing sporophylls and sporangia although their arrangement is uncertain. Subtending bract 5mm long, up to 4mm wide (quarter distance from distal end) tapering to a basal attachment with the strobilus axis.

Discussion. These specimens are of uniform size with the subtending bract still attached indicating a simple structure, probably a pollen-bearing cone. Details of the sporophylls are not preserved. The bracts appear to have been fleshy at their distal and basal ends (which have preserved a darker colour) with a vascular trace along the central region.

These bracts are unlike those of extant conifers, especially families expected to be prevalent in Southern Hemisphere deposits — the Podocarpaceae and Araucariaceae. They are, however, strikingly similar to the bracts surrounding developing male inflorescences of *G. biloba*, which suggests the strobili are immature *Ginkgo* pollen organs. These bracts are consistent with a more mature *Ginkgo* male strobilus (Fig. 28G) which is clearly subtended by two bracts. The bracts of *G.*

Fig. 28. A-E, *Ginkgo australis* (McCoy) comb. nov. A, leaf dissected into six spatulate segments, NMVP167552, × 1. B, leaf dissected into fourteen ultimate segments, NMVP167553, × 1. C, leaf dissected into twelve segments, NMVP167554, × 1. D, leaf dissected into ?ten segments, NMVP167555, × 1. E, several leaves with long petioles arising from the same ?short shoot, NMVP167556, × 1. F-H, *Ginkgo* male strobilus. F, isolated pollen cone, NMVP167575, × 3. G, isolated pollen cone subtended by two sterile bracts, NMVP167576, × 3. H, basal portion of pollen cone showing sporangia located terminally on lateral stalks arising from the strobilus axis, NMVP167577, × 3.

biloba exhibit a wide variation in size, shape and colouring and while some persist until the strobili are mature, many drop or are shed separately from the short shoot. Also preserved at Koonwarra are numerous isolated bracts which may also be of *Ginkgo* origin. These are discussed below as 'Isolated bracts or cone scale type 1'.

Division CONIFEROPHYTA

The absence of attached fertile organs or preserved cuticle makes it difficult to place the conifer shoots from Koonwarra in extant families. The different leaf types are not definitive of any particular family, e.g. in extant families awl-shaped leaves are to be found in the Podocarpaceae (some *Podocarpus* L'Her. *ex* Pers., *Dacrydium* Sol.), Araucariaceae (*Araucaria*), Cupressaceae (*Callitris* Vent. juvenile), and Taxodiaceae (*Athrotaxis* D. Don, *Cryptomeria* D. Don, *Taiwania* Hayata). In deciding the most probable affinities of the remaining foliage, it is necessary to consider the phytogeography of extant Southern Hemisphere conifers.

The Araucariaceae is well represented in Australia, New Zealand, and particularly in New Caledonia. Cone scales, interpreted as araucarian, from the Victorian Lower Cretaceous, and from the middle Mesozoic of India (*Araucarites cutchensis*) and Africa (*A. rogersi* Seward 1903), indicate that this family was well represented in the Gondwana flora of that age. The Cupressaceae is represented in Australasia by *Callitris, Actinostrobus* Miq., *Diselma* Hook. f. and *Libocedrus* Endl., although its fossil record is meagre. The Podocarpaceae is, in terms of present day population, distribution and species diversity, the dominant Southern Hemisphere conifer family. The richest concentration in the Australasian region is in New Zealand and New Caledonia but there are several genera in Tasmania and on the Australian mainland. In contrast, the Taxodiaceae is essentially a Northern Hemisphere family although three species of *Athrotaxis* are endemic to Tasmania (Curtis, 1975).

Florin (1940), discussing the Mesozoic and Tertiary confiers of the Southern Hemisphere, emphasized the lack of Northern Hemisphere coniferous elements in the floras, and allied most of the foliage (particularly from the Mesozoic) with the Podocarpaceae and the *Eutacta* and *Colymbea* sections of *Araucaria*. Although insufficient Victorian Lower Cretaceous material (then thought to be Jurassic) was available to Florin in 1940, he did undertake a detailed study of *Bellarinea barklyi* (Florin 1952) which he considered to belong to the Podocarpaceae.

Another indication of the expected foliage types is the evidence from the dispersed microfloras. Dettmann (1963, 1981, this memoir) noted a number of coniferalean microspore taxa from the Victorian Lower Cretaceous, mostly belonging to the Podocarpaceae (*Microcachryidites* Cookson *ex* Couper, *Podocarpites* Cookson *ex* Couper, *Podosporites* Rao) and Araucariaceae (*Araucariacites* Cookson *ex* Couper). Cheirolepidaceous pollen (*Classopollis* Pflug *emend.* Pocock & Jansonius) is sparsely represented.

It is probable that most of the conifer foliage preserved in the Victorian Lower Cretaceous belongs to the Araucariaceae or Podocarpaceae, possibly ancestral types, with a slight chance the Taxodiaceae, and even the Cheirolepidaceae, is represented. Plant remains of the Cupressaceae may also be present.

Order CONIFERALES

Family ARAUCARIACEAE

ARAUCARIA A.L. Juss. 1789

ARAUCARIA sp. cf. A. HETEROPHYLLA (Salisb. 1807) Franco 1952 (Fig. 29A–F)

Material. NMVP167617-167623.

Description. Coniferous shoots, preserved lengths up to 60mm, 12–25mm wide, consisting of an axis bearing spirally arranged leaves. Leaves up to 15mm long × 2mm thick (compressed), erect, awl-shaped (probably keeled), arising at 60° to the axis, attachment adnate and decurrent, apices acute.

Discussion. The shoots ascribed to this species differ slightly from one another in leaf size and leaf frequency along the shoot. A similar range of variation is exhibited within extant species of *Araucaria* (e.g. *A. heterophylla, A. cunninghamii* Sweet 1830), and on this basis the fossil shoots are placed in a single taxon. Allocation to the Araucariaceae is based on external shoot morphology and supported by association with araucarian cone scales. This is not completely satisfactory as awl-shaped leaves are borne by some extant Podocarpaceae, Cupressaceae and Taxodiaceae, and the possibility that the shoots belong to one of these families cannot be discounted. Within *Araucaria*, the awl-shaped leaves indicate the shoots would be most satisfactorily placed in the section *Eutacta* Endl. *emend.* Wilde & Eames.

Fig. 29. *Araucaria* sp. cf. *A. heterophylla* (Salisb.) Franco. A, medial portion of leafy shoot, NMVP167617, × 2. B, distal portion of leafy shoot, NMVP167622, × 2. C, NMVP167618, × 2. D, NVMP167619, × 2. E, NMVP167621, × 2. F, NMVP167623, × 2.

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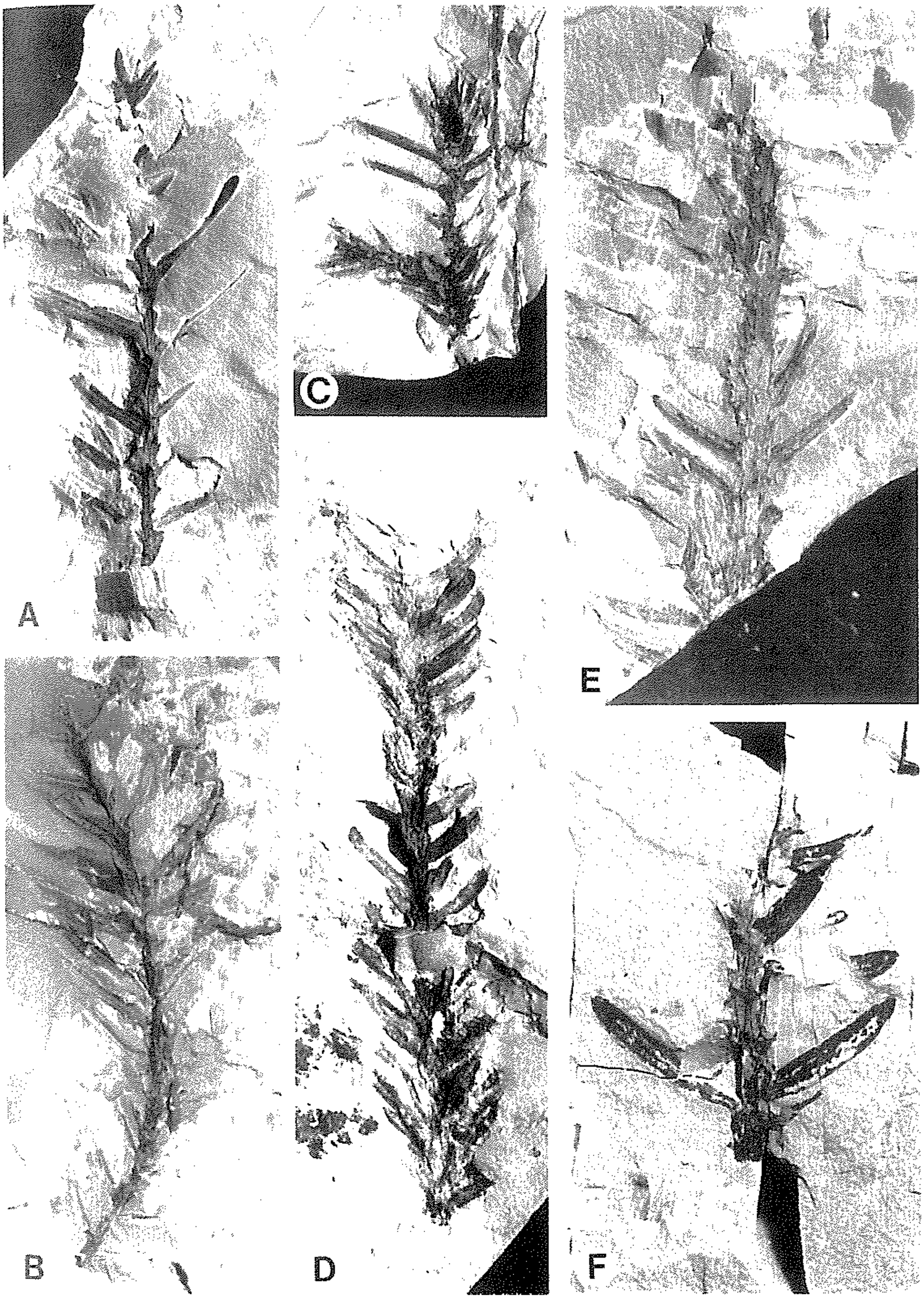

ARAUCARIA sp. (Fig. 30A)

Material. NMVP167626.

Description. Coniferous shoot, preserved 90mm long (incomplete), 5mm wide, consisting of an axis bearing small, spirally arranged, imbricate, appressed, awl-shaped to scale-like leaves. Leaves varying in size along the shoot from 1mm × 0.5mm to 3mm × 1mm, elliptical, venation uncertain, attachment uncertain but probably by a wide leaf cushion. Growth ?monopodial, lateral branches arising from the main axis, similarly bearing awl-shaped, scale leaves.

Discussion. The foliage on this specimen appears the same as *Brachyphyllum gippslandicum*; however, closer inspection shows it to differ in shape of the leaves, which are narrower and more elliptical, and the variation of leaf size along the shoot. The latter character is common in extant species of *Araucaria* and occurs in response to changes in growing conditions. This specimen is rather indistinct because mineral leaching has distorted its outlines.

Associated with this foliage is a cone axis that, although without organic connection, lies so closely parallel to the shoot in the same bedding plane that it is tempting to assume the two were once attached. The cone axis shows characters exhibited by the Araucariaceae, which increases the probability of their affinity. It is, however, discussed immediately below as an araucariacean seed cone axis type 1.

SEED CONE AXIS type 1 (Fig. 30A–C)

Material. NMVP167578, 167626.

Description. Cone axis, 30mm × 10mm, covered with numerous, small, spirally arranged, cone scale scars. Scars depressed, rhomboidal, approximately 1mm wide.

Discussion. These axes, one of which is associated closely with *Araucaria* foliage (Fig. 30A), are covered with numerous scars which indicate the point of attachment of shed cone scales, and are most probably of araucarian affinity. It is impossible to conclude from the cone axes whether they are more closely related to *Agathis* Salisb. or *Araucaria*, or which cone scales originated from the plant.

SEED CONE AXIS type 2 (Fig. 30D–G)

Material. NMVP167627, 167628.

Description. Cone axis, preserved lengths up to 60mm, 14mm wide, covered with spirally arranged cone scale scars. Scars depressed, semicircular, 1.6mm across.

Discussion. These cone axes are not attached to foliage. One axis (Fig. 30D,E) appears to be preserved in close association with a *Brachyphyllum gippslandicum* shoot but closer examination reveals they are in different bedding planes. These axes belong to a different taxon than the smaller araucariacean axes (Fig. 30A–C). Presumably both axis types are from cones which had shed their scales and seeds prior to fossilization.

NMVP167628 (Fig. 30F) has 4–5 scars in its width (compressed) and NMVP167627 (Fig. 30D,E) has about 20 scars in its length, which gives an estimate of about 200 scales per cone. Several unattached cone scale types, including one which is definitely araucarian, are preserved at Koonwarra, but there is no evidence to allow association of cone axes with scales.

ARAUCARIA CONE SCALE (Figs 31A–D, 36L–N)

1904	*Araucarites* sp. A; Seward, p.181, fig.42.
1908	*Araucarites* sp.; Chapman, p.219, pl.35, fig.6.
1954a	*Araucarites cutchensis* Feistmantel; Medwell, p.98, figs 18,19.
1954a	?Araucarian cone scale; Medwell, p.99, fig.17.
1954b	*Araucarites cutchensis* Feistemantel; Medwell, p.20.

Material. NMVP167624–167642.

Description. Detached cone scale complex (i.e. seed, ovuliferous scale, and bract scale intimately fused), varying in size from 12mm × 7mm to 24mm × 10mm, cuneate, widest at distal end and tapering to 1–2mm at the point of attachment to the cone axis. Cone scale complex thinly winged, bearing a distal spine up to 12mm long.

Discussion. These cone scales vary considerably in size and slightly in shape. The thin lateral wings are not pronounced and, judging from their dark

Fig. 30. A, *Araucaria* sp. and Seed cone axis type 1, portion of leafy shoot showing the appressed awl-shaped, scale leaves which vary in size up and down the shoot. Associated seed cone axis (which has shed its seeds and cone scales) attributed to the Araucariaceae, NMVP167626, ×2. B,C, Seed cone axis type 1. B, isolated seed cone axis, NMVP167578, ×2. C, enlargement from B showing rhomboidal cone scale scars, NMVP167578, ×5.5. D–G, Seed cone axis type 2. D, incomplete seed cone axis, NMVP167627, ×2. E, counterpart of D, NMVP167627, ×2. F, incomplete seed cone axis, NMVP167628, ×2. G, enlargement of F showing semi-circular cone scale scars, NMVP167628, ×5.5.

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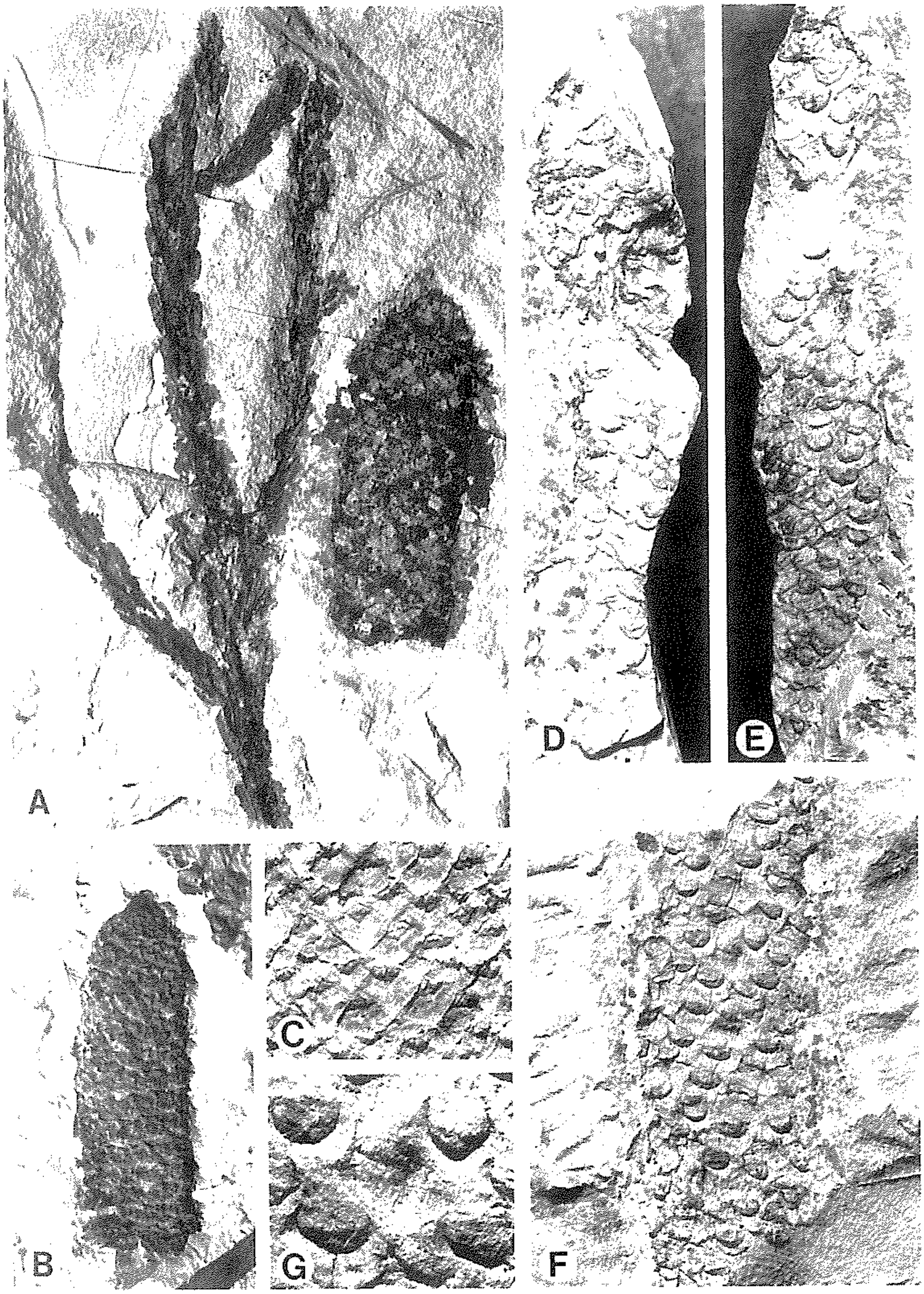


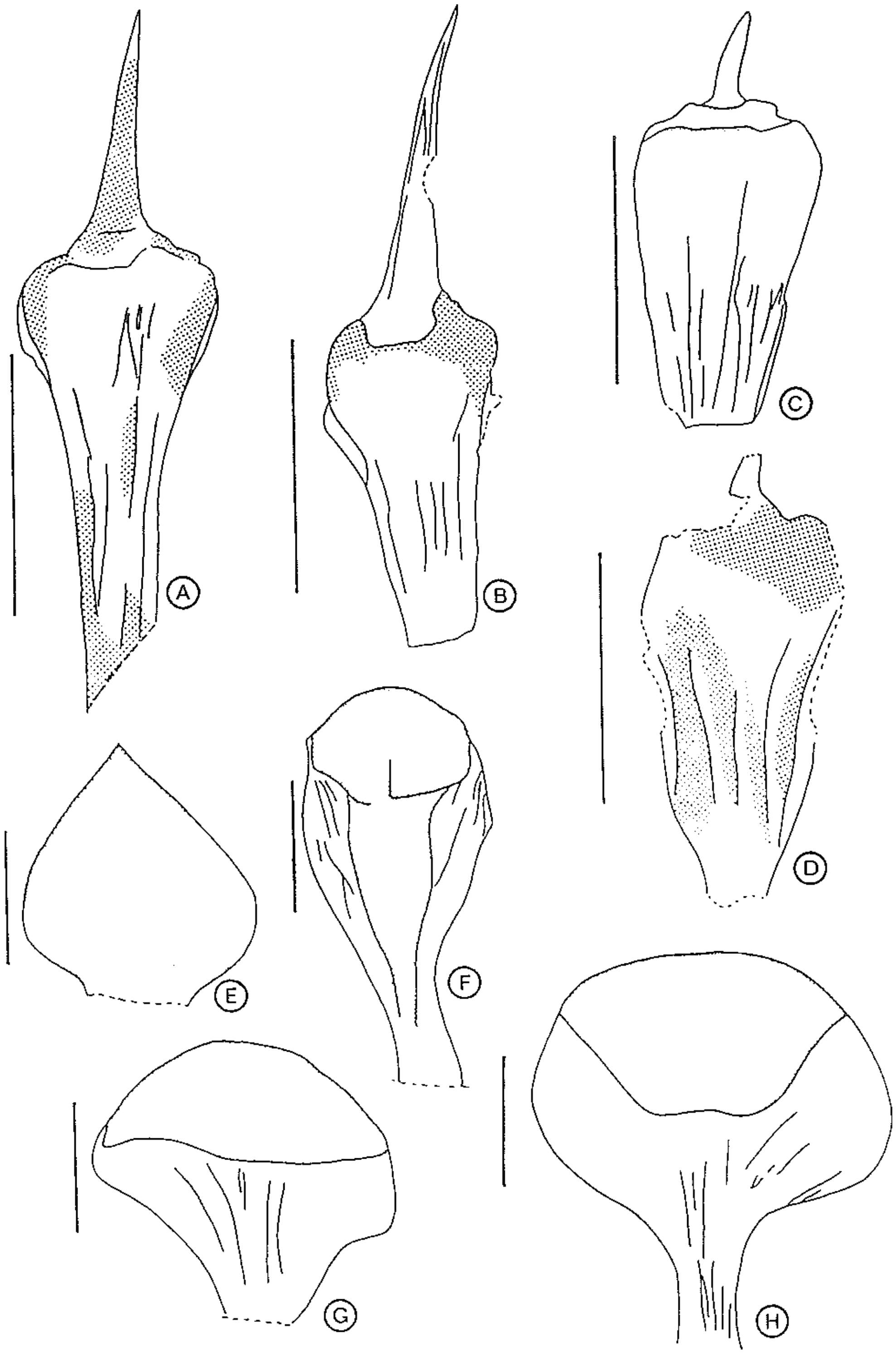
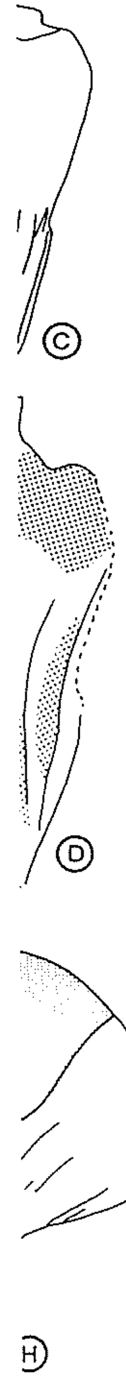


Fig. 31. A–D, *Araucaria* cone scale. A, NMVP167630. B, NMVP167632. C, NMVP167640. D, NMVP167633. E–H, Isolated bract or cone scale type 1. E, NMVP167646. F, NMVP167647. G, NMVP167645. H, NMVP167643. Scales A–D = 10mm; E–H = 5mm.



NMVP167633. E-
H, NMVP167643.

colour, appear to have been woody. Not all of the cone scales have distal spines preserved, possibly because the spines were at high angle to bedding when lying on sediment and sheared off when the rock was cleaved. These scales closely resemble ovuliferous scales of some extant species of *Araucaria*, particularly *A. heterophylla*, which exhibit similar range of size and shape, often within a single cone (i.e. the distal and basal scales are shorter than those medially). They were probably shed by disintegration of the cone, the method of dispersal of extant araucarians.

Despite the uncertainty of foliage type, their gross morphology allows their assignment to *Araucaria* section *Eutacta*. It is possible that they belonged to one of the foliage types or cone axis attributed to the Araucariaceae above.

Family PODOCARPACEAE

BELLARINEA Florin 1952

BELLARINEA BARKLYI (McCoy 1874) Florin 1952 (Fig. 32E,F)

1874 *Zamites* (*Podozamites*) *barklyi* McCoy, p.33, pl.8, fig.1.
1952 *Bellarinea barklyi* (McCoy) Florin, p.179, pl.1, figs 1-6; pl.2, figs 11-15.
1954a *Bellarinea barklyi* (McCoy) Florin; Medwell, p.100.

Material. Holotype (by monotypy) NMVP12220 from Bellarine, Victoria. Other material NMVP12221, 12222 from Bellarine and NMVP167624, 167625 from NMVPL425.

Description. See Florin (1952). Branchlets straight to slightly curved, up to 100mm × 40mm, axis 1mm wide. Leaves bifacial, linear, slightly recurved, up to 32mm × 3mm, spirally arranged but appearing to arise in two lateral ranks at 40-90° to the axis due to twisting of the leaf bases. Leaf margins parallel, apices sub-acute, bases constricted and decurrent, midvein persistent from base to apex. Leaves closely spaced but not overlapping, four per 10mm along each side of the axis.

Leaves hypostomatic with two broad longitudinal stomatal bands, stomata haplocheilic (Florin, 1952).

Discussion. Both pieces of foliage collected at Koonwarra, although incomplete, were toward the smaller limit of Florin's size range, the individual leaves measuring 15mm × 1.5mm. In external appearance they closely resemble leafy shoots of species of *Taxodium* A. Rich. and *Metasequoia* Miki *ex* Hu & Cheng (Taxodiaceae), and some species of *Podocarpus*. Florin, on consideration of leaf cuticle, attributed this species to the Podocarpaceae, allying it to some extant members of the genus *Podocarpus* section *Stachycarpus* Endl. *emend.* Buchholz & Gray, notably *P. ferrugineus* D. Don 1832 and *P. spicatus* R. Br. 1838. Florin concluded sufficient uniqueness in stomatal arrangement to justify generic separation.

BRACHYPHYLLUM Brongn. 1828

BRACHYPHYLLUM GIPPSLANDICUM McCoy 1892 (Fig. 32A-D)

1892 *Brachyphyllum gippslandicum* McCoy *in* Stirling, p.13.
1900 *Brachyphyllum gippslandicum* McCoy; Stirling, p.5, pl.3, figs 10-14.
?1904 cf. *Brachyphyllum* sp.; Seward, p.182, fig.44.
1908 *Brachyphyllum gippslandicum* McCoy; Chapman, p.217, pl.35, fig.3.
1909 *Brachyphyllum gippslandicum* McCoy; Chapman, p.110.
1954a *Brachyphyllum gippslandicum* McCoy; Medwell, p.99, pl.6, fig.26; text-fig.10.

Material. Lectotype (designated Medwell, 1954a) NMVP15705 from Albert River, Victoria. Other material NMVP167597-167616.

Description. Coniferous shoots, portions preserved up to 150mm long, 2-4mm wide, consisting of an axis bearing small, spirally arranged, imbricate, closely appressed, scale leaves. Leaves of uniform size along any one branch, 1-3mm long × 1-2mm wide, ovate-rhomboidal, venation uncertain, attachment uncertain but probably by the whole width of the leaf base. Growth monopodial, main axis giving off lateral branches which in turn give rise to smaller branches, all similarly bearing small scale leaves. Seed more or less spherical, at least 4mm across, borne singularly and terminally on a branch, probably subtended by a fleshy receptacle.

Discussion. This species is the most common conifer in the Koonwarra flora, occurring mostly as small portions of sterile foliage. The small imbricate scale-like leaves immediately bring to mind extant species of the Cupressaceae and Podocarpaceae, although the spiral leaf arrangement of *B. gippslandicum* suggests affinity with the Podocarpaceae (as opposed to the whorled, or opposite and decussate leaves of the Cupressaceae). *Athrotaxis* is also a possibility but is discounted by the interpretation of the fertile specimen.

The structure borne terminally on the lateral branch (Fig. 32C) is interpreted as an ovule or seed, and its appearance is characteristic of a large number of extant podocarps. The seed which, on account of its remaining attached to the shoot is probably immature, is round in compressed shape, 4mm across, and apparently subtended by a receptacle. The small lateral appendage may be aborted ovules or a short continuation of the sterile axis. However, if this interpretation is incorrect and this structure is an immature seed cone *B. gippslandicum* may be a member of the Taxodiaceae, possibly belonging to *Athrotaxis*. It is also worth noting that in the Yorkshire Jurassic flora *Brachyphyllum* type foliage is attributed to the Araucariaceae (Harris, 1979).

Assuming the affinity of *B. gippslandicum* is with the Podocarpaceae, its position within that family — based on both foliage and seed characters — lies with the *Dacrycarpus* Endl. section of *Podocarpus*, in particular *P. dacrydioides* A. Rich. 1832; or with *Dacrydium*, e.g. the New Zealand species *D. bidwilli* Hook. f. 1878, *D. biforme* Pilger 1903, *D. kirkii* F. Muell. 1868, and *D. colensoi* Hook. 1843. A more definite classification may be possible if specimens with attached pollen cones and preserved cuticles are discovered.

PODOSTROBUS Rao & Bose 1971

PODOSTROBUS ELONGATUS sp. nov. (Fig. 33)

1973 Lycopodiales? cones; Douglas, p.47, pl.10, figs 1-3.

Etymology. Latin *elongatus* — elongate.

Material. Holotype NMVP167580. Paratypes NMVP167581-167583. Other material NMVP167584-167595.

Diagnosis. Cone (probably pollen-bearing), up to 45mm long (usually about 30mm) by 4.5mm wide, consisting of a central axis 0.6mm thick, bearing numerous spirally arranged, overlapping sporophylls. Sporophylls ovate, 1.5mm × 0.8mm, hypopeltate, with stalks 1mm long and of minimal width.

Discussion. These strobili, which were tentatively recorded as Lycopodiales cones by Douglas (1973) had, based on their colour and three dimensional preservation in the sediment, a woody axis and fairly solid sporophylls. Although no traces of pollen sacs can be seen and none of the strobili have any sterile foliage attached, the hypopeltate sporophylls and the apparently woody habit are more indicative of conifers than lycopods. The most probable reason for the lack of associated foliage and microsporangial remains is that most conifers abscisse the male cones separately after the pollen sacs have dehisced, thus most unattached male cones will be of mature size but will have shed their pollen. Also arguing against lycopod affiliation is the almost complete absence of lycopodiaceous sterile foliage in these sediments.

The long, narrow strobili with between 60 and 100 sporophylls are indicative of Araucariaceae or Podocarpaceae; the araucarians are represented in the Victorian Lower Cretaceous by numerous cone scales, and the podocarps by sterile foliage. Extant araucarian male strobili are usually shed with several subtending sterile bracts or scale leaves, a condition not observed on any of the Koonwarra cones, suggesting they are more likely to belong to the Podocarpaceae.

Although much shorter than the Victorian cones (less than 15mm) the Indian species of *Podostrobus* are equivalent in shape and arrangement of sporophylls. Although the Koonwarra cones do not have microspores preserved (the Indian *Podostrobus* cones had bi- and trisaccate pollen grains) their external morphology is sufficiently similar to allow their inclusion in the same genus.

INCERTI ORDINIS

ISOLATED BRACT OR CONE SCALE type 1 (Figs 31E-H, 36G-K)

Material. NMVP167643-167656.

Description. Isolated bracts or cone scales varying in size and shape, 5mm × 8mm to 15mm × 7mm to 15mm × 15mm, ovate to obovate to broadly spatulate, apices usually rounded (although one specimen has an acute apex), margins sometimes membraneous (almost winged). Texture uncertain but most specimens are preserved darkest in colour about the distal region, with evidence of four or five (or possibly more) impersistent vascular traces entering the scale from the base.

Discussion. The wide range of variation exhibited by the specimens ascribed to this scale type suggests that more than one taxon may be represented. They are grouped because of their general similarities and the uncertainty of their nature and systematic position. It is not possible

Fig. 32. A-D, *Brachyphyllum gippslandicum* McCoy. A, portion of leafy shoot, NMVP167597, ×1. B, portion of leafy shoot, NMVP167600, ×1. C, portion of leafy shoot, with a solitary seed/ovule located distally on one of the lateral branches, NMVP167599, ×1. D, apical portion of leafy shoot, NMVP167598, ×1. E-F, *Bellarinea barklyi* (McCoy) Florin. E, medial portion of leafy shoot showing the leaves of only one side of the axis, NMVP167624, ×2. F, apical portion of leafy shoot, NMVP167625, ×2.

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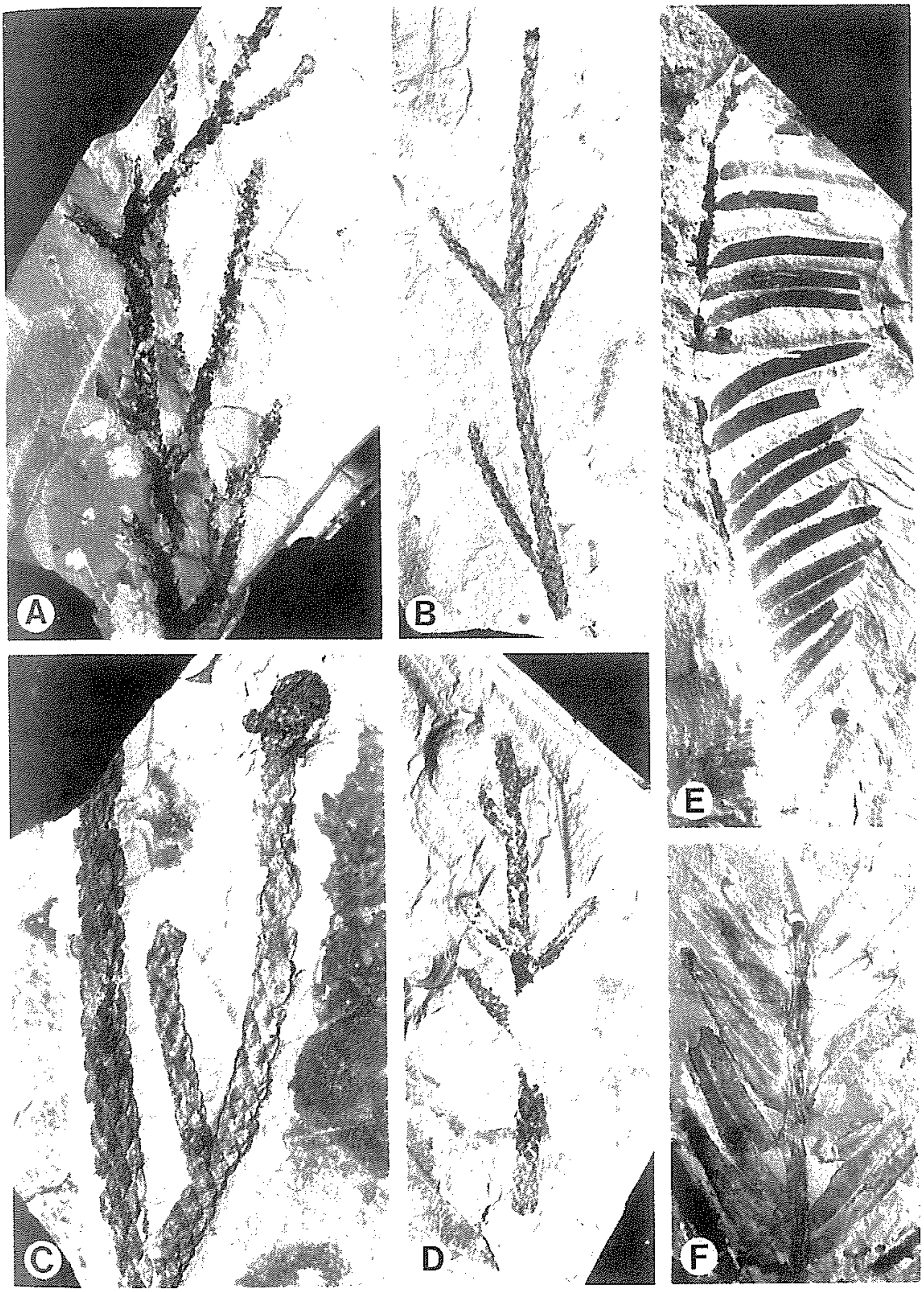

to determine whether they are cone scales associated with seeds (e.g. conifer), bracts which subtended fertile organs, or whether they had any association with fertile structures. None have seeds attached although there are several isolated winged and unwinged seed types preserved at Koonwarra with which they may have been associated. They do resemble the fleshy bracts which subtend the male strobili of the extant *G. biloba* in size and shape, and in the variation of these two characters. Associated *Ginkgo* leaves and male strobili (Figs 27E–J, 36A–C) have similar but smaller bracts attached basally.

Although this bract type has been listed with the other isolated scale types and seeds at the end of the Coniferophyta section, it is possible that they are derived from another plant group. There is no evidence that any elements of the cryptogamic flora preserved at Koonwarra bore such scales, and no extant lower plants have equivalent structures. The Pentoxylales, which is represented at Koonwarra by leaves, pollen organs, and possibly by seed bearing structures, may have had a short shoot branching system equivalent to *G. biloba* and bracts subtending its fertile organs in a similar manner to that species. Vishnu-Mittre (1953) described *Sahnia nipaniensis*, (a pentoxylalean pollen-bearing organ from the Jurassic of the Rajmahal Hills, India) subtended by an involucre of bracts in its immature stages.

ISOLATED BRACT OR CONE SCALE type 2 (Figs 34A–E, 36O,P)

Material. NMVP167657–167671.

Description. Isolated bracts or cone scales varying markedly in size although only slightly in shape, 35mm × 15mm to 9mm × 2mm (although some of the shorter scales are up to 3mm wide), spatulate, apices obtuse. Texture uncertain but most specimens are preserved darkest in colour at their distal and basal ends, with evidence of one medial vascular trace entering the base of the scale and persisting to the apex.

Discussion. Although variable in size, uniformity of overall shape and appearance indicates a single species. Their nature and systematic position remain uncertain. The darker preservation of their distal and basal ends suggests a woody habit (or at least a thicker transverse section) and may indicate the site of a seed which has been shed or is possibly still preserved attached. On account of their consistent shape and probably woody habit they are considered more likely to be ovuliferous scales from a coniferalean cone than bracts which subtended, or were associated with, a vegetative or fertile structure.

WINGED SEED type 1 (Figs 35A–E, 36D,E)

1904 *Araucarites* sp. B; Seward, p.181, fig.43.

Material. NMVP167674–167689.

Description. Seed 8mm × 2mm, oblanceolate, surrounded by a flat lateral wing about 1.5mm wide. Overall shape roughly triangular.

Discussion. Some doubt remains as to whether these specimens are actually seeds, or delicate *Araucaria*-like seed cone scale complexes which lack distal spines and are preserved with the appearance of a seed with papery wings.

WINGED SEED type 2 (Figs 35F,G, 36F)

Material. NMVP167672, 167673.

Description. Seed 6.5mm long by 1.5mm wide, oblanceolate, with two laterally extended wings. Each wing about 10mm long by 35mm wide, joined laterally along the whole length of the seed, tapering to the base of the seed but extending further distally to an acute point.

Discussion. The same uncertainty noted for the Winged Seed Type 1 also applies to this taxon. Their appearance suggests they are most likely conifer seeds, but an attempt at further classification is tenuous. Possibilities include the free seeds of *Agathis* or taxodiaceous-types. There are several types of Isolated Bracts or Cone Scales which may have been associated with these seeds, or Winged Seed Type 1.

WINGED SEED type 3 (Figs 35H–J, 36S,T)

Material. NMVP167699–167724.

Description. Seed 2.5mm × 1.5mm, obovate, with two laterally extended wings. Each wing falcate, about as wide as the seed and slightly longer (extending further distally) giving the seed and wing complex an overall reniform outline. Wings usually equal in size but occasionally differing slightly.

Fig. 33. Podostrobus elongatus sp. nov. A, NMVP167580, ×4. B, NMVP167581, ×4. C, specimen showing the microsporophylls from two angles; 1, longitudinal section (distal sporophylls). 2, distal faces (basal sporophylls), NMVP167583, ×4. D, NMVP167582, ×4. E, enlargement of A showing hypopeltate sporophylls in longitudinal section, NMVP167580, ×10. F, enlargement of B showing hypopeltate sporophylls in longitudinal section, NMVP167581, ×10.

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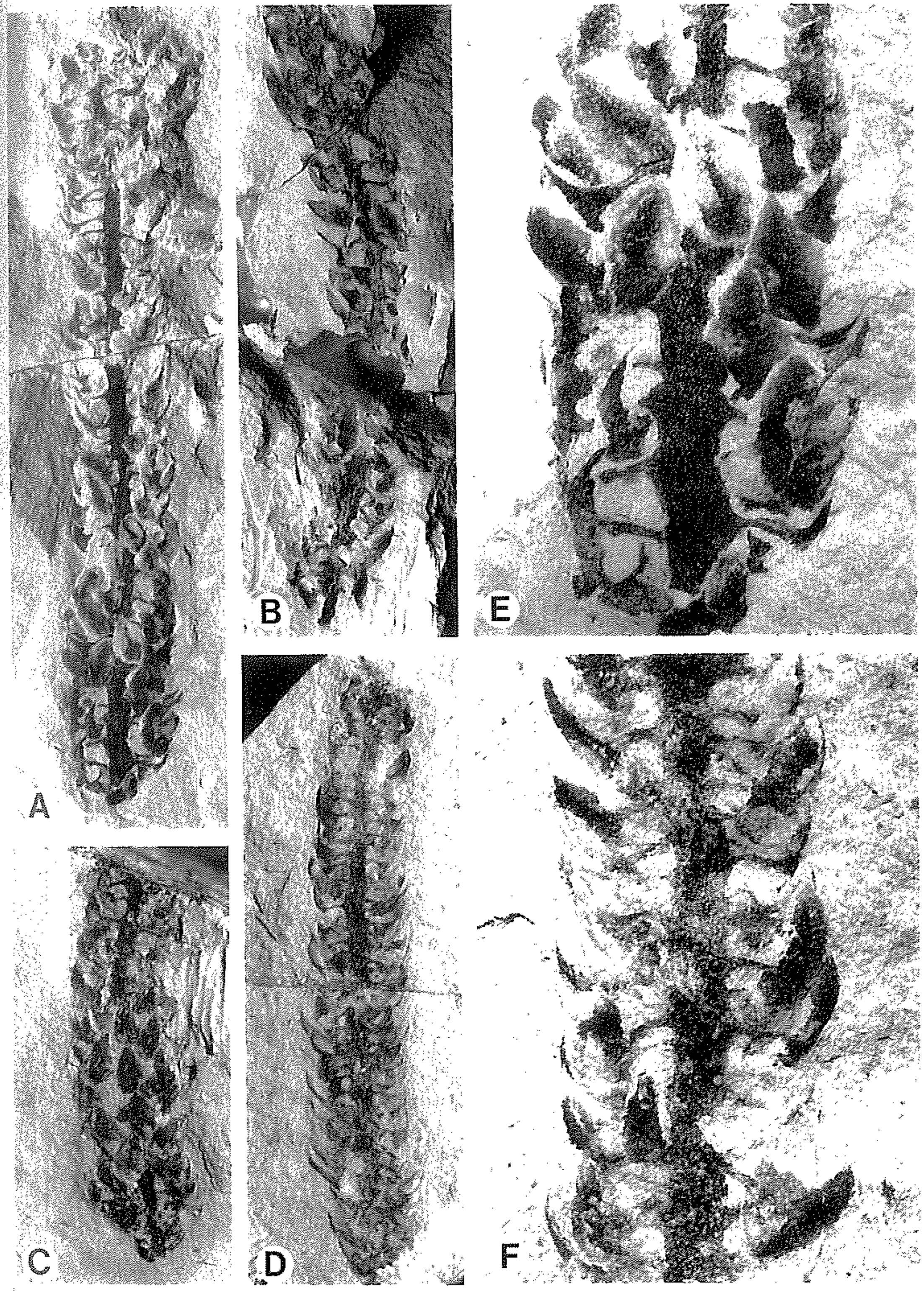


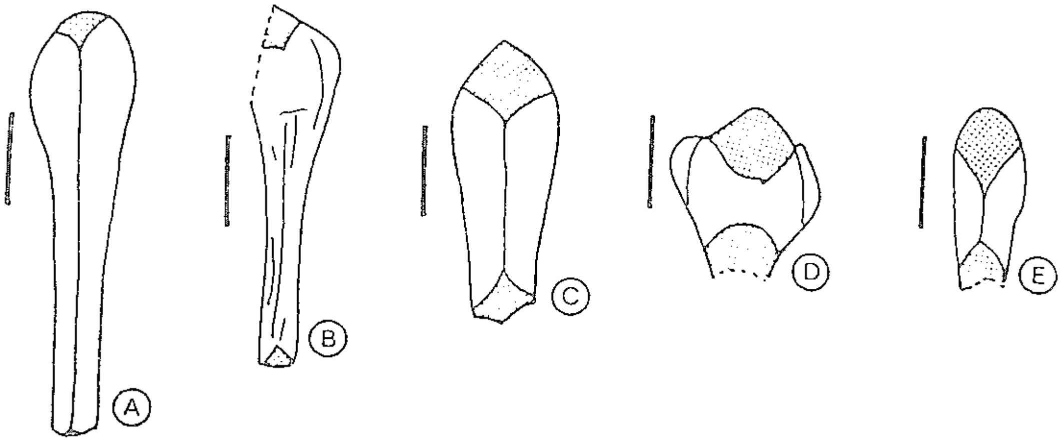


Fig. 34. Isolated bract or cone scale type 2. A, NMVP167661. B, NMVP167657. C, NMVP167662. D, NMVP167660. E, NMVP167664. Scale = 2mm.

Discussion. These specimens, in contrast to the first two winged seed types, are undoubtedly seeds, but their affinity is equally uncertain. If coniferalean, they may have been associated with one of the 'Isolated bract or cone scale' types also preserved. They are very similar to seeds of the extant Tasmanian species *Athrotaxis cupressoides* D. Don 1839, and may represent an extinct species of that genus. *Athrotaxis*-type plants had a wide distribution in the early Tertiary and are known from sediments of that age in Patagonia, Queensland, and Tasmania (Townrow, 1965). It is possible that similar species existed during Early Cretaceous times.

A seed so apparently well adapted for wind dispersal could possibly have been shed some distance from its site of preservation and even carried part of the way by water. A consequence of this could be the absence of any other evidence in the same sediments of the taxon concerned. This could be similarly true for any of the winged seed types described.

ISOLATED WINGLESS SEEDS (Fig. 36W–Z)

1904 *Carpolithes* sp. A; Seward, p.182, fig.46.
1904 *Carpolithes* sp. B; Seward, p.183.

Material. NMVP167725–167741.

Discussion. These solitary wingless seeds are variable in size and shape and probably derived from several different taxa, but because of the gradational size series it is difficult to determine probable limits of taxa. They range from small round seeds 1mm in diameter to large elliptical seeds 12mm long by 7mm wide, the intermediates varying slightly in shape — some ovate, others (e.g., Fig. 36X) having one obtuse and one acute end.

Affinities of these seeds are uncertain, but one may speculate by considering associated foliage types. *Taeniopteris daintreei* (Pentoxylales), *Ginkgo australis*, and *Bellarinea barklyi* (Podocarpaceae) would be expected to have had seeds similar to these, as would any podocarpaceous conifers and any pteridosperms that were present (possibly *Thinnfeldia* sp. cf. *T. indica* and *Phyllopteroides lanceolata*). It is probable that some of these seeds are from seed-bearing organs similar to those discussed and illustrated below (Fig. 38A–D) but it is unwise to relate them too closely when the maturity of the preserved fertile organ is not known.

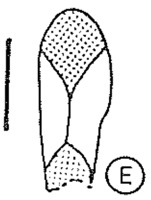
Assignment to the often-used fossil seed genus *Carpolithes* Schlotheim neither enhances their taxonomy nor elucidates their affinities. Their correct systematic positions may be determined if specimens either with preserved anatomical structure or with connected foliage or fertile organs are discovered.

AWNED SEEDS (Fig. 36U,V)

1963 *Hemitrapa*? sp.; Douglas, p.23, pl.3, figs 2–5; pl.4, figs 3, 4.
1969 *Hemitrapa*? sp.; Douglas p.225, pl.44, figs 3, 4, text-fig.4,4.

Material. NMVP167747–167761.

Description. Isolated seeds with two spines arising laterally one each side of the seed. Seeds 2.5mm long, up to 1mm wide at point of attachment of spines (three-fifths distance from base), tapering to a pointed base and apex. Spines 3mm long, thin, orientated as a distal continuation of the seed margin (outline), slightly recurved toward their ends.



62. D, NMVP167660.

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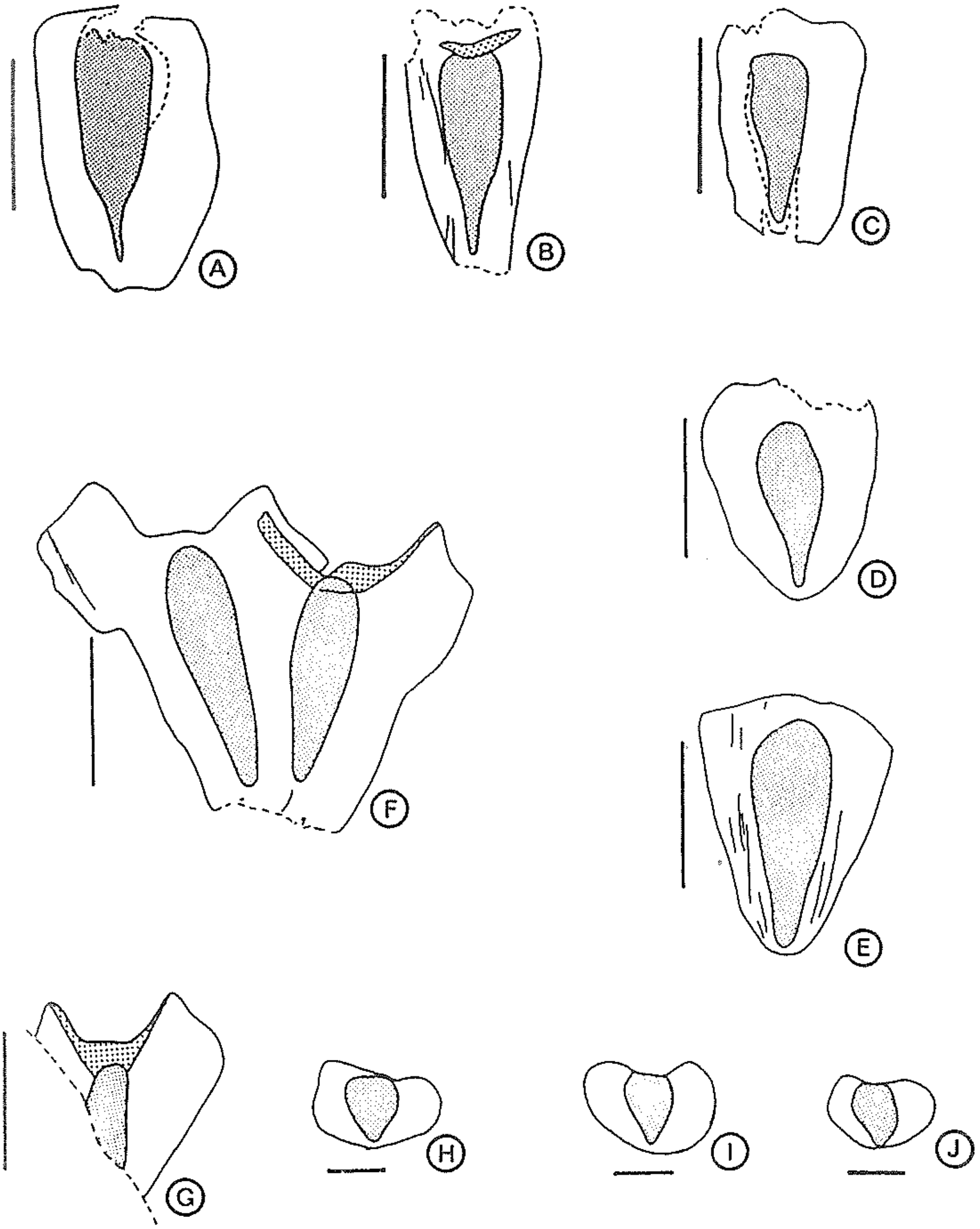

Fig. 35. A–E, Winged seed type 1. A, NMVP167681. B, NMVP167682. C, NMVP167688. D, NMVP167674. E, NMVP167675. F,G, Winged seed type 2. F, NMVP167672. G, NMVP167673. H–J, Winged seed type 3. H, NMVP167703. I, NMVP167704. J, NMVP167722. Scales A–G = 5mm, H–J = 2mm.

Discussion. These small, isolated seeds are difficult to match with any co-occuring foliage. Douglas (1963, 1969) compared them with nuts of early Tertiary aquatic angiosperms (*Hemitrapa* spp.) described from Japan by Miki (1952). The seeds from Koonwarra are much smaller than Miki's *Hemitrapa* specimens (2.5mm long compared with 28–60mm) but are similar in shape to several of the species which have only two spines.

Although it is tempting to include these small seeds here as angiosperms, there is no evidence of angiosperm-like leaves to support such a classification. *Hemitrapa* is discarded here in favour of a more general term to avoid the implication of classification to the angiosperms.

SEED BEARING STRUCTURE type 1 (Figs 37, 38A)

Material. NMVP167742.

Description. Seed bearing structure, 85mm long, consisting of an axis 2.5mm wide bearing megasporophylls for its entire length (28 sporophylls were counted but there are probably others concealed under the specimen in the part and counterpart). Sporophylls up to 11mm long, arising from the axis at an 80-90° angle and curving distally, each subtending an ?oval seed which appears to be fused to the sporophyll. The sporophylls on the distal portion of the strobilus appear less developed and are probably immature. The arrangement is lax and open, and the sporophylls are free and distant from each other with little or no overlap. Habit woody.

Discussion. This fertile structure is probably from a gymnospermous plant but its position within that group is uncertain. It has a very lax, open sporophyll arrangment but judging from the texture, amount of carbon remaining, and the three dimensional preservation in the sediment, it had a woody habit. There is no evidence of subtending bracts, either at the base of each sporophyll or the base of the strobilus, but it is presumably a compound structure. The curve of the basal portion of the axis suggests this strobilus may have been pendulous. It appears to have had a gradual maturation of seeds distally along the axis.

No modern conifers have seed cones of this type — certainly not so open or with differential seed maturation so apparent and both extant and fossil ginkgoalean ovules are not subtended by such prominent bracts. The fossil strobilus is similar in several ways to the seed cones of the Yorkshire Jurassic cycad *Beania mamayi* Thomas & Harris 1960 (see Harris, 1964). Although the sporophylls are not as distinctly stalked or spatulate as those of *B. mamayi*, their probable spiral arrangement and maturation distally along the strobilus is similar. It is possible that this seed bearing structure belongs to the Cycadales, although none of the associated leaf types have been allocated to that order.

SEED BEARING STRUCTURE type 2 (Fig. 38B,C)

Material. NMVP167743, 167744.

Description. Seed bearing structure with seven seeds evident but possibly as many as fifteen. Seeds round to slightly oval, 3.0-3.5mm across, apparently without subtending bract, arrangement uncertain, attachment probably sessile. Axis or peduncle not evident. Complete structure about 10mm across (compressed).

Discussion. These structures are possibly seed bearing organs of the Pentoxylales. They have been described here separately because of the difficulty in equating them with the specimens of *Carnoconites cranwellii* from Smythe Creek, Apollo Bay (Drinnan & Chambers, 1985). The Koonwarra fructifications are larger, their seed arrangement is less compact, and they show no evidence of micropyles — the latter character is a consistent feature of *C. cranwellii*. These features could be attributed to greater maturity whereas Drinnan & Chambers noted several characters of *C. cranwellii* which suggested that those fossils represent immature organs. The comparison of impressions (Koonwarra structures) with compressions (*C. cranwellii*) may also account for some difference in appearance. The Victorian Early Cretaceous leaves attributed to the Pentoxylales, although exhibiting wide variation in size and shape, have all been ascribed to one natural species, *Taeniopteris daintreei* McCoy, which precludes (at least at this stage) the treatment of these fructifications as another

Fig. 36. A-C, *Ginkgo* male strobilus (immature). A, pollen cone with subtending bract, NMVP167697, ×4. B, pollen cone with subtending bract, NMVP167529, ×4. C, pollen cone with subtending bract, NMVP167528, ×4. D,E, Winged seed type 1. D, NMVP167674, ×3. E, NMVP167675, ×3. F, Winged seed type 2. Two seeds compressed together, NMVP167672, ×3. G-K, Isolated bract or cone scale type 1. G, NMVP167645, ×2. (Note thickened distal edge, and evidence of several vascular traces entering the bract from its base). H, NMVP167646, ×2. I, NMVP167644, ×2. J, NMVP167647, ×2. (Note thickened distal edge and central area). K, NMVP167643, ×2. (Note thickened distal edge). L-N, *Araucaria* cone scale. L, NMVP167629, ×2. (Note most of the distal spine has separated from the cone scale). M, NMVP167631, ×2. (Note the prominent distal spine). N, NMVP167633, ×2. O,P, Isolated bract or cone scale type 2. O, NMVP167657, ×4. P, NMVP167658, ×5.5. (Note thickened distal edge). Q, Cruciform structure type 1, NMVP167763, ×10. (Note two of the "bracts" are larger than the other two; all four are joined by their bases to a circular disc). R, Cruciform structure type 2. NMVP167762, ×10. (Note all four "bracts" are equal in size, and have a reticulate pattern and thickened margins; they appear to be joined basally but not at a disc). S,T, Winged seed type 3. S, NMVP167722, ×6. T, NMVP167723, ×7. U,V, Awned seeds. U, NMVP167748, ×5. V, NMVP167749, ×5. W-Z, Isolated wingless seeds. W, NMVP167725, ×2.5. X, NMVP167727, ×3. Y, NMVP167728, ×4.5. Z, NMVP167729, ×4.5.

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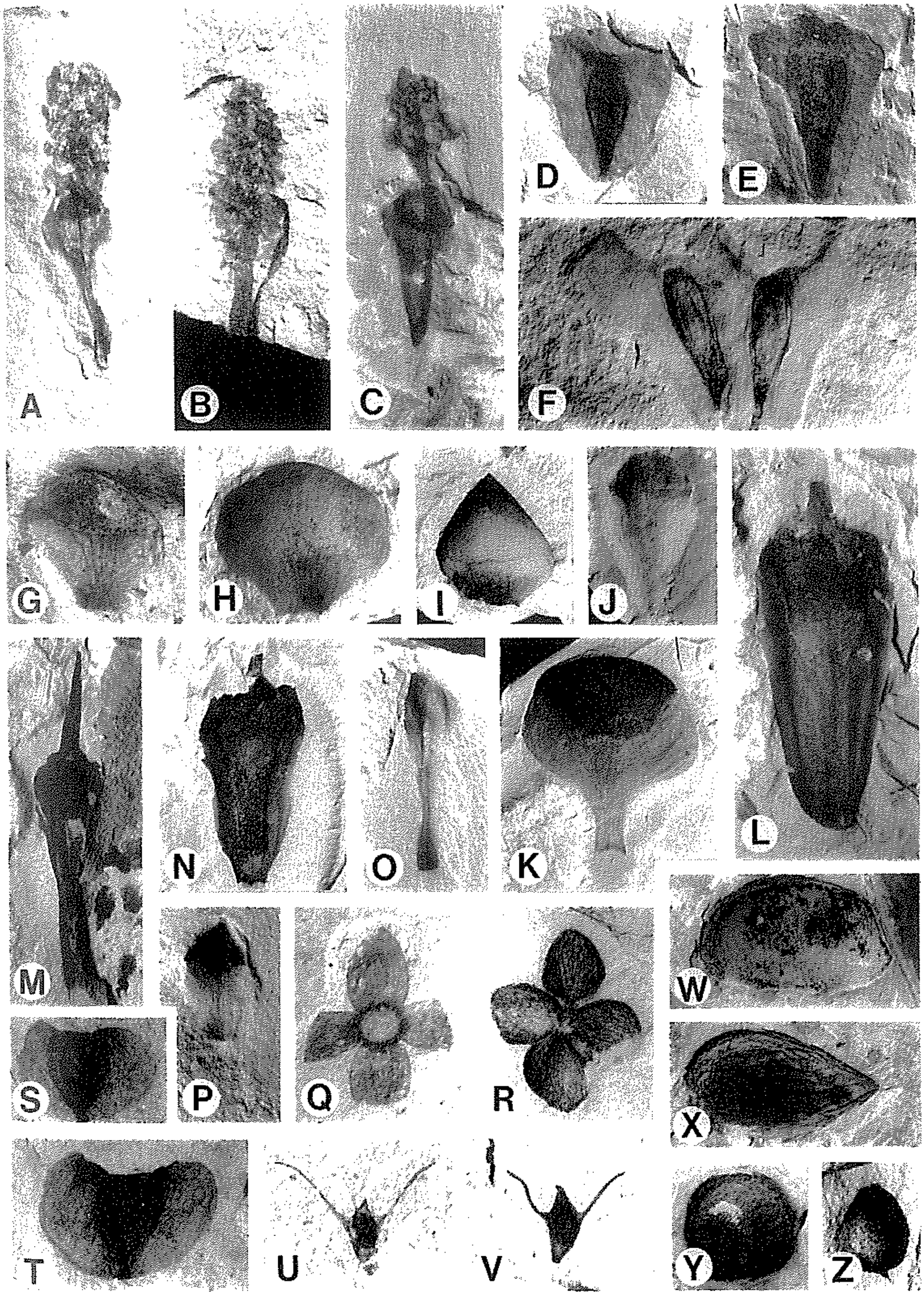

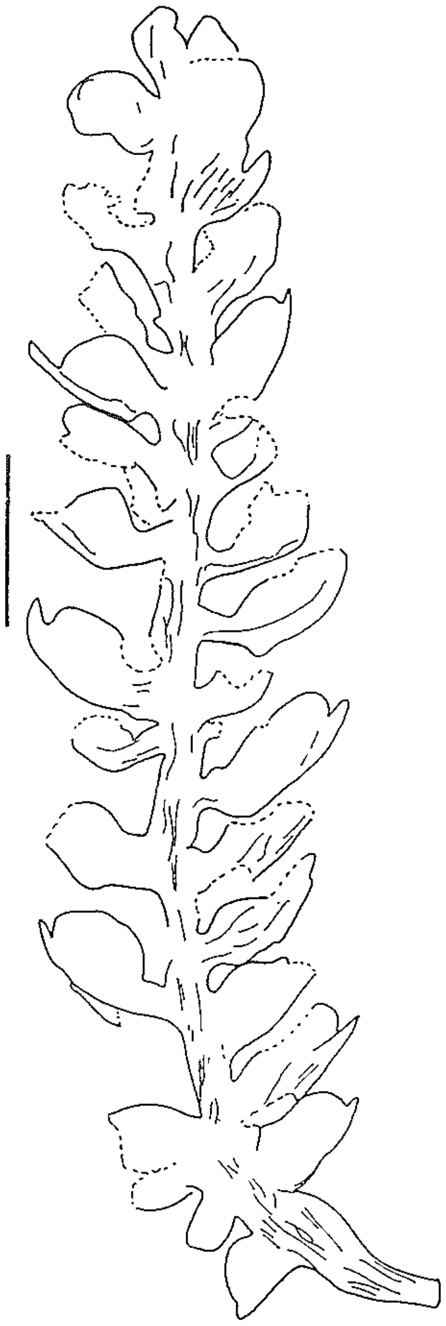

Fig. 37. Seed bearing structure type 1. NMVP167742. Scale = 10mm.

species of *Carnoconites*. Excepting the Pentoxylales, it is difficult to suggest the affinity of a structure bearing apparently bractless seeds in this manner.

SEED BEARING STRUCTURE type 3 (Fig. 38D)

Material. NMVP167745, 167746.

Description. Seed bearing structures incomplete, size and shape unknown but, as preserved, up to 60mm across, bearing up to 26 seeds (counted). Seeds round, ?bilateral, approximately 7mm across and 3mm in transverse section, without associated bracts, arrangement uncertain. Axis or peduncle not evident.

Discussion. As with the previous seed bearing organ it is as difficult to place these specimens outside the Pentoxylales as it is to equate them with *Carnoconites cranwellii*. Different stage of maturity is again a possible explanation which links the three types and explains the size difference between them.

They may, however, be the seed bearing organs of *Ginkgo australis*. *Karkenia* Archangelsky, Mesozoic fructifications attributed to the Ginkgoales and recorded from the Ticó flora (Archangelsky, 1965) and the Lower Cretaceous of the U.S.S.R. (Krassilov, 1969, 1982), has numerous stalked ovules/seeds arising from a central axis. Peduncles cannot be seen in these two Koonwarra fossils; it is possible that either they have not been preserved or the seeds were sessile. The crinkled appearance of the remains of several seeds of NMVP167745 is consistent with the compression of fleshy seeds similar to those of the extant *Ginkgo biloba*, and possibly also of the extinct Pentoxylales.

Because of the poor state of preservation of these particular structures and the uncertainties which accompany that condition, they have been described only as seed bearing structures.

PLANTAE indet. (Fig. 38E)

1973 *Isoetes*? sp.; Douglas p. 50, pl. 12, figs 1,2.

Material. NMVP167596.

Description. Portion of stem 20mm × 1.5mm, with a whorl of six or seven branches arising at a node. Branches incomplete (preserved up to 22mm long), 0.5mm wide, bearing a solitary ?pair of

Fig. 38. A, Seed bearing structure type 1, NMVP167742, × 1. unattached fertile organ showing apparent gradual maturation of seeds distally along the axis. B,C, Seed bearing structure type 2. B, NMVP167743, × 4. C, NMVP167744, × 4. D, Seed bearing structure type 3. NMVP167746, × 1.5. (Note several seeds compressed obliquely indicating probable bilateral symmetry; no axis or peduncles are evident). E, Plantae indet., portion of axis with a ?whorl of branches, NMVP167596, × 4. (Note central vascular trace preserved a darker colour and ?pair of small scale-like leaves on two of the branches).

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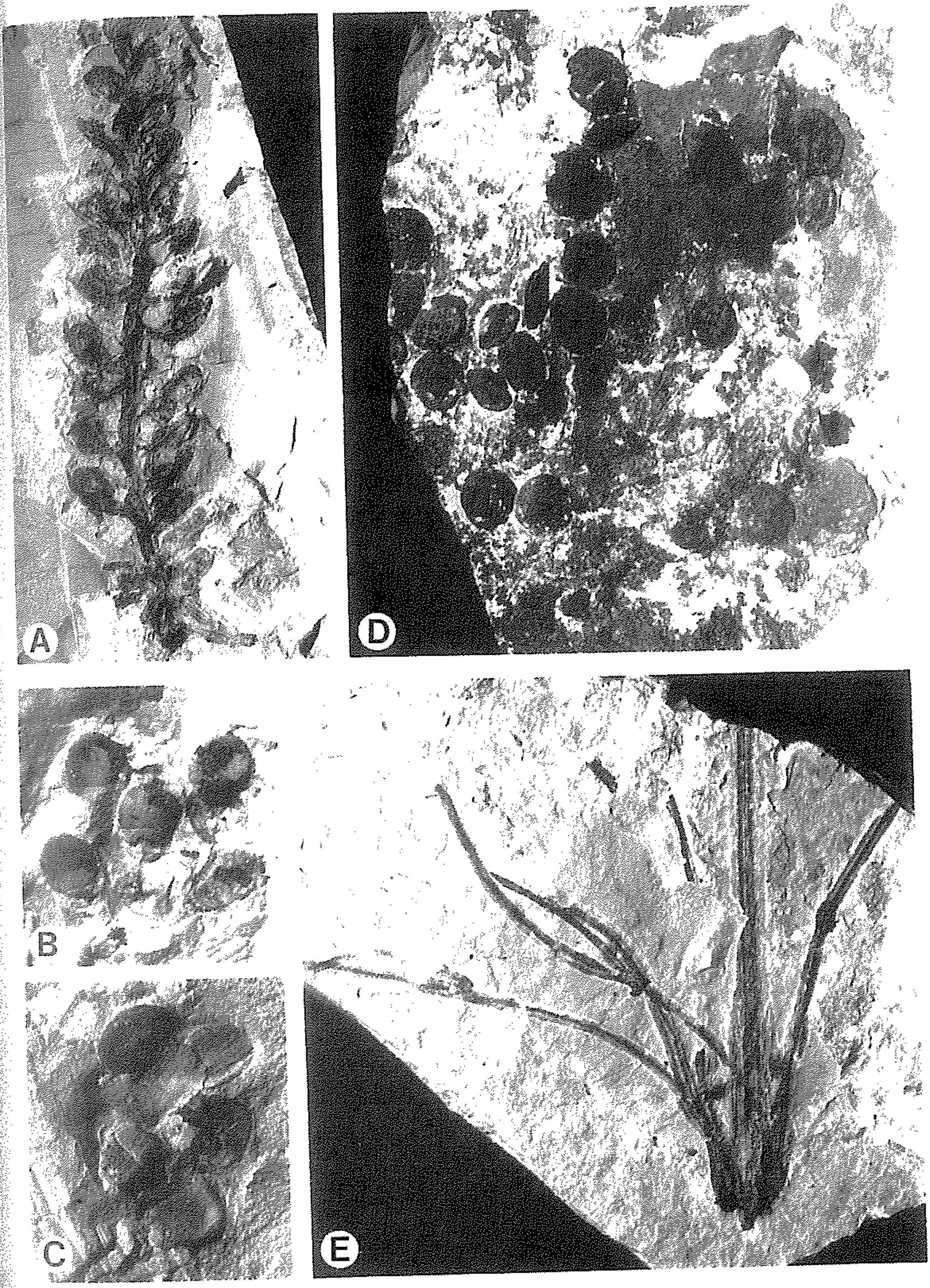

scale-like leaves about 12mm from their base. Leaves 1mm long. Stem and branches smooth (i.e. show no evidence of longitudinal ridges), and appear to have had one or more central vascular strands (preserved brown) and a non-vascular cortex (preserved yellow).

Discussion. This plant fragment is difficult to interpret. Douglas (1973) tentatively allocated it to *Isoetes* but the main stem, which appears to be central amongst the whorl of branches, is much thicker and presumably much longer than the branches, a feature inconsistent with the Isoetales (in which all the leaves are more or less equal in size and arise from near the stem apex). The whorl of branches occurs at the basal end of this specimen only because the main axis broke at that node. *Equisetum* has a similar habit but its vascular system usually preserves as longitudinal ridges on the stem, not as a central vascular core. Fossilized shoots of the Callitroideae (Cupressaceae) would be expected to have more prominent scale leaves sheathing the stem axis, although they may be a considerable distance apart.

The small scale-like leaves of the specimen are not easily interpreted, but their preservation is consistent with the opposite decussate nature of most *Ephedra* L. species. No fertile structures are evident. It is impossible to be certain of affinities with *Ephedra*, but its overall appearance bears marked similarity to the extant *E. distachya* L. 1753. Dettmann (1981) noted that *Ephedra*-like pollen is a minor element in sediments of similar age in Western Australia and the Great Artesian Basin.

CRUCIFORM STRUCTURE type 1 (Fig. 36Q)

Material. NMVP167763.

Description. Small cruciform structure consisting of four free parts joined to a circular disc 0.8mm in diameter. Parts of two sizes: two opposite parts 1.5mm long by 1mm wide, ovate, apices acute, fused basally to the central disc by a width of 0.7mm; the other two parts are narrower (0.7mm wide) and presumably shorter (they are incomplete), and are joined to the central disc by a lesser width (approx. 0.5mm).

Discussion. Although this small fossil looks remarkably like an angiosperm perianth, there is no conclusive evidence either in available morphology or in the other components of the Koonwarra flora which allows the classification of this specimen with the flowering plants. The structure has four parts apparently of two different sizes (opposite parts are equal), of which three are either broken or compressed back onto themselves at their distal ends. This latter feature of their preservation suggests they had a supple rather than a rigid nature.

Determination of the affinity of a structure of this type is frustrated by the two different sizes of parts although this feature may be an artifact of preservation. The structure may in fact be a dehisced capsule of a liverwort belonging to the Jungermanniales or the Metzgeriales which has broken from the seta, or even a dehisced capsule of an *Andreaea* Hedwig type moss which has broken apart at its distal end.

CRUCIFORM STRUCTURE type 2 (Fig. 36R)

Material. NMVP167762.

Description. Small cruciform structure consisting of four free parts joined basally at a central point. Parts of equal size 1mm long by 0.6mm wide, more or less oval, apices rounded, margins thickened, attachment to central point sessile. Surface pattern of parts reticulate.

Discussion. This structure differs from the previous type of cruciform structure in that its parts are equal in size, have thickened margins and a reticulate surface pattern, and although they are attached at a central point there is no evidence of a circular disc. The parts have not preserved flat in the sediment but are slightly convex, suggesting a habit of sufficient rigidity to retain their shape. The reticulate pattern of the surface is compact, but it is uncertain whether the reticulation represents venation or cell outlines.

The parts do not appear to be four separate sporangiate structures, but are possibly the four parts of a dehisced spore-containing organ, e.g. the sporphyte capsule of a jungermannialean or metzgerialean liverwort, or an *Andreaea*-like moss. Its similarity to perianth parts of an angiosperm flower is more marked than that noted for the previously described cruciform structure, but that determination is similarly prevented by the absence of recognizable angiosperm leaf remains.

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