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STEMS WITH ATTACHED *DICROIDIUM* LEAVES FROM THE IPSWICH COAL MEASURES, QUEENSLAND, AUSTRALIA.

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A single large block of massive siltstone with bands of medium to fine sandstone from the Late Triassic Blackstone Formation of the Ipswich Coal Measures of Queensland has revealed three stems each bearing fascicles of *Dicroidium elongatum* leaves. Two stems are preserved parallel to the bedding plane and the third is a vertically compressed and coalified stem passing at c. 45° through the matrix. The specimens show a single leaf or fascicles of from two to four leaves attached to protuberances or short shoots arranged spirally up the stems. This is the first occurrence in the fossil record of the multiple attachment of leaves and the growth habit of the plants in the ubiquitous Gondwana genus *Dicroidium*.
□ Triassic, Ipswich, fossil flora, *Dicroidium* leaves, stem attachment.

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DICROIDIUM – THE ENIGMATIC GONDWANA TRIASSIC PLANT

The forked leaves ascribed to *Dicroidium* have been known since Morris (1845) described the first specimens from the Triassic of Tasmania. Gothan (1912) established the new genus *Dicroidium* to accommodate certain *Thinnfeldia*-like fronds with a forking rachis from Gondwana. On the basis of close association and similarities of cuticles Thomas (1933) affiliated the male pollen-bearing organ *Pteruchus* and the female ovulate structure *Umkomasia* with *Dicroidium*. These fertile structures and *Dicroidium* have been reviewed by Anderson & Anderson (2003) and classified as gymnosperms in the Class Ginkgoopsida, Order Umkomasiales and the Family Umkomasiaceae that is restricted to the Triassic.

Dicroidium leaves range in form from simple to pinnate to bipinnate and tripinnate and have been recorded from all Gondwana continents. They are common to dominant in many Gondwana Triassic fossil plant assemblages. Anderson & Anderson (2003) noted that *Dicroidium* was present in 75 of their 100 taphocoenoses (TCs = assemblages) from the Molteno Formation of South Africa. In 54 of these TCs *Dicroidium* was mono-dominant to co-dominant. In the Middle Triassic Benolong Flora from near Dubbo NSW leaves of *Dicroidium* and the ginkgoalean *Sphenobaiera* formed the bulk of the preserved plant material (Holmes, 1982). *Dicroidium* leaves

were recorded as the most commonly preserved fossils in the rich and diverse Middle Triassic Nymboida Flora from the Nymboida Coal Measures of northern NSW (Holmes & Anderson, 2005). In the open cast coal mines at Leigh Creek in South Australia thin beds of 'paper coal' are composed of *Dicroidium zuberi* cuticles (K. Holmes pers. obs. 1997). Rich assemblages from South America have been described by Artabe (1985) and Gnaedinger & Herbst (1998; 2001). While the leaves of *Dicroidium* are abundant and widespread throughout Triassic Gondwana (as reviewed by Anderson & Anderson, 2003) clues to the habit of the plant that bore the leaves are limited.

Petriella (1978) reconstructed *Dicroidium* as a palmiform tree with a substantial trunk to 10m high, while various other authors have speculated that *Dicroidium* ranged from shrubs to tall trees (Retallack, 1980; Anderson & Anderson, 1982; Anderson et. al., 1998; Anderson & Anderson, 2003) or was a large tree (Taylor, 1996). The whole-plant reconstruction by Retallack & Dilcher (1988, fig.10) showed a tall deciduous forest tree in a seasonally wet lowland.

The first convincing specimen of leaf attachment was of two leaves attached apically on an elongated stem from the Molteno Formation of South Africa (Anderson & Anderson, 1983, Pl. 88, fig. 1). Another incomplete specimen (Anderson & Anderson, 1983, Pl.88, fig. 2)

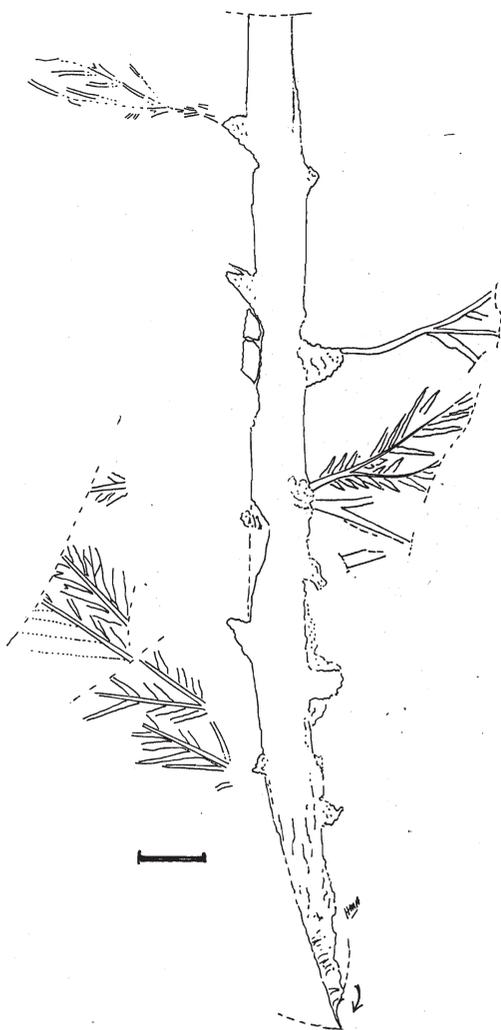


FIG. 1. Line-drawing (R1) of *Dicroidium elongatum* stem and leaves based on part and counterparts QMF52275C,D,E. Scale = 10mm

suggested that the leaves were attached in a fascicled manner to a stem. The reconstruction by Anderson and Anderson (2003, p. 257, text fig.5) was based on these specimens.

Archangelsky (1968) argued a case for the affiliation of silicified logs of *Rhexoxylon* and *Dicroidium* leaves. During a Mesozoic Terrestrial Ecosystems Congress Field Trip to view exposures of the Ischigualasto Formation in southern Argentina WBKH and HMA observed shale beds packed with *Dicroidium* leaves in close association with large petrified logs of *Rhexoxylon*



FIG. 2. Stem with *Dicroidium elongatum* leaves attached. QMF52275C, counterpart of QMF52275D. Scale = 10mm

but with no evidence of attachment. This was probably the same occurrence as that described by Archangelsky. *Rhexoxylon* has also been recorded in South Africa in the "Red Beds" now termed the Elliot Formation (Walton, 1923) and usually dated as Jurassic which would be well beyond the time range of *Dicroidium*. Meyer-Berthaud et al. (1993) described permineralised twigs from Antarctica as *Kykloxylo*n and suggested that the stems bore *Dicroidium fremouwensis* leaves as described by Pigg (1990), but the leaves have not been found in organic connection. In a



FIG. 3. Stem with *Dicroidium elongatum* leaves attached. QMF52275D. Scale = 10mm.

paper describing *Umkomasia uniramia* Axsmith et al. (2000, figs 6, 8) illustrated a *Dicroidium odontopteroides* leaf apparently contiguous with, or overlain by, a stem of a plant with long and short shoot morphology. By analogy with extant plants bearing long and short shoot morphology (e.g. *Ginkgo biloba*) it would be unlikely in the extreme for a plant with this growth morphology to bear a leaf on the long shoot section of a stem subsequent to the formation of well-developed short shoots. On the illustrated Antarctic specimen even the short shoots are in a leafless state although still bearing the ovulate fructifications. The close association of the *Dicroidium* leaf with the stem bearing short shoots suggests an affiliation but this is not exclusive as other leaves (e.g. *Heidiphyllum*, *Taeniopteris*) are reported as being present in the same deposit. Cúneo et al. (2003) described a

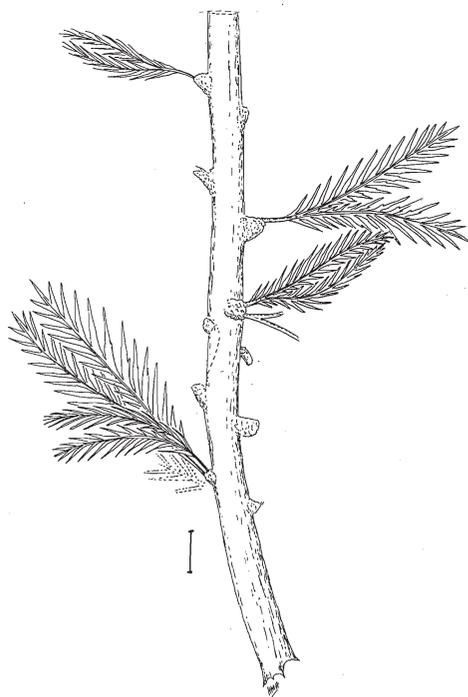


FIG. 4. Partial reconstruction (R3) of *Dicroidium elongatum* stem with some leaves. QMF52275C, D, E. Scale = 10mm

Triassic in situ forest in the Fremouw Formation of Antarctica consisting of 99 petrified standing stumps that indicated a forest density of c. 270 trees/hectare. The wood corresponds with that described by Del Fueyo et al. (1995) as *Jeffersonioxylon*. Based on the diameter (60cm) of the largest stump and the maximum number of growth rings (86) it was estimated that the forest may have reached a height of more than 30m, with an average canopy height between 14 and 25m. The sediments associated with the stumps contain mats of *Dicroidium* leaves. While there is no evidence of attachment their exclusive occurrence indicates that the *Dicroidium* leaves were produced by the trees now preserved as the in situ stumps.

NEW MATERIAL OF STEMS WITH ATTACHED LEAVES

In 2005 during a plant fossil collecting trip in the Ipswich District, LAF recovered some plant fossils from a large block of grey siltstone with paler thin bands generally less than 3.5mm thick of cross-bedded medium to fine sandstone. The



FIG. 5. Branching stem with *Dicroidium elongatum* leaves attached. QMF52275B. Scale = 10mm.

nature of the block indicates the sediments were deposited during gentle current activity from periodic overbank flooding events. The block as found was bounded on two sides by oblique joint fractures. The collecting site was in the old Dinmore Quarry near Ipswich (Pattimore, 1998) in heaps of overburden dumped from the nearby, now worked-out, open-cast mines that exploited the coal seams in the Late Triassic Blackstone Formation of the Ipswich Coal Measures, south-east Queensland (Playford & Rigby, 1988). The stratigraphic horizon and exact source of the specimens in this overburden material is not known.

The initial specimens were two individual horizontal stems each bearing fascicles of attached *Dicroidium elongatum* leaves together with the counterparts. Recognising the importance of the find, further material was later collected from the original shattered block including some radiating groups of leaves and two large vertically adjacent fragments showing a semi-vertical coalified stem and indications of fascicles of leaves radiating into the matrix. By now the remains of original large block were in fragments and dispersed. The specimens



FIG. 6. A fascicle comprising a large and small leaf of *Dicroidium elongatum* attached to the stem on right side. QMF52275A, counterpart QMF52275B. Scale = 10mm.

illustrated and described were all recovered from the single original block.

The collection comprises two horizontal stems with attached fascicles of *Dicroidium elongatum* leaves and blocks showing a coalified semi-vertical branched stem with fascicles of leaves radiating into successive layers of the matrix. Leaves and horizontal stems are preserved as compressed carbonaceous material or have been replaced or stained with iron oxide. A few fragments of *Dicroidium odontopteroides* leaves are scattered through the matrix and as a layer in a lower coarser sandstone band. We have endeavoured to reassemble the whole block from the collected material, but with only partial success as some of the intermediate fragments are missing. Minimal chipping of specimens has been carried out. Further detailed disengagement of some of the partially hidden leaf fascicles may reveal additional information. The total collection represented by 17 pieces has been allocated the single Queensland Museum Fossil Number QMF52275 with the individual pieces identified with upper case letter suffixes, as QMF52275A to QMF52275Q (to avoid confusion, letters I, L and O have not been used).



FIG. 7. Line drawing (R2) of branching stem with attached *Dicroidium elongatum* leaves; based on part QMF52275A and counterpart QMF52275B. Scale = 10mm.

The collection is housed in the Palaeontological Department of the Queensland Museum, Brisbane.

THE LEAF-BEARING STEMS

Two separate horizontally compressed stems are preserved with attached fascicles of *Dicroidium elongatum* leaves. The stem and its counterpart (Figs 1–4) is c. 160mm long and 10mm wide and shows individual leaves and two fascicles of leaves attached. For most of its length the stem is compressed parallel to the bedding plane but basally the stem curves downwards into the sediment. The second specimen and its counterpart (Figs 5–7) is a portion of a woody stem 180mm long and c. 14mm wide. A lateral branch, c. 6mm wide is attached to the main stem at c. 45°. A fascicle of two leaves is attached at c. 45° near the base and another leaf fascicle at a high angle at 65mm along the stem. Further fragments of fascicles are aligned in the matrix as though originally attached to the stem. The swollen leaf bases of the attached fascicles and the irregularly spaced protuberances along the stems of both the above specimens probably represent short shoots.

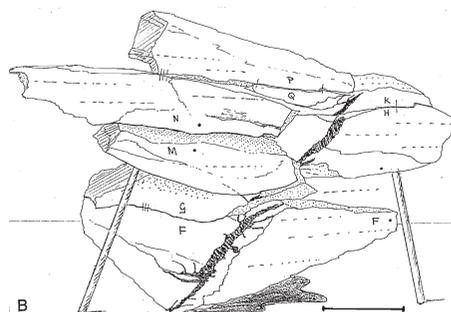


FIG. 8. *Dicroidium elongatum* leaf fascicle. A, QMF52275H and J upper surface; B, Counterpart of fascicle in Fig. 8A, (portion only), QMF52275K lower surface. Scale = 10mm.

A third compressed and coalified stem with cleat structure is preserved in a semi-vertical position passing upwards through the matrix on the margin of four blocks, for a length of 270mm (Figs 9). Near the base the width is c. 20mm then contracting to 10mm distally. Fascicles of leaves (Figs 8, 10) radiate horizontally into the matrix at close intervals adjacent to the mid to upper section of the stem. Coalified roots radiate from the base and up the main stem there is evidence of some lateral branches. A frontal view of the blocks encompassing the main stem is illustrated in Fig. 9. The schematic sketches (Figs 10A, 10B) show the three dimensional placement of leaf fascicles. Figs 11 and 12 are serial depictions of the upper and lower surfaces of the blocks adjacent to the main coalified stem and show the arrangement of leaves preserved horizontally in the matrix. A separate leafless coalified stem c. 0.5mm in diameter passes vertically through the matrix (see Fig. 11, S1). It cannot be established whether the two stems illustrated in Figs 1–7 connect with the semi-vertical stem or are independently preserved fragments. Also a connection between the fascicles



FIG. 9. A, Frontal view of reassembled blocks QMF52275F–Q associated with the semi-vertical stem. Scale = 100mm; B, Schematic sketch of reassembled blocks shown in Fig. 10A. Scale = 100mm.

of leaves (QMF52275R) shown in Fig. 13 and any stem is missing.

DICROIDIUM LEAVES AND THEIR ATTACHMENT

The forked leaves from this assemblage while differing greatly in size, are uniformly pinnate to slightly bipinnatifid. They fit well into *Dicroidium elongatum*, a variable morpho-taxon, often with many intergrading forms that have in the past and even to the present, been placed in several genera, species, varieties or formae (Carruthers, 1872; Tenison Woods, 1883; Shirley, 1898; Walkom, 1917; Frenguelli, 1943; Jones & deJersey, 1947; Hill et al., 1965; Retallack, 1977; Holmes, 1982; Anderson & Anderson, 1982: 2003; Artabe, 1985; Gnaedinger & Herbst, 2001; Holmes & Anderson, 2005). Pattermore & Rigby (2005) argued for the retention of the genus *Xylopteris* for this form of leaf based on the presence of a male fructification apparently attached apically to a *Dicroidium elongatum* leaf. We have examined the specimen in the Queensland Museum and consider the leaf and fructification to be two separate entities.

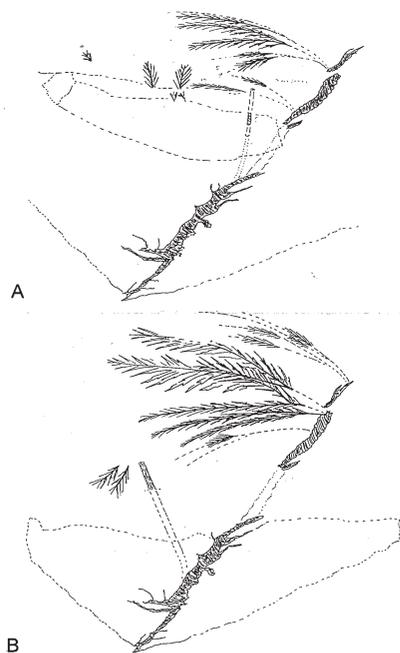
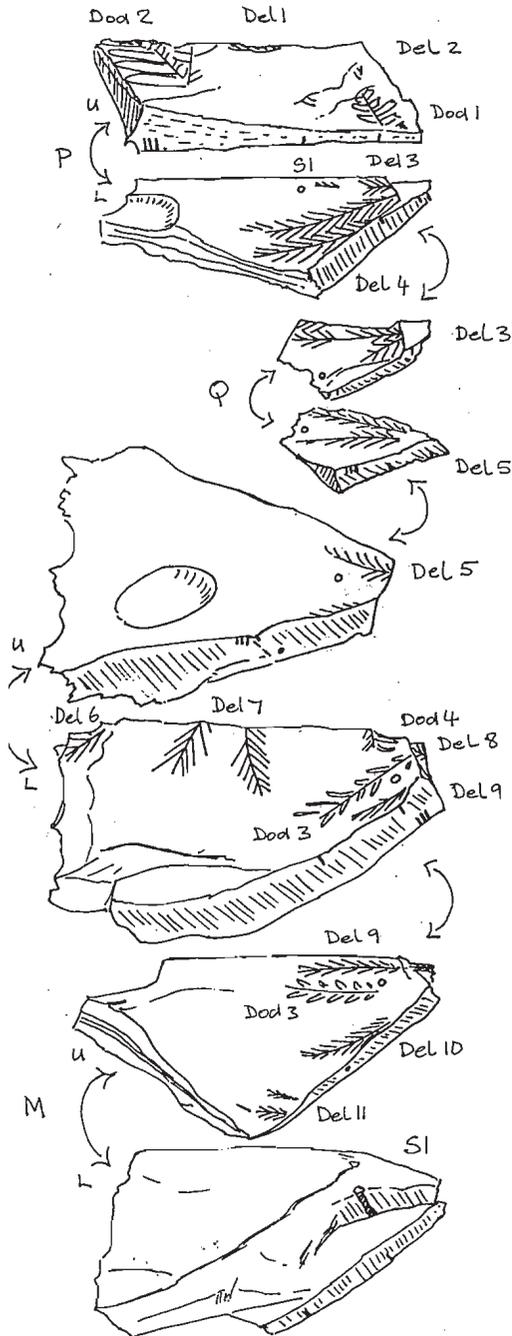


FIG. 10. Partial reconstruction of foliage associated with the semi-vertical stem. A. Based on blocks QMF52275M–Q. B. Based on blocks QMF52275F–K.

In the present material, leaves are attached in close groups of from one to four to a swelling or protuberance on a slightly tapering and sympodially branching stem. The grouping of several leaves is here regarded as a fascicle but may be a close spiral on a poorly developed short shoot. Previously published illustrations of incomplete groups of *Dicroidium* leaves (e.g. *Trichomanides elongata* of Shirley, 1898, pl.10, fig. 3; also from the Blackstone Formation and *Dicroidium odontopteroides*, Anderson & Anderson, 1982, pl.88, fig. 2) suggest a similar fascicular arrangement. The reconstruction of *D. odontopteroides* by Anderson & Anderson (2003) depicts a fascicle of leaves terminal on an elongated stem.

In our Dinmore material the leaves are variable in length (even in the same fascicle (Figs 6, 7) ranging from 50mm–160mm long. Fascicles comprising mostly three leaves ranging in length from 140–160mm (Figs 8, 10) radiate into the matrix parallel to the bedding plane from the semi-vertical stem. Based on the few attached fascicles the angle of attachment to the stem ranges from 45°–90°. Additional fragments of fascicles are aligned in the matrix in the



Note that slivers of matrix may be missing between some of the slabs.

QMF52275P Upper surface

D.el. 1. Small portion of leaf at block margin.

D.el. 2. Small distal portion of forking leaf in alignment with main stem.

D.od. 1. Fragment of leaf.

D.od. 2. Portion of forked leaf.

QMF52275P Lower surface

Stem 1. Coalified stem vertical through slab (indicated by a circle).

D.el. 3. Forked leaf; base concealed in matrix.

D.el. 4. Distal portion of frond. This leaf and *D.el.* 3. are aligned with main axis and probably from a common base.

QMF52275Q Upper surface

D.el. 3. As above.

D.el. 4. As above but smaller fragment preserved.

QMF52275Q Lower surface

D.el. 5. Forked leaf, base missing; in alignment with main axis.

QMF52275N Upper surface

D.el. 5. As above; smaller fragment of leaf preserved.

QMF52275N Lower surface

D.el. 6. Small portion of leaf.

D.el. 7. Distal portion of forked leaf.

D.el. 8. Portion of leaf aligned with main axis.

D.el. 9. Portion of leaf aligned with main axis.

D.od. 3. Fragment of leaf.

D.od. 4. Fragment of leaf.

S. 2. Stem aligned with main axis.

QMF52275M Upper surface

D.el. 9. Portion of leaf aligned with main axis; basally passing down through matrix.

D.el. 10. Portion of leaf aligned with main axis.

D.el. 11. Portion of leaf aligned (?) with main axis.

D.od. 3. Fragment of leaf.

S. 2. Stem passing through matrix.

QMF52275M Lower surface

S1. Stem preserved vertically through all slabs and here exposed over a 15mm length with a diameter of 6mm.

S3. Stem exposed on two sections of the slab and aligned with main axis.

Key

S = Stem

D.el. = *Dicroidium elongatum*

D.od. = *Dicroidium odontopteroides*

Figure 9B

FIG. 11. Serial depictions of the upper and lower surfaces of blocks to show position and alignment of the leaves and stem branches associated with semi-vertical axis. Based on blocks QMF52275M-Q.

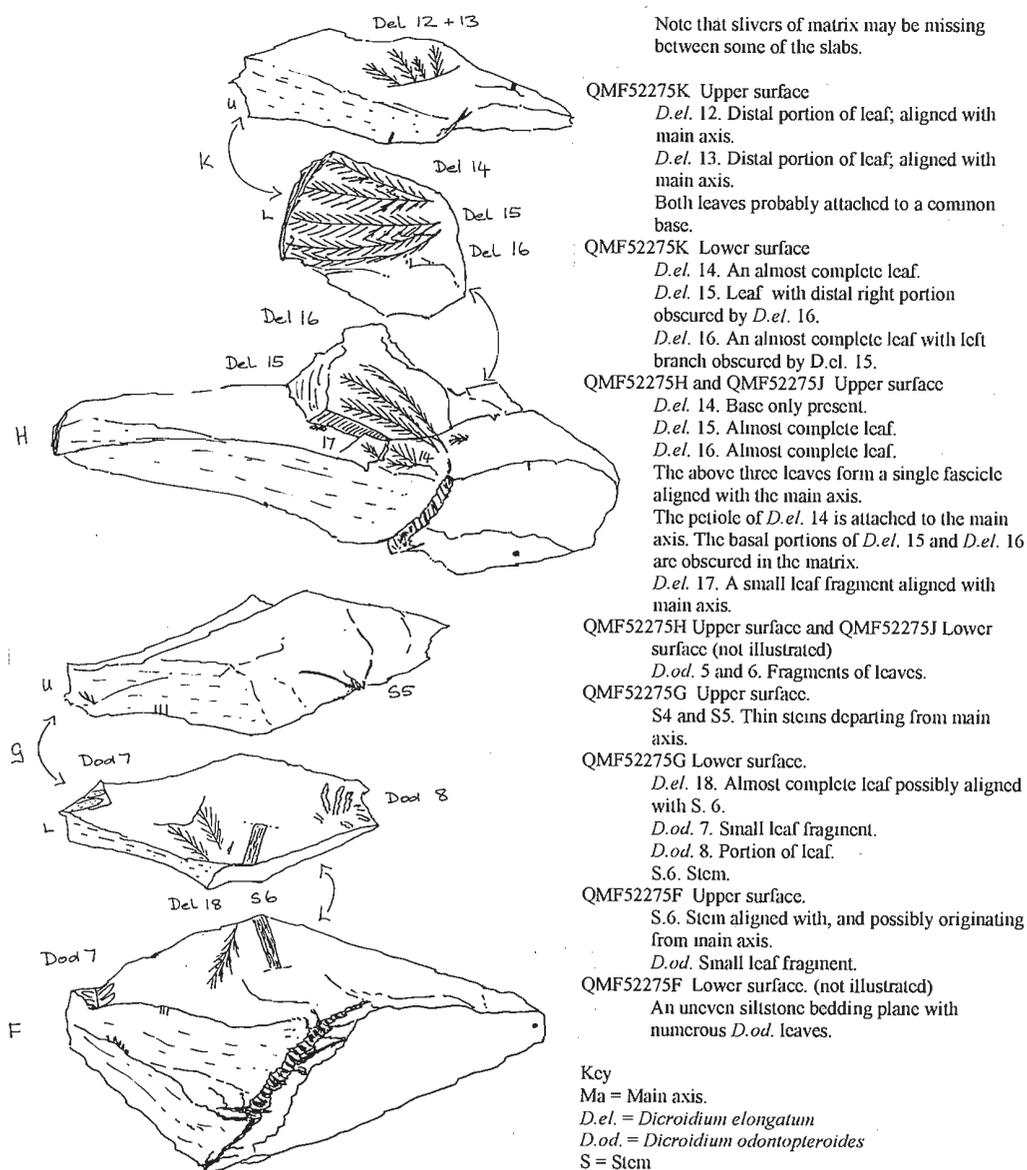


FIG. 12. Serial depictions of the upper and lower surfaces of blocks to show position and alignment of the leaves and stem branches associated with semi-vertical axis. Based on blocks QMF52275F–K.

correct position to also have been attached to the stem. The spacing between fascicles or leafless protuberances ranges from 15mm to c. 20mm apart. The R3 reconstruction (for definitions see Anderson & Anderson, 2003, p.44) of this horizontal stem (Fig. 4) depicts only the leaves actually preserved on the fossil together with its leafless short shoots. When compared with the

abundance of leaves attached to the semi-vertical stem (Figs 10–12) this stem in life would have had much denser foliage. Another block QMF52275R and S (Fig. 13) of uncertain relationship to the above stems shows portions of three or possibly four adjacent fascicles each composed of three leaves to 90mm long. The irregular arrangement of the fascicles and protuberances along the



FIG. 13. Portions of four associated *Dicroidium elongatum* leaf fascicles. QMF52275R. Scale = 10mm.

compressed stem suggests a spiral arrangement in life and the probability that they were short shoots. The Antarctic stem described by Axsmith et al. (2000) as bearing a *Dicroidium* leaf on a long shoot also bears well-developed widely-spaced leafless short shoots that show evidence of leaf scars, a feature not well-preserved on the protuberances on the stems of the Dinmore material which are carbonaceous compressions.

DISCUSSION

This important new find of stems with attached *Dicroidium elongatum* leaves provides an insight into the habit of this particular *Dicroidium* plant. The attached and adjacent groups of leaves described here as fascicles probably represent closely-spaced spirals of leaves on short shoots similar to those seen in extant *Ginkgo biloba* first to second year short shoots. The short shoots themselves are also closely arranged spirals along the stems. The extreme variability in size of the leaves in a single fascicle (Figs 5–7) is also closely similar to that of *G. biloba*.

The stem preserved in a semi-vertical position (Fig. 8A, B) suggests a small woody branching shrub or young tree in its position of growth in a waterway, being bent at an angle during a period of high current activity and with its spiral of leaf fascicles becoming preserved horizontal to the bedding plane by the later gently accumulating layers of sediment. Its small shrub-like size as preserved provides no indication of possible size at maturity. The two horizontally preserved leaf-bearing stems (Figs 1–7) appear to be independent as no connection has been established with the third semi-vertically preserved stem (Figs 9, 10). They are probably detached branches from separate plants possibly of tree size.

ACKNOWLEDGEMENTS

Dr Barry McKelvey has provided information on the possible origin and nature of the fossil-bearing sediments. WBKH acknowledges support from the Betty Mayne Research Fund.

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