

# The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 10. Miscellaneous Foliar (*Rochipteris*) and Fertile Genera (*Fraxinopsis*, *Tomiostrobus*, *Umkomasia*, *Weltrichia*)

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Miscellaneous megafossil plants are described from two quarries in the Middle Triassic (Ladinian) Nymboida Coal Measures in northern New South Wales, Australia. These include the isoetalean lycopod *Tomiostrobus*; the petriellalean leaf *Rochipteris*, the fertile megasporophyll *Umkomasia* and associated dispersed seeds; the male bennettitalean *Weltrichia*, and a possible gnetalean winged seed *Fraxinopsis*. The Nymboida Flora, with *Dicroidium* the dominant element, is the most intensively collected and best documented flora of the Gondwana Australian Triassic with 60 genera and 121 species described in ten publications. The flora is of global importance in highlighting the re-establishment of peat-forming plant communities some 10 million years after the end-Permian extinction event.

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## INTRODUCTION

The Triassic Period, framed by the end-Permian and end-Triassic extinctions, is a unique time in Earth's history with world wide correlations largely based on marine strata and their fossils which are rarely of plant origin. The land during the Triassic consisted of the supercontinent Pangea with the southern area hosting a distinctive Gondwana flora (Kustatscher et al., 2018). In this paper, further plants from Nymboida Coal Measures of the Nymboida Sub-basin in northern New South Wales of eastern Gondwana, i.e. present day Australia, are reported from Middle Triassic (Ladinian) strata. The Nymboida megafossil flora is of global importance in highlighting the re-establishment of peat-forming

plant communities some 10 million years after the end-Permian extinction event, which saw the collapse of mire communities across Gondwana and Cathaysia (Mays et al., 2020).

This is the tenth paper of a series describing the Middle Triassic (Ladinian) Nymboida megafossil flora: Part 1 of this series (Holmes 2000) described the Bryophyta and Sphenophyta; Part 2 (Holmes 2001) the Filicophyta; Part 3 (Holmes 2003) other fern-like foliage; Part 4 (Holmes and Anderson 2005a) the genus *Dicroidium* and its fertile organs, *Umkomasia* and *Pteruchus*; Part 5 (Holmes and Anderson 2005b) the genera *Lepidopteris*, *Kurtziana*, *Rochipteris* and *Walkomiopteris*; Part 6 (Holmes and Anderson 2007) the Ginkgophyta; Part 7 (Holmes and Anderson 2008) the Cycadophyta; Part 8 (Holmes et al. 2010) the genera

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*Nilssonia*, *Taeniopteris*, *Linguifolium Gontriglossa* and *Scoresbya*; Part 9 (Holmes and Anderson 2013a) the genera *Heidiphyllum*, *Voltziopteris* and *Rissikia* with affiliated fertile structures and leaves tentatively attributed to *Yabeiella*. A summary of the flora and geological setting was presented by Holmes and Anderson (2013b) and, together with the plants described here, a total of 60 genera and 121 species of vegetative macro-plants have been recorded. The Nymboida Flora is the most intensely collected and best documented flora of the Australian Triassic. Trailing second is the Ipswich Flora which had 63 species recorded by Jones and de Jersey (1947). This figure needs revision of most species and updating to include subsequent descriptions by Pattemore and Rigby (2005) and Pattemore (2016a, b).

Additional specimens of the following taxa are described here: the isoetalean lycopod *Tomiostrabus*; the petriellalean leaf *Rochipteris*; the fertile megasporophyll *Umkomasia* and dispersed seeds (both associated with the leaf *Dicroidium*); the male bennettitalean *Weltrichia*, and a possible *Fraxinopsis* (a winged seed belonging to the Gnetopsida). These specimens derive from the Coal Mine and Reserve quarries, and a description of the localities with a summary of the geology was provided by Flint and Gould (1975), Holmes (2000) plus Holmes and Anderson (2013b). The specimens in this paper were collected by the authors, unless otherwise indicated in the text. They are housed in the Australian Museum, Sydney and designated with an AMF (Australian Museum Fossil) number. The original collection number is in brackets.

### CLASS LYCOPODIOPSIDA

In contrast to the arborescent lycopods found in the Palaeozoic, the Mesozoic lycopod fossils are slender pseudo-herbaceous plants, most notably from the Lower Triassic and are well known globally. These have been described and reviewed by various researchers (Grauvogel-Stamm and Lugardon, 2001; Kustatscher et al., 2010; Moisan and Voigt, 2013) and particularly from the Australian Triassic by Retallack (1975, 1997). The herbaceous lycopods from the Triassic are related to the extant quillworts (*Isoetes*) which grow in moist habitats. Fossil allies have been reported as early as the Devonian to more recent times (Taylor et al., 2009). Significant post Triassic Australian macro records of *Isoetes* are from: the Cretaceous of Western Australia based on a whorl of leaves and megasporangia as *I. elegans* (McLoughlin, 1996) and Victoria based on corms with leaves as *I.*

*bulbiformis* (Drinnan and Chambers, 1986) plus *I. abundans* (McLoughlin et al., 2002); the Cenozoic of Tasmania based on megaspores and leaves as *I. reticulata* (Hill, 1988); the Miocene of New South Wales based on an isoetalean whorl of leaves (Holmes and Anderson, 2019).

This is the first record of lycopods from the Nymboida Flora. It contributes to the knowledge of similar sterile and fertile macro lycopod material found elsewhere in the Australian Triassic (Ash, 1979; Holmes and Ash, 1979; Pattemore and Rigby, 2005; Retallack, 1975, 1997). Of significance are the permineralized lycopsid remains, including cones, described from the Lower Triassic of the Bowen Basin, Australia, by Cantrill and Webb (1998).

### Order Isoetales

#### Family Isoetaceae

*Tomiostrabus australis* (Ash 1979) Sadovnikov  
1982

Figure 1A–H

#### Material

AMF 159177a (5729a) and counterpart 159177b (5729b), Reserve Quarry.

#### Description

Portion of an isoetalean conical corm (stem), width c. 30 mm, woody, carbonaceous, bearing numerous leaves. The sterile leaves are incomplete, parallel sided, length greater than 30 mm and c. 5 mm wide. The sporophylls (fertile leaves) have an expanded base c. 7 mm wide and a narrower parallel-sided extensions with total lengths unknown. Three sporophylls and possibly a fourth are visible.

#### Discussion

The isoetalean corm (Fig. 1A–H) is placed in this species based on the nature of the sporophylls that are similar in size and morphology to those described by Retallack (1997). It shows a portion of the woody corm preserved in 3D as part and counterpart with numerous leaves and sporophylls attached but none is visible for its full length. The sporophylls (Fig. 1D) clearly have the expanded basal fertile portion and the apical area consisting of a narrower parallel-sided leaf as was illustrated by Retallack (1997, fig. 1). They can also be compared to the more complete specimen illustrated by White (1986, fig. 193) which bore some fertile sporophylls. The 3D nature of the fossil is further reflected in the photograph taken from the underside of the slabs (Fig. 1H), which illustrates the continuation of the leaves in the sediment and from the edge shows that the corm dips down at

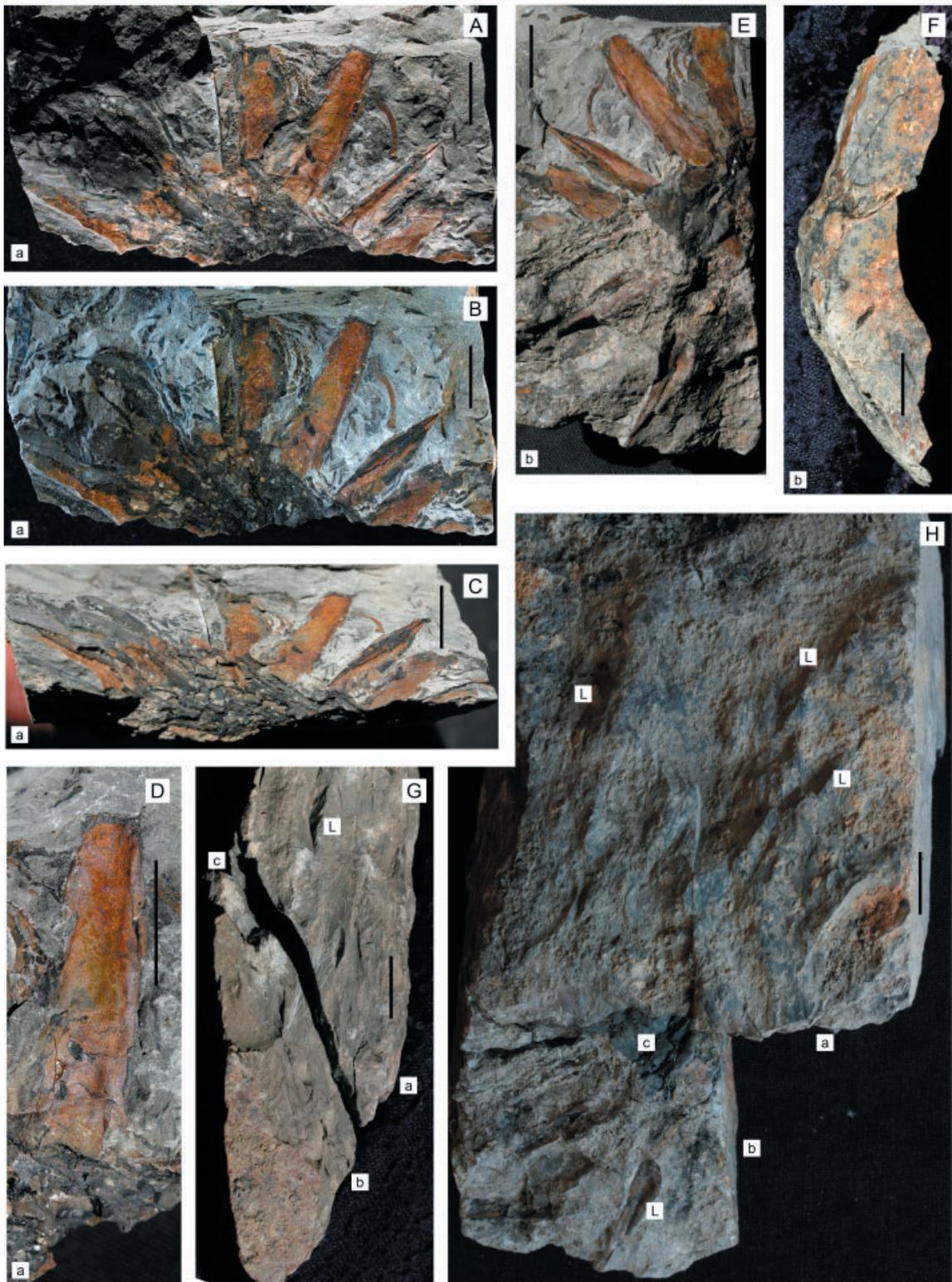


Figure 1. [A–H] *Tomiostrobus australis* AMF 159177; [A–C] side ‘a’ from three different light angles; [D] individual sporophyll from side ‘a’ close up; [E] side ‘b’ partial counter part of side ‘a’; [F] side ‘b’ edge on view to show curvature of specimen; [G] side ‘a’ and ‘b’ showing overlap from the edge; [H] the reverse side of ‘a’ and ‘b’ showing the 3D nature of the fossil and extension of leaves ‘L’ and centre of corm ‘c’; (scale bar = 10 mm).

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an angle (Fig. 1G). The counterpart slab (Fig. 1E) represents the right hand side of the specimen in (Fig. 1A) and an additional portion not present in the other. Similarly, the left hand side of the specimen (Fig. 1A) does not occur on the counterpart. The curvature of the corm is illustrated in lateral view (Fig. 1F) and demonstrates the continuation of the leaves in the sediment, features that are also visible in the lateral views shown in Fig. 1G. This lycopod corm shows a superficial similarity to the Nymboida specimens previously described as fern leaf bases by Holmes (2003, figs 33, 34). However, most of those published specimens are definitely fern leaf bases as shown by the rhachis bearing fern pinnules (Holmes, 2003, fig. 33A, B).

### *Tomiostrubus* sp. A

Figure 2 A–C

#### Material

AMF 159178 (5748), Coal Mine Quarry.

#### Description

Portion of an isoetalean corm (stem) bearing numerous leaves, length 120 mm and width 100 mm. The leaves are 60 mm or longer and up to 7 mm wide, parallel-sided and apically taper to an acute tip, the base and attachment to the corm is not clearly preserved.

#### Discussion

This lycopod (Fig. 2A) is similar to the one identified as *Tomiostrubus australis* above in having a central conical corm and numerous leaves attached. Although the leaves are more numerous and fairly complete there is no evidence of sporophylls to permit a more definite identification. This may be what Retallack (1997, fig. 7) referred to as an immature specimen. Such vegetative material may have been more common, due to previously being overlooked and regarded as roots or leaf bases of ferns.

Walkom (1925a, p. 220, pl. 30, figs 1, 2) described two stems from the Narrabeen Stage of the Hawkesbury Series that he placed in “*?Williamsonia* sp. (Stems)”. The larger stem (fig. 1) has numerous leaf scars (some rhombic) spirally arranged and the identity is difficult to ascertain. The smaller stem (fig. 2) has what he referred to as “leaf bases or petioles” and is possibly a lycopod as the leaves are similar to the Nymboida specimen. Walkom (1925a, p. 220, pl. 29, figs 7–8) also described fertile structures as “*?Williamsonia* sp. (flowers)” and these were reclassified by Anderson et al. (2019) as “cf. *Umkomasia feistmantelii* (Holmes & Ash 1979)

Holmes” being typical split open *Umkomasia* cupules which may look like ‘flowers’.

### *Lycopod* sp. A

Figures 3A–E, 4A, B

#### Material

AMF 159179 (5805X in 4 pieces) stem with leaves, AMF 159180 (5805Y in 3 pieces) stem/root, Reserve Quarry.

#### Description

A stem > 130 mm long and c. 30 mm wide bearing numerous, closely spaced, spirally attached leaves c. 40 mm long and 1.5–2 mm wide.

#### Discussion

This lycopod stem (Fig. 3A–C) AMF 159179 (5805X) (referred to as ‘X’) shows a close resemblance to extant *Lycopodium* in bearing numerous, small and closely spaced leaves. These are all evenly aligned at an angle of c. 15° to the stem. The lower part of the specimen has clearly preserved leaves (Fig. 3B, C) but, distally, the stem is visible along the edge of the slab as a carbonaceous streak that dips into the sediment at an angle of 30° (Fig. 3A the arrows point to the continuation of the stem, Fig. 4B see sketch at upper right on side Xa). This lycopod occurs on four slabs (Fig. 4B) with one labeled ‘Xa’ and the counterpart of that as ‘Xb, c’. The lower portion of the lycopod is on ‘Xd’ and the counterpart is missing. Although these three slabs all connect, it was preferable not to glue the narrow margins together.

On the same slab, at a lower level, is a stem or root/rhizome AMF 159180 (5805Y) (referred to as ‘Y’), 210 mm long and 18 mm wide with numerous circular scars c. 3 mm in diameter (Figs 3D, E; 4A, B). The main specimen is on the slab ‘Ya’ with a small counterpart portion on ‘Yb’ and a larger portion ‘Yc’ which occurs on the underside of the lycopod slab ‘Xd’, not illustrated but arrow in sketch (Fig. 4B) indicates the position. The close association with the lycopod stem (X) in the same block may indicate that this stem/root (Y) is linked and is of lycopod origin. Of palaeoecological interest is that the slab also bears two leaves of *Lepidopteris madagascariensis* (Holmes and Anderson 2005) shown as a sketch (Fig. 4B). These leaves may have grown alongside the lycopod in a moist environment. Furthermore, the silty matrix and lack of good bedding planes on these slabs possibly indicates a fairly fast burial and probable autochthonous preservation.

This Nymboida lycopod shows some similarity to the two illustrated lycopods from the Lower

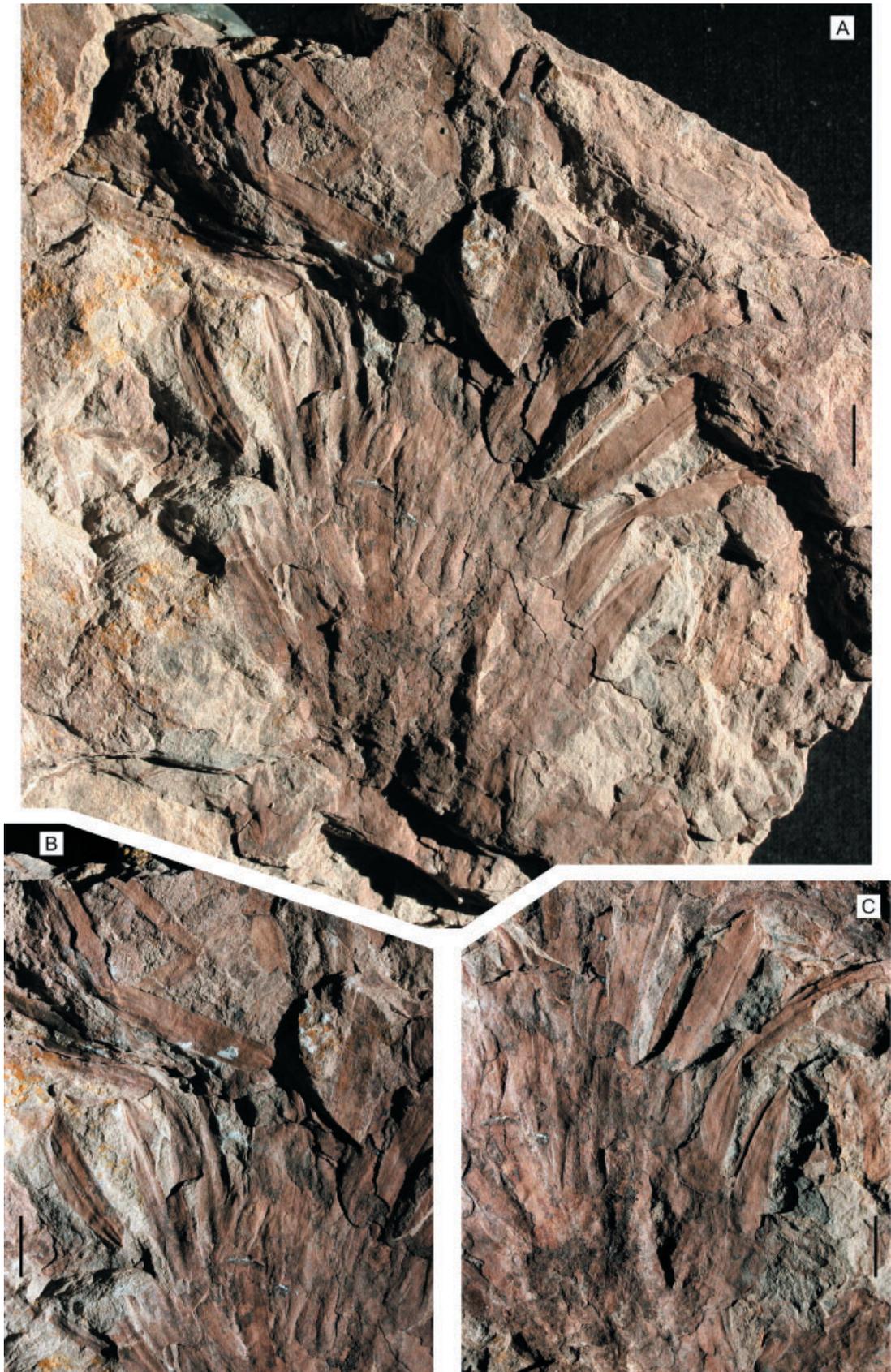


Figure 2. [A–C] *Tomiostrobus* sp. A. AMF 159178; [A] corm near base with numerous leaves attached; [B, C] different light angles to show overlapping leaves; (scale bar = 10 mm).

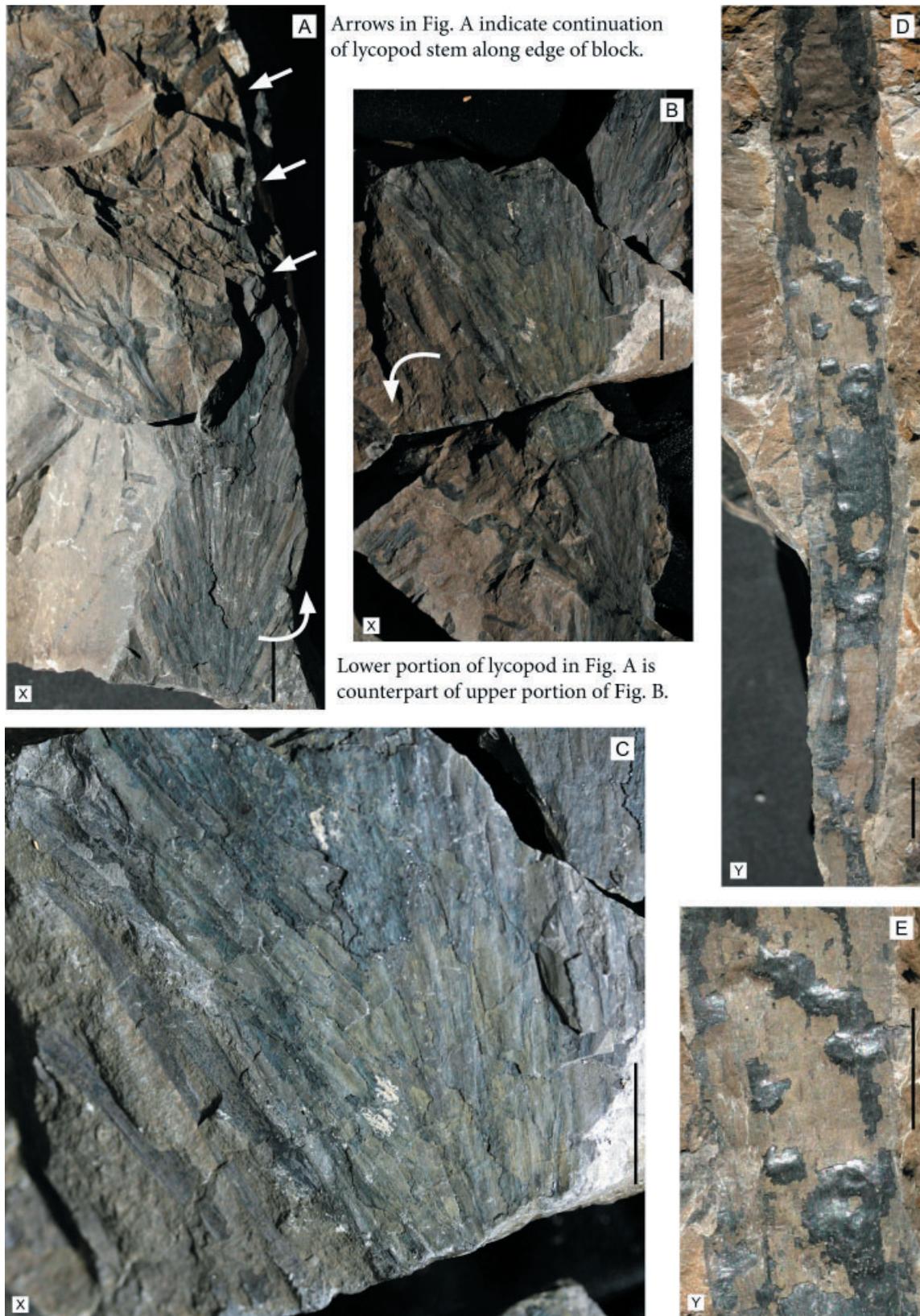


Figure 3. [A–C] *Lycopod* sp. A., AMF 159179 stem ‘X’; [D–E] AMF159180 stem/root ‘Y’; the relationship of these two specimens is shown in Fig. 4; (scale bar = 10 mm).

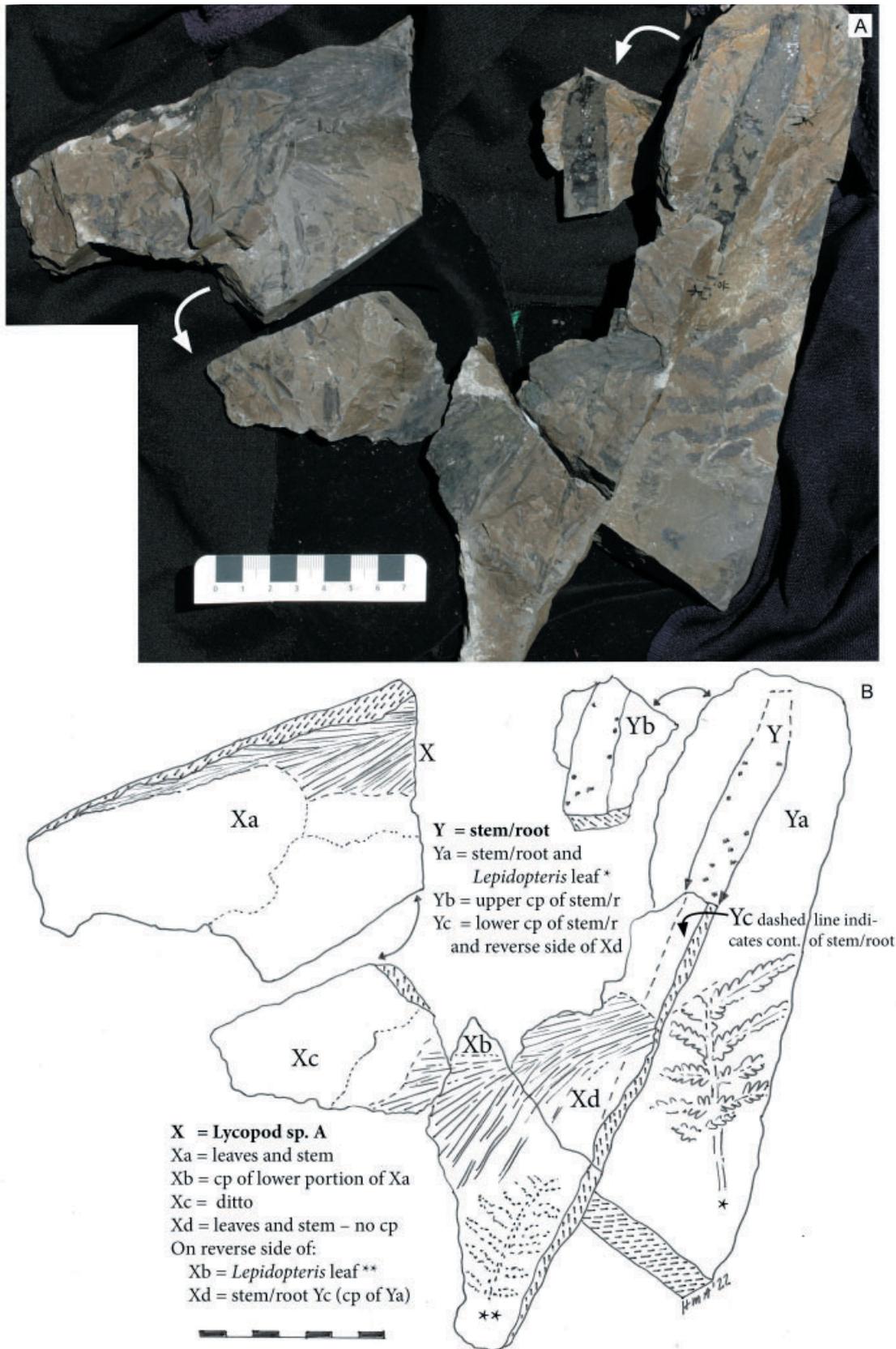


Figure 4. [A, B] *Lycopod* sp. A., AMF 159179 stem 'X'; AMF 159180 stem/root 'Y'; showing the relative position of these two specimens and the numbering of the separate pieces a-d that all derive from the same block; (scale bar = 70 mm).

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Jurassic of Queensland by Pattemore and Rigby (2005, fig. 2 A, B). Their larger one shows a dichotomising axis and both have numerous leaves attached, with a maximum length of 20 mm and width of 1.5 mm i.e. about half the length of the Nymboida leaves.

### CLASS GINKGOOPSIDA

Certain plants previously placed in the pteridosperms (seed ferns) were grouped by Meyen (1987) in the class Ginkgoopsida. This classification has been followed by Anderson et al. (2007) in their compendium of the gymnosperm families. Here we describe additional fossils that have come to our attention since the publication of fossils belonging to Umkomasiaceae (Holmes and Anderson 2005a) and Petriellaceae (Holmes and Anderson 2007). The latter family includes *Kannaskoppia*, which is unique in the Triassic of Gondwana in having both female organs and leaves attached to the same stem as described by Anderson and Anderson (2003). This is a rare phenomenon in the fossil record and from Nymboida, despite over 40 years of collecting, no specimens showing organic attachment of fertile structures have been found. However, attached *Rochipteris* leaves were reported from the Nymboida flora by Holmes and Anderson (2007). From the Ipswich Flora three stems with numerous *Dicroidium* leaves attached were described by Anderson et al. (2008). *Umkomasia* and its attached seeds are well known since first described by Thomas (1933). They were previously described by Holmes (1987) and Holmes and Anderson (2005a) from the Nymboida Flora. Additional dispersed seeds most probably belonging to this genus are described here as different 'Forms' and not as species.

#### Order Umkomasiales Family Umkomasiaceae *Umkomasia* sp. B

Figure 5A–G

#### Material

AMF 159181 (5746), collected by Lance Fitness and Alan Carlsburg (the counterpart is AMF145066 with a *Dicroidium* sp. published by Anderson et al. 2019) from the Reserve Quarry; AMF 159182 (5771); AMF 159183 (5773), the latter two specimens were collected by John Riley from the Coal Mine Quarry.

#### Description

Large oval cupules up to 23 mm long and 15 mm wide occurring in pairs and attachment unknown.

#### Discussion

The close clustering of the cupules on AMF

159181 (5746) (Fig. 5A, B) suggests that they probably came from the same strobilus. The cupules shows varying degrees of preservation and probably consist of two pairs. The most complete cupule (c1) is 23 by 15 mm and shows a portion of the pedicel/peduncle along the upper carbonaceous edge. How this is attached to the axis or the other cupules is not evident. The cellular structure on cupule (c1) also occurs on cupule (c3). These cupules are larger than those of *Umkomasia cupulata* and *U. grandis* from the Molteno Flora and *U. feistmantelii* from the Lorne Basin Flora as depicted in the Key to *Umkomasia* Species by Anderson et al. (2019, fig 2). These are regarded as possibly a new and separate species, but since the present specimen is incomplete and does not show the diagnostic features of attachment, it is here described as *Umkomasia* sp. B. Note that a previous species named *Umkomasia* sp. A, was recorded from Nymboida by Holmes and Anderson (2005a, fig. 22C).

Another cluster of similar cupules occurs on AMF 159182 (5771) (Fig. 5C–E) and appears to represent two pairs of cupules. The upper two cupules are closely aligned and the lower two cupules both retain cellular structure, which may represent epidermal cells. This cluster occurs on a slab with a leaf (Fig. 5C) belonging to the *Dicroidium dubium* complex (Holmes and Anderson 2005a). The partially split open cupule with two lobes AMF 159183 (5773) (Fig. 5F) is included here as the size and shape is similar.

At the Southern African Molteno Formation locality of Morija, *Umkomasia grandis* is clearly associated with large *Dicroidium zuberi* leaves (Anderson and Anderson, 1983, 2003). In the Nymboida Flora, the most likely associate foliage of *Umkomasia* sp. B is also *D. zuberi* (Holmes and Anderson, 2005a), which has the largest leaves of all the various species identified.

#### *Umkomasia* sp. c.f. *U. feistmantelii*

Figure 6A–E

#### Material

AMF 159184 (5776) Coal Mine Quarry, collected by John Riley.

#### Description

An open cupule c. 20 by 20 mm, split into four lobes with a short pedicel, the lobes show parallel cellular structure.

#### Discussion

This cupule is 'star shaped' and spread out to show four lobes that are similar in size and shape (Fig. 6A). A portion of an attached pedicel is visible for a

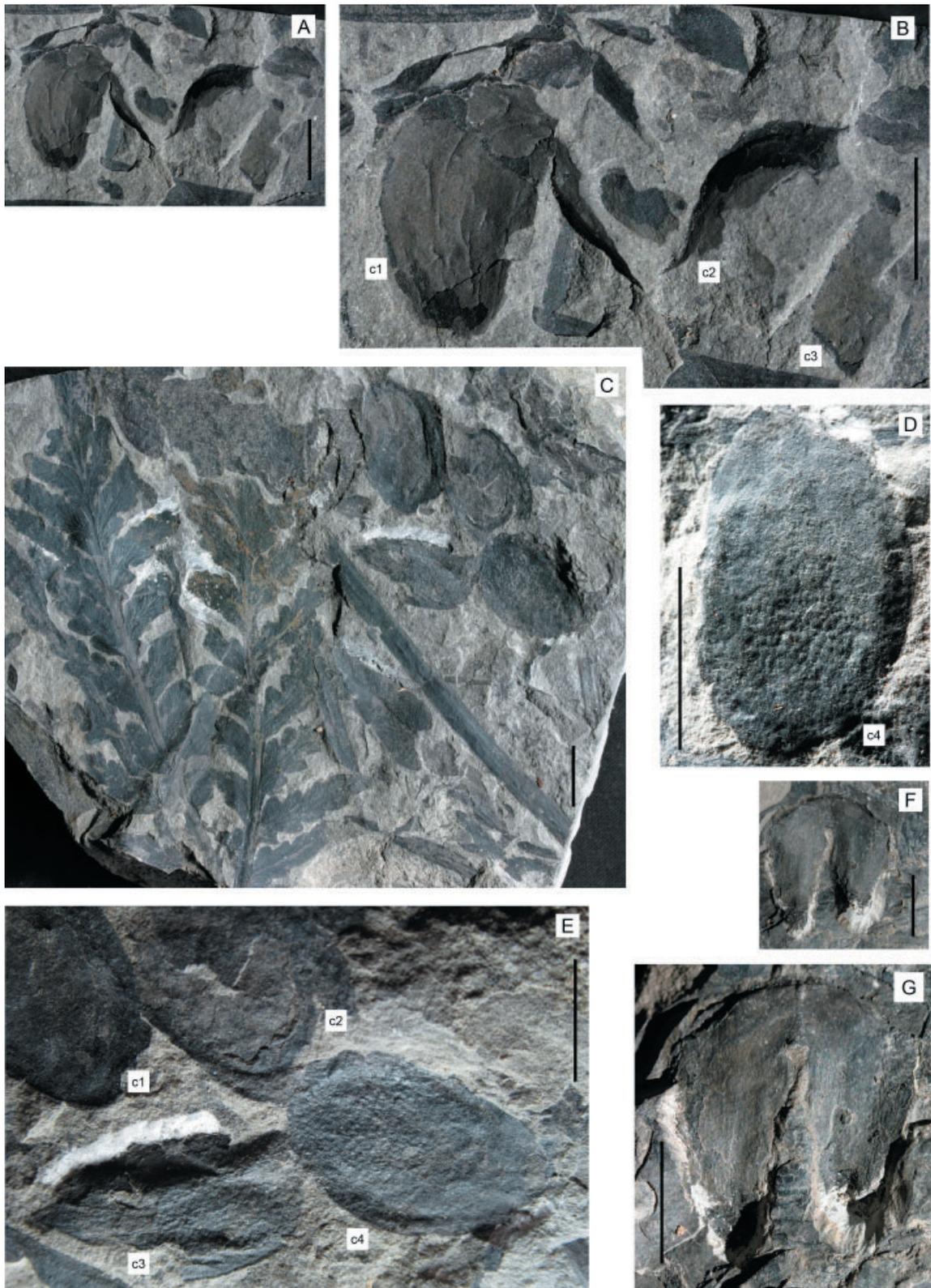


Figure 5. [A–G] *Umkomasia* sp. B cupules; [A–B] AMF 159181, a complete cupule ‘c1’ with attached pedicel alongside a pair of cupules ‘c2’, ‘c3’, similar cellular structure is evident on the cupules ‘c1’, ‘c3’; [C–E] AMF 159182 two pairs of cupules in a cluster showing cellular structure and occurring close to a *Dicroidium dubium* leaf; [E–G] AMF 159183 an isolated cupule split into two visible lobes; (scale bar = 10 mm)

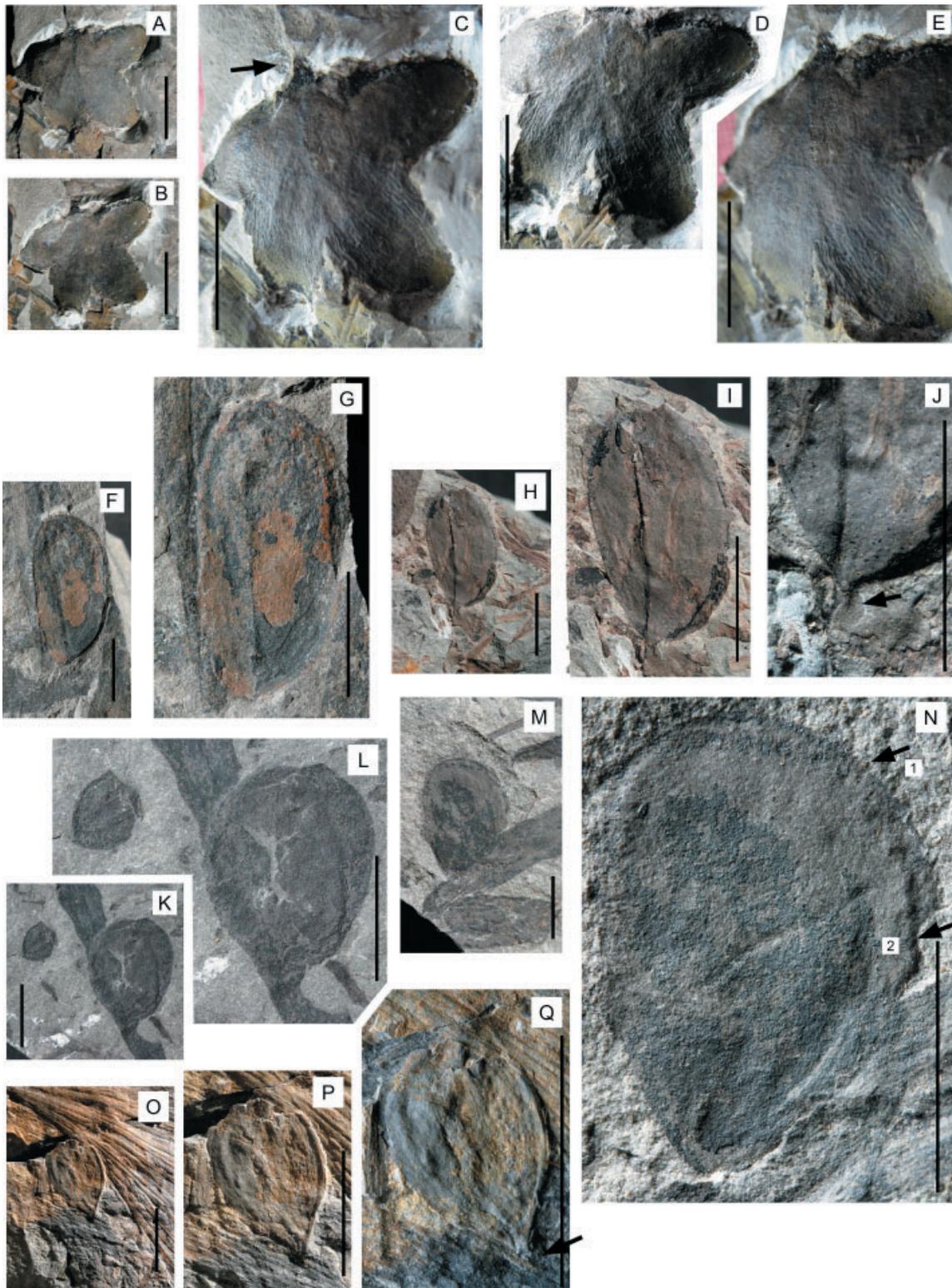


Figure 6. [A–E] *Umkomasia* sp. cf. *U. feistmantelii* AMF 159184, a cupule with attached pedicel (indicated by arrow) and split into four lobes showing cellular structure, angular view in Fig. E. [F–N] *Umkomasia* seeds Form A (large); [F–G] AMF 159186; [H–J] AMF 159187 with arrow indicating micropyle in fig. J; [K, L] AMF 159188a with a small, unidentified seed alongside; [M, N] AMF 159189 with arrows pointing to possible insect damage, of numerous piercing ‘1’ and marginal feeding ‘2’. [O–Q] *Umkomasia* seeds Form B (ovate), AMF 159190 seed with an acute apex and bifid micropyle indicated by arrow; (scale bar = 10 mm).

length of 1 mm (Fig. 6C). The lower two lobes show parallel cellular structure (Fig. 6C–E) and dip into the matrix, an effect of their partial three-dimensional preservation. This cupule is similar in size to *U. feistmantelii* from the Lorne Basin as described by Holmes and Ash (1979) under the name *Karibacarpon feistmantelii* and placed in *Umkomasia* by Anderson et al. (2019). As discussed by Anderson et al. (2020) it is probably associated with *Dicroidium zuberi* var. *feistmantelii* occurring at the same locality. Similar but smaller open cupules (AMF 125092, 125094) have previously been described from Nymboida by Holmes and Anderson (2005a, figs 22 F, D). Another open cupule (AMF 125093) has very distinctive markings, which sets it apart (Holmes and Anderson 2005a, fig. 22E). Similar ‘star shaped’ cupules were described from Mount Piddington in the Sydney Basin by Walkom (1932, pl.5, figs 3–5) and Retallack (1980, fig. 21.9F) and were identified as *Umkomasia feistmantelii* by Anderson et al. (2019). These differ in being smaller than AMF 159184 (5776) and by the numerous cupules being attached to the main axis of the strobilus.

***Umkomasia* sp. c.f. *U. distans***  
Figure 7A, B

**Material**

AMF 159185a, b (5806a, b), Coal Mine Quarry.

**Description**

Dissociated strobilus with a cluster of numerous cupules probably all derived from the same strobilus. Cupules c. 5 x 5 mm with a few split open. Peduncles are present but main axis and pedicels are not clearly aligned.

**Discussion**

This specimen (Fig. 7A, B) is similar to *U. distans* described previously from the Nymboida Flora (Holmes 1987, Holmes and Anderson 2005a). The attachment of the cupules is not clear but, as they lie some distance from the peduncle, they are taken as being pedicellate and not sessile as occurs in *U. sessilis* (Holmes 1987). The cupule size is similar to both species as illustrated in the Key to *Umkomasia* Species (Anderson et al. 2019, fig. 2). Some cupules are split open and show the typical ‘star shape’ (Fig. 7B).

***Umkomasia* seeds Form A (large)**  
Figure 6F–N

**Material**

AMF 159186 (5772) collected by John Riley;

AMF 159187 (5765); AMF 159188a, b (5747a, b); AMF 159189 (4020); all samples from Coal Mine Quarry.

**Description**

Isolated ovate seeds, large 17–23 x 11–13 mm with a narrow wing c. 1 mm wide and bearing a bifid micropyle c. 1 mm long.

**Discussion**

These large seeds are similar in size and shape to the cupules described above as *Umkomasia* sp. B. The typical bifid micropyle is visible on seed AMF 159187 (5765) (Fig. 6J). Possible insect damage by piercing (numerous pits) and marginal feeding is visible along the margin of the seed AMF 159189 (4020) (Fig. 6N).

***Umkomasia* seeds Form B (ovate)**  
Figure 6O–Q

**Material**

AMF 159190 (4173), Coal Mine Quarry.

**Description**

An isolated, ovate seed of medium size 12 by 8 mm, with narrow wing c. 0.5 mm wide and a fairly acute apex bearing a clear bifid micropyle c. 1 mm long.

**Discussion**

This seed (Fig. 6O–Q) differs from *Umkomasia* seeds Form A in being smaller and having a fairly acute apex. It is similar in size and shape to the cupules known for *U. geminata* from the Ipswich Flora (Pattimore and Rigby 2005, fig. 3B) and *U. monopartita* from the Molteno Flora (Anderson and Anderson 2003). These species have not as yet been recorded from Nymboida.

***Umkomasia* seeds Form C (small)**  
Figure 7C–K

**Material**

AMF 159191 (4697) Reserve Quarry; AMF 159192z (5586z) (a single seed near a cluster of three shown in Fig. 8H) Reserve Quarry; AMF 159193 (5733) Reserve Quarry; AMF 159194 (4636) Coal Mine Quarry.

**Description**

Isolated seeds, ovate, small 7–10 mm by 5–8 mm with narrow wing c. 0.25 mm wide and bifid micropyle c. 0.5 mm long.

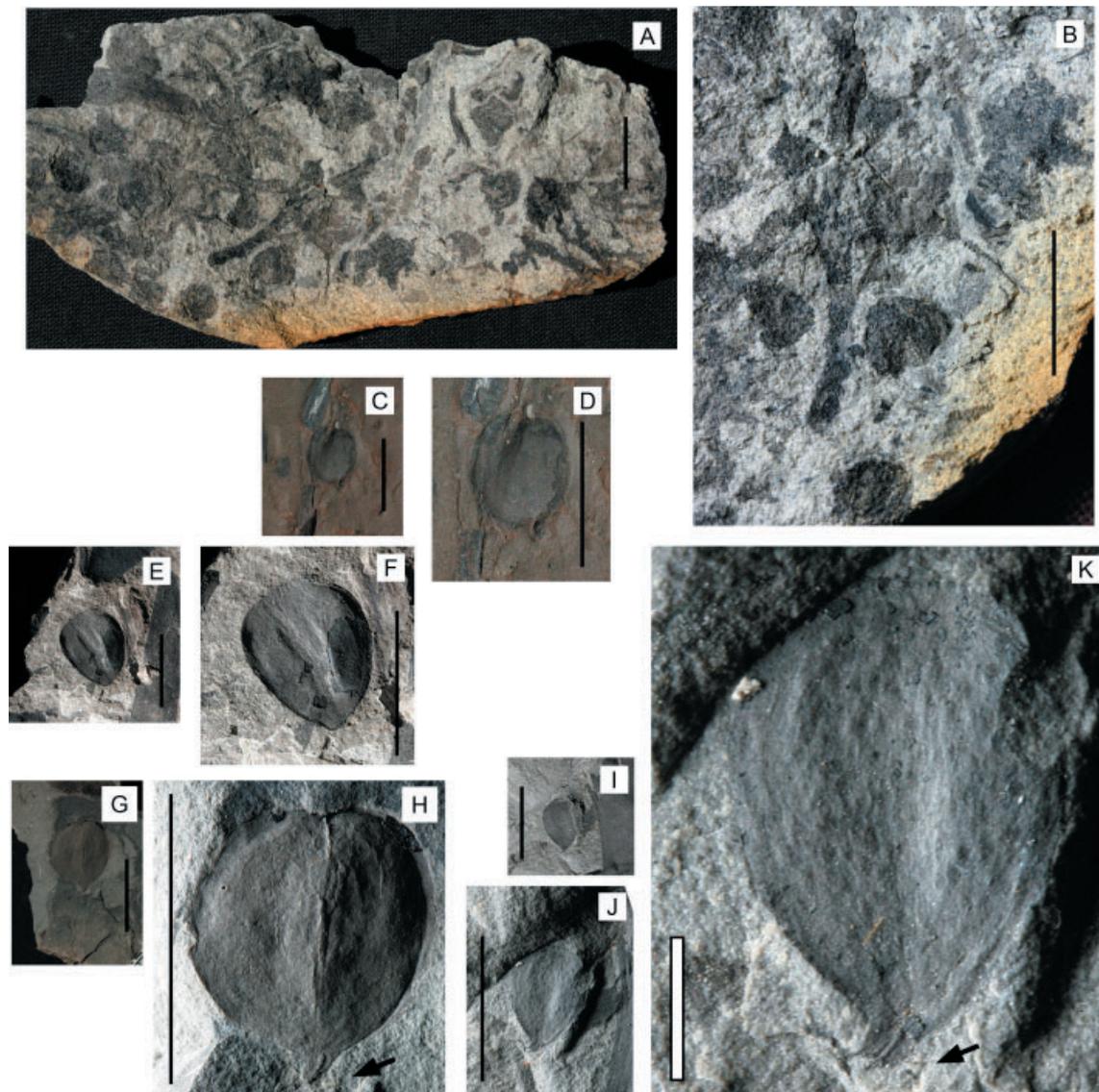


Figure 7. [A, B] *Umkomasia* cf. *U. distans* AMF 159185b strobilus with some open cupules. [C–K] *Umkomasia* seeds Form C (small); [C, D] AMF 159191; [E, F] AMF 159192z single seed (near a cluster of three shown in fig. 8H); [G, H] AMF 159193; [I–K] AMF 159194 with regular cellular structure; (arrows indicate micropyle); (scale bar = 10 mm, except in Fig. 8K = 2.5 mm).

### Discussion

These isolated seeds (Fig. 7C–O) could derive from *U. distans* or *U. sessilis* (recorded from Nymboida, by Holmes 1987, Holmes and Anderson 2005a) as both have cupules similar in size and shape. Such isolated seeds were described previously from Nymboida and commonly have a distinct bifid micropyle (Holmes and Anderson 2005a, fig. 21D). Similar seeds were recorded by Anderson and Anderson (2003) from the Molteno Flora and by Barale et al. (2009) who described the microscopic structure of possible *Umkomasia* seeds (ovules) with

bifid micropyles from a peat deposit in Zambia. Some regular cellular structure occurs on the surface of an isolated seed (Fig. 7K), placed in this group based on shape but could possibly belong elsewhere.

### *Umkomasia* seeds Form D (circular)

Figure 8A–K

### Material

AMF 159195 (5123) (cluster of seeds) Reserve Quarry; AMF 159196 (4805) Reserve Quarry; AMF 159197w, x, y (5586w, x, y) Reserve Quarry, a

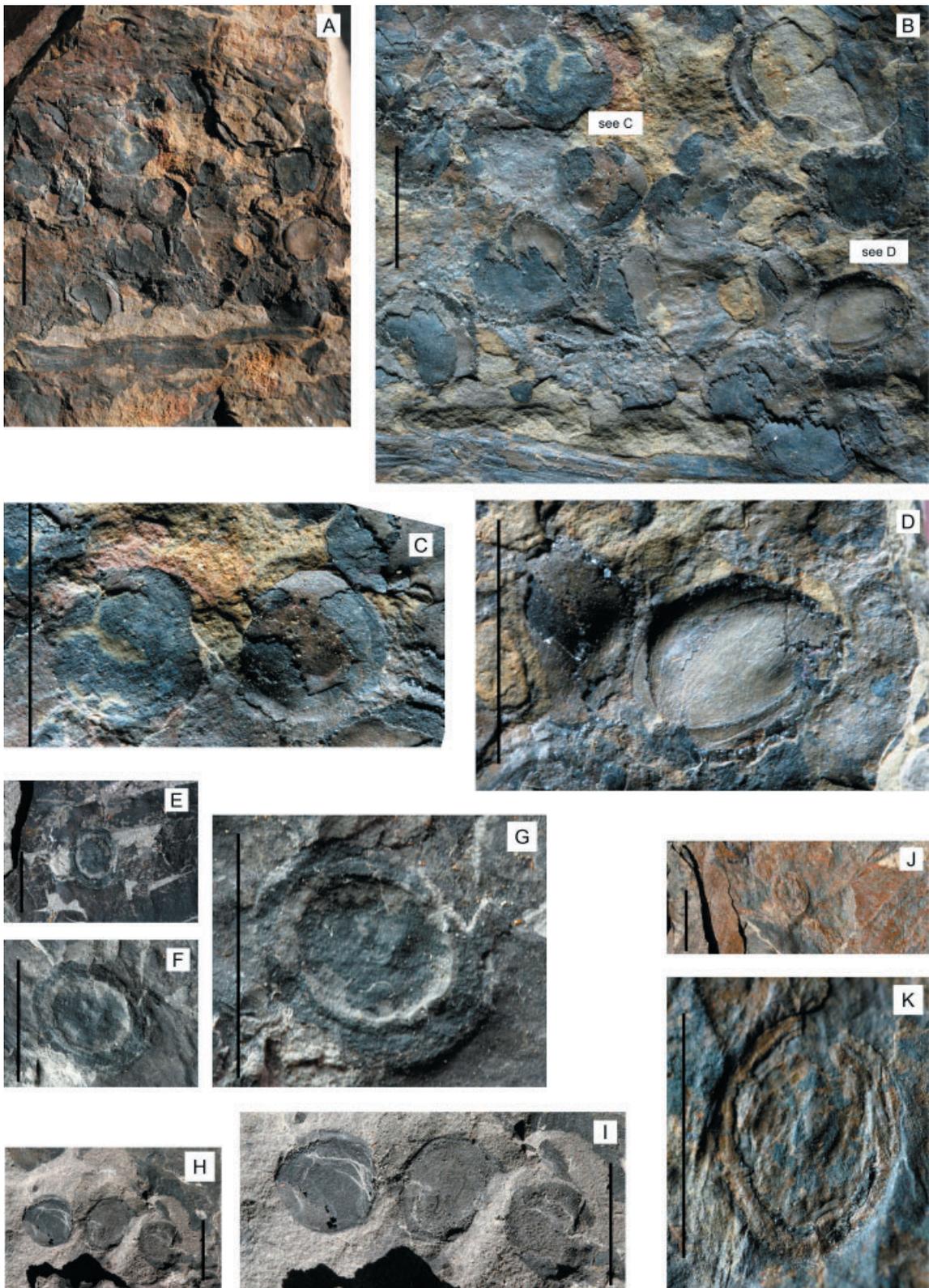


Figure 8. [A–J] *Umkomasia* seeds Form D (circular); [A–D] AMF159195 numerous seeds occurring in a close cluster; [E–G] AMF 159196 an isolated seed; [H–I] AMF 159197 ‘w, x, y’, cluster of 3 seeds (near a single shown in fig 7E); [J–K] AMF 159198 seed with irregular markings; (scale bar = 10 mm).

cluster of three seeds near a single (shown in Fig. 7E); AMF 159198 (5745) Coal Mine Quarry.

**Description**

Isolated seeds circular to slightly oval, small 8 x 7–8 mm with a clear narrow wing c. 1 mm width surrounding the central portion.

**Discussion**

These seeds are similar to the Form C seeds but are more circular with a distinct wing and occur isolated or in clusters. Some irregular markings occur on the surface of an isolated seed (Fig. 8K). The close cluster (Fig. 8A–D) probably indicates an origin from the same parent structure. Another close cluster of three seeds occurs on slab AMF 159197w, x, y (5586w, x, y) (Fig. 8H) near a single seed labeled ‘z’ which is not circular (Fig. 7E).

Somewhat similar seeds were described by Retallack (1980, 1983) from various localities in New Zealand as *Carpolithus macleayi* and were affiliated with leaves of *Linguifolium* based on associations at the same localities. Three taxa of *Linguifolium* have been described from Nymboida (Holmes et al. 2010) making this a possibility but the leaves are rare to very rare (Holmes and Anderson 2013). Based on the distinct wing they can also be compared to the “un-described seeds” illustrated from the Molteno Flora (Anderson and Anderson 2003, pl. 150, fig. 9 is close in size and pl. 149, fig. 1 is c. a third larger). However, in the Molteno Flora there is no apparent association of these seeds with *Linguifolium* as they occur at separate localities. Hill et al. (1965, pl T8, fig 8) illustrated a “Gymnospermous seed” which is of similar size but has a wider more distinct wing. These seeds from Nymboida are provisionally placed in *Umkomasia* even though they may, with more information, prove to belong to some other genus.

***Umkomasia* seeds form E (ovate 3D)**

Figure 9A–N

**Material**

AMF 159199a, b (3534/5) with three similar seeds labeled ‘X, Y, Z’) Coal Mine Quarry; AMF 159200 (4525) a close cluster of five seeds; Coal Mine Quarry; AMF 159201 (5587) single seed, Reserve Quarry.

**Description**

Isolated ovate seeds, small 6–8 mm by 3–5 mm, with narrow wing c. 0.5 mm wide, distinct smooth convex surface.

**Discussion**

On AMF 159199 (3534/5) are a number of seeds with 3 being clear (‘X, Y, Z’). They are ovate with a possible stalk (Fig. 9D). At some angles it may look like a micropyle which it is not. The single seed AMF 159201 (5587) (Fig. 9L) has a clear wing on one side which may represent the outer layer of the seed as indicated by some carbonaceous matrix along the margin of the seed. This wing is not clearly evident in the other seed cluster (Fig. 9H). Alongside the seed (Fig. 9L, to right) is another small indistinct seed, which may belong here. The close cluster of five seeds in AMF 159200 (4525) (Fig. 9H–K) most probably indicates derivation from a single strobilus or fruit.

The characteristic 3D preservation, smooth convex surface and ovate shape clearly link these seeds and distinguish them from all the other forms described here. Pole and Raine (1994, figs 5I–M, 7H) illustrated a cluster of five small, ovate seeds from the Pollock Road locality in New Zealand that closely resembles the cluster recorded here. These seeds may prove to belong to some genus other than *Umkomasia*.

**Order Petriellales  
Family Petriellaceae  
*Rochipteris* sp. A  
Figure 10A–D**

**Material**

AMF 159202 (5774), Reserve Quarry, collected by Alan Melbourne.

**Description**

A well preserved incomplete leaf, base missing, dichotomising irregularly up to three times resulting in 13 leaflets up to c. 7 mm long and 0.2–0.5 mm wide.

**Discussion**

This well preserved incomplete leaf (Fig. 9A–D) has the base missing while the tips appear to be mainly complete. It has leaflets dividing thrice as preserved and in the complete leaf it would be at least to four times. Venation is partially evident as parallel and dichotomising (Fig. 10D) but confirmation of the diagnostic anastomoses occurring in *Rochipteris* cannot be made.

The leaf is regarded as belonging to *Rochipteris* due to the similarity with leaves having very narrow segments as described by Herbst et al. (2001), Anderson and Anderson (2003) and Bomfleur et al. (2014). Various *Rochipteris* species have previously

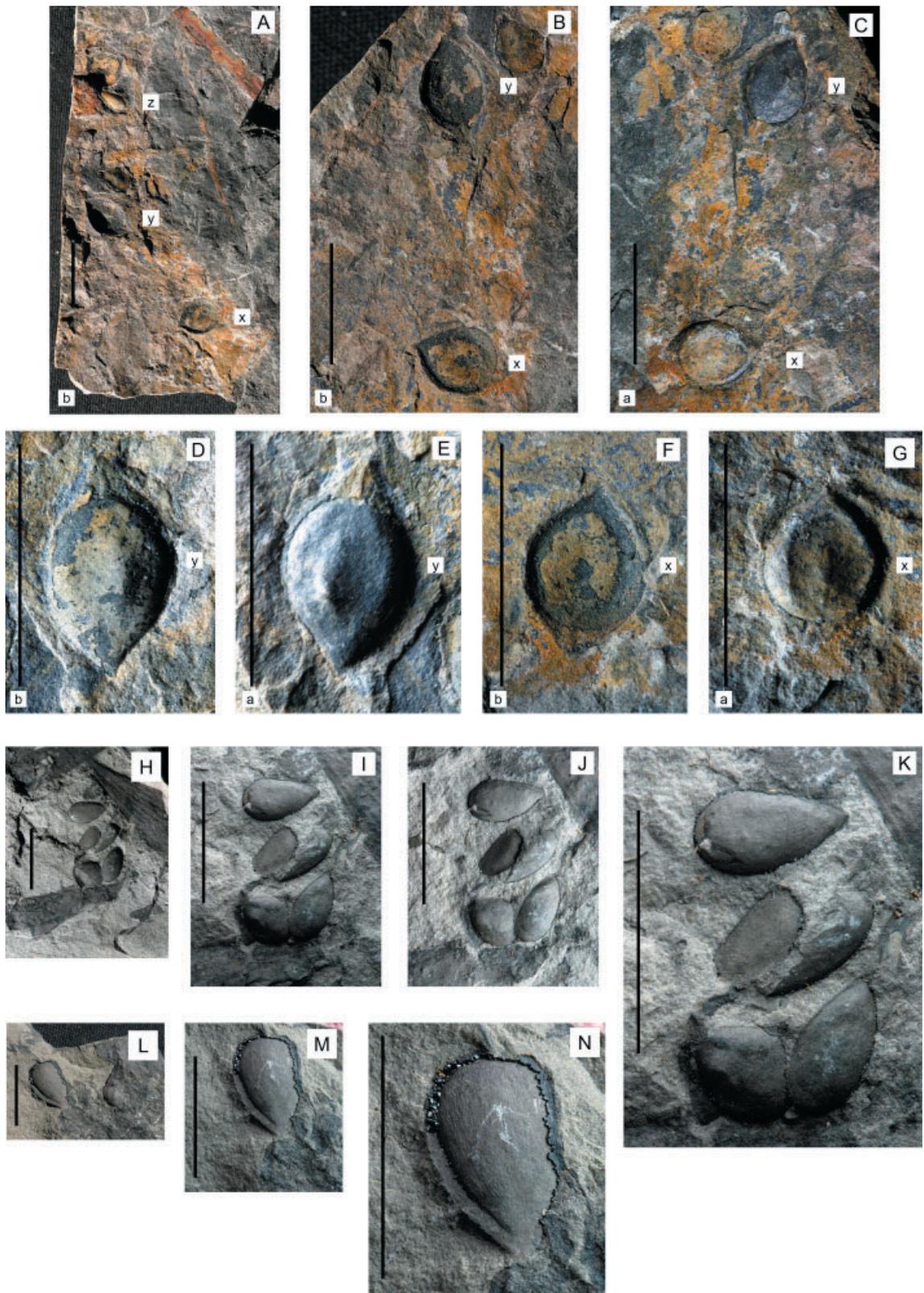


Figure 9. [A–N] *Umkomasia* seeds Form E (ovate 3D); [A–G] AMF 159199a, b, [A, B] three similar seeds ‘x, y, z’ on side b (counterpart), [C] ‘x, y’ on side a, [D–G] close ups of seeds ‘x, y’; [H–K] AMF 159200 close cluster of 5 seeds probably derived from the same fruit; [L–N] AMF 159201 ovate seed with narrow wing and second partial one alongside in fig. L; (scale bar = 10 mm).

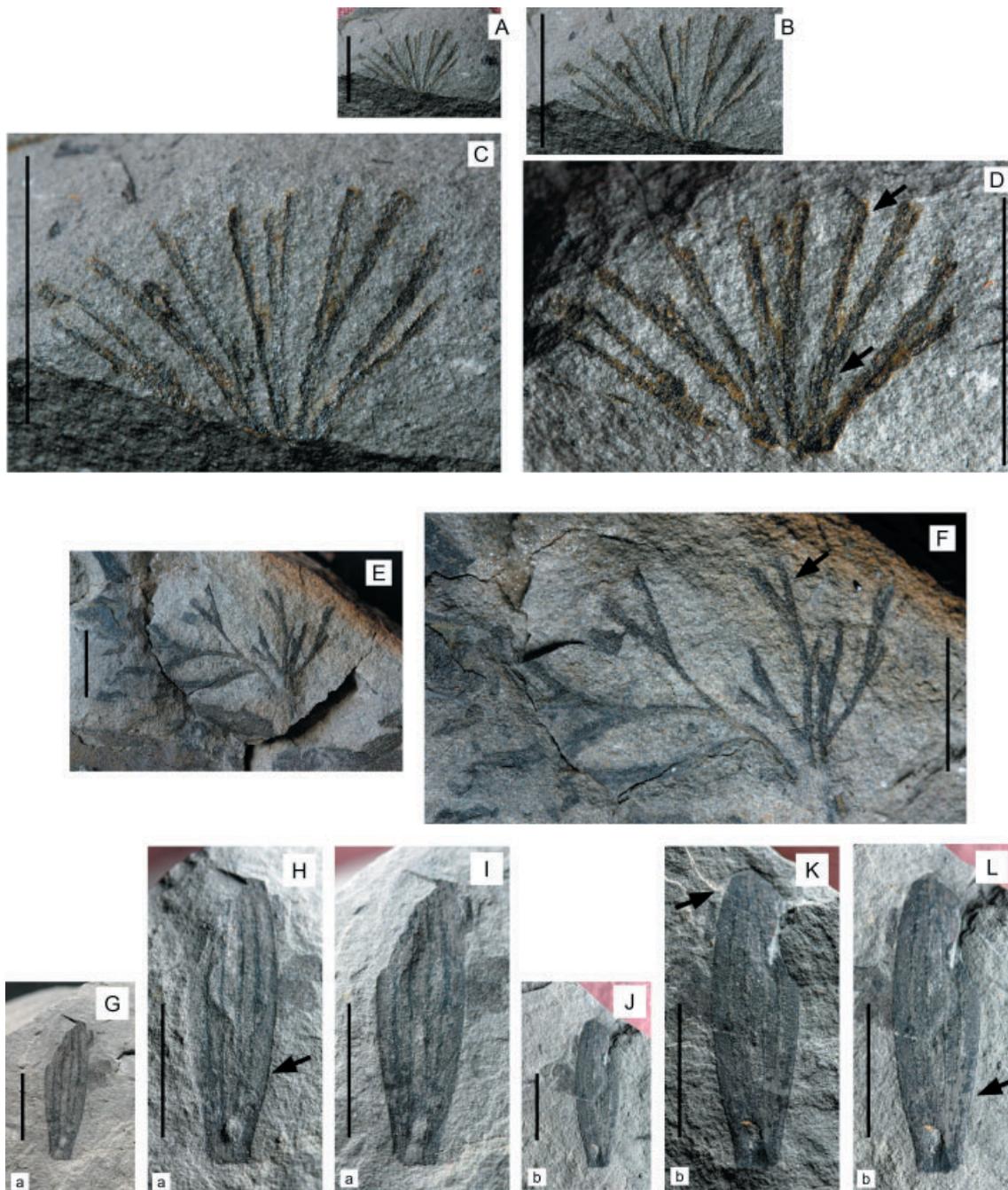


Figure 10. [A–D] *Rochipteris* sp. A, AMF 159202, arrows indicate areas where parallel venation is evident. [E, F] *Rochipteris* sp. B, AMF 159203, arrow indicates where forking vein is evident. [G–L] *Fraxinopsis* sp. A, AMF 159206a, b; [G–I] side a; [J–L] side b (counter part); arrow in fig. H indicates the marginal vein, in fig. K the veins converging near tip and in fig. L an anastomosis; (scale bar = 10 mm).

been described from the Nymboida Flora by Holmes and Anderson (2005b) but no leaves as finely divided as this leaf. A recent study of Molteno *Rochipteris* leaves from South Africa (J.M. Anderson and H.M. Anderson in preparation) shows a great variation in leaf size and division but very rarely show segments

as narrow as this specimen. The more irregular nature of the dichotomy in this leaf favours the placement in *Rochipteris*.

Dichotomising leaflets also occur in *Sphenobaiera* found in the Nymboida Flora by Holmes and Anderson (2007) but *S. nymbolina* is a significantly

larger leaf (over 145 mm long with wider leaflets). This specimen and the following one (*Rochipteris* sp. B) are not considered to be liverworts as they do not occur in groups nor form a rosette as those recorded from the Nymboida Flora, as Thalloid Fossil sp. A and B by Holmes (2000).

***Rochipteris* sp. B**  
Figure 10E, F.

**Material**

AMF 159203 (5776), Coal Mine Quarry.

**Description**

An incomplete leaf c. 30 mm long and 30 mm wide, base missing, dichotomising irregularly up to three times resulting in 14 leaflets each c. 1 mm wide and up to 6 mm long, shows a tripartite division of leaf.

**Discussion**

The leaf is attributed to *Rochipteris* on the basis of the tripartite division of the leaf and the narrow lamina. The leaflets divide at least thrice and venation is partially evident as a single dichotomising vein in the upper part (Fig. 10E). This specimen is separated from the one described above by being twice as large with more irregular dichotomies of the lamina which are wider apart. As was discussed for *Rochipteris* sp. A this specimen was not regarded a liverwort and does not resemble any of the other described Nymboida fossils.

CLASS BENNETTITOPSIDA

This class encompasses gymnospermous plants with compact multi-ovulate “gynoecia” associated with various cycad-like leaves, which typically have syndetocheilic stomata. An overview was given by Taylor et al. (2009, pp. 722–741) and they are recorded rarely from the Triassic but are common in the Jurassic and Cretaceous. Recent work suggests that Bennettitales may extend back to at least the late Permian (Blomenkemper et al. 2021) and may have persisted to the Oligocene (McLoughlin et al. 2011). A useful classification was provided by Anderson et al. 2007 who placed the Bennettitopsida in three orders namely Bennettitales (eight families), *Fredlindiales* (one family), and *Pentoxylales* (two families). The fertile organs are relatively rare in Gondwana but have a wide distribution. A very well preserved *Williamsonia* showing sterile bracts, interseminal scales and seeds was described by Barboni and Dutra

(2013) from the Carurrita Formation of Brazil of Late Triassic or Early Jurassic age. From the Mesozoic of Australia, several *Williamsonia* species and *Fredlindia* were described by McLoughlin et al. (2017). From the Triassic Molteno Formation in South Africa, the female genera *Fredlindia* and *Lindtheca* and the male microsporangiate “flower” *Weltrichia* were described by Anderson and Anderson (2003). The previous record of bennettitopsidan from the Nymboida Flora was limited to the leaf *Halleyoctenis brachypinnata* (Holmes and Anderson 2008). Based on cuticular studies of *Halleyoctenis* from the Molteno Flora by Anderson and Anderson (1989, 2003) the genus was shown to belong to Bennettitopsida. The first records of *Weltrichia* from the Nymboida Flora are described below.

**?Order**

**?Family**

*Weltrichia* (Braun 1847) Harris 1969  
***Weltrichia* sp. A**  
Figure 11A–E

**Material**

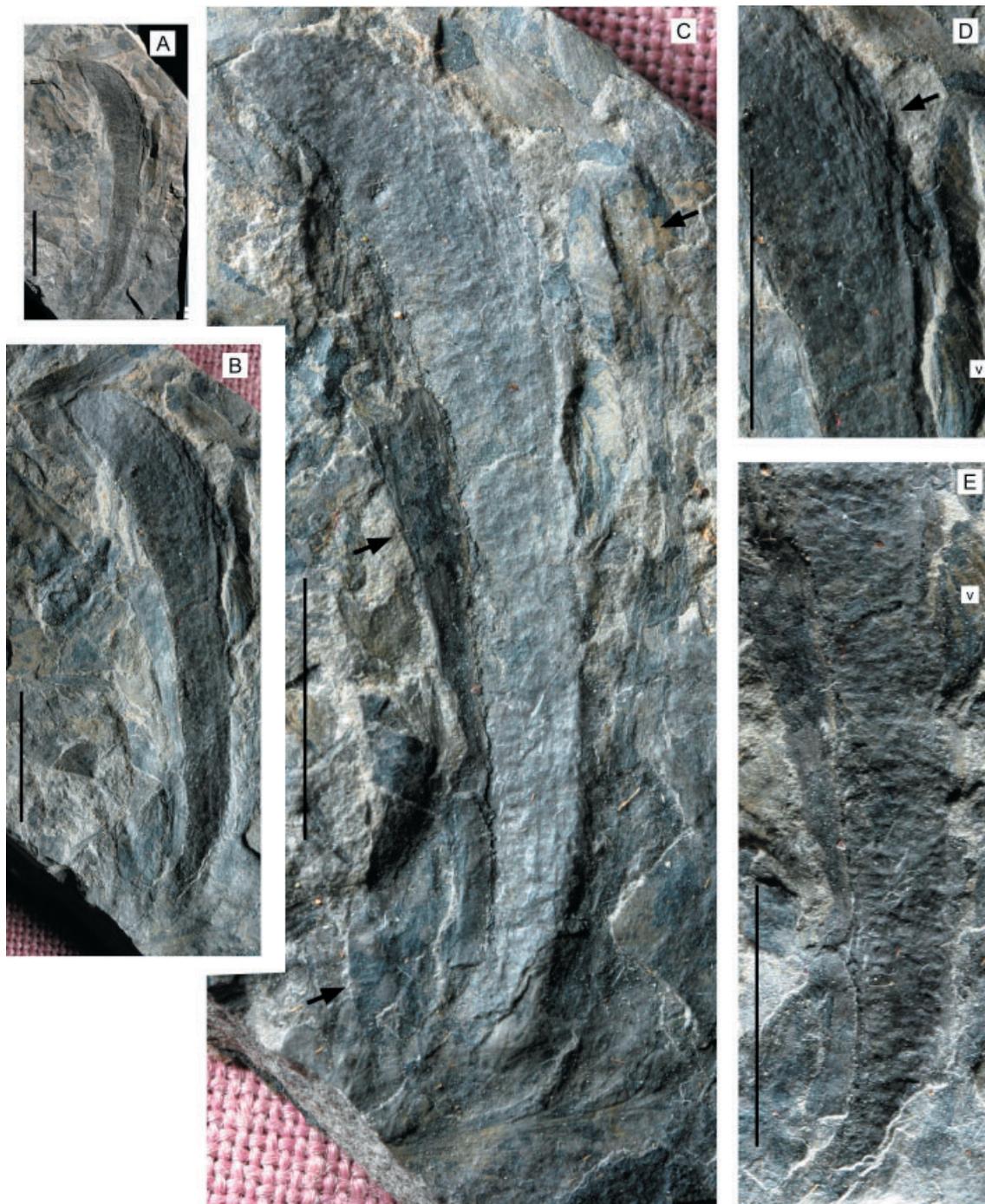
AMF 159204 (5777) Coal Mine Quarry, collected by John Riley.

**Description**

A specimen with a complete lobe, a partial second and a third lobe alongside and a possible fourth on the opposite side. The largest lobe is 49 mm long and 6 mm wide near the upper section, narrowing to 3 mm at the base. Fine irregular markings cover the entire lobe and some striations occur in the upper part. The second lobe is smaller, 35 mm long and 4 mm wide with parallel striations along the margin, especially towards the tip.

**Discussion**

The specimen has one complete lobe, and to the left a fairly complete second lobe plus a third incomplete lobe alongside, with only the bottom part evident, and a possible fourth on the other side which is difficult to discern amongst other plant matter (Fig. 11C the lobes are indicated by arrows). Although the specimen is incomplete there is sufficient preservation to identify it as a *Weltrichia* species based on the shape of the most complete lobe. The faint spherical depressions (Fig. 11C, two near centre of lobe) are similar to the *Weltrichia* sp. indet illustrated by Anderson and Anderson (2003, pl. 135, figs 6, 7) from the Molteno Flora. These depressions can be compared to those in *Weltrichia sol* Harris as illustrated by Meyen (1987, fig. 61k) which has pollen synangia on the upper



**Figure 11. [A–E] *Weltrichia* sp. A. AMF 159204; [C] enlargement with arrows indicating the lobes 2 and 3 to LHS and a possible further lobe on the RHS of the main lobe; [D] arrow indicates the striations (hairs) on the upper part of the main lobe; [E] low lighting highlights the irregular markings covering the main lobe; (veins of a *Dicroidium* leaflet are indicated by ‘v’); (scale bar = 10 mm).**

part of the lobe and “resiniferous organs denoted by circles” on the lower part. The striations along the edge (Fig. 11D, see arrow) are somewhat similar to the hairs occurring on the bracts of *Cycadolepis* (compare

Anderson and Anderson, 2003, pl. 136). These are not to be confused with the veins of a *Dicroidium* leaf fragment alongside (Fig. 11E, in lower right hand corner). A few faint lines parallel to the margin in the

lower part of the lobe may represent veins (Fig. 11C). The main lobe is covered with irregular markings which show up especially under low light (Fig. 11D). Whether this is a wrinkling effect as a result of fossilisation is unknown. But a similar effect is present in the Molteno *Weltrichia* specimens especially in *W. helvetirara* (Anderson and Anderson, 2003, pl. 135, figs 4, 5). The general shape is similar to *Weltrichia regalis* as illustrated by Anderson and Anderson (2003, pl. 135, figs 1–3) from the Molteno Flora but it differs by the lobes being larger and spatulate. From the Australian Triassic two *Williamsonia* species have been described by McLoughlin et al. (2018) and as there is no evidence that these are female structures (no interseminal scales and seeds) they could also represent the male *Weltrichia*. The specimen from Paddy’s Gully near Esk *W. eskensis* has c. 20 lobes up to at least 28 mm long and 3 mm wide. Their other specimen from Denmark Hill in Ipswich *W. ipsvicensis* has c. 11 lobes each up to 38 mm long and 11 mm wide, and shows evidence of venation. This species is somewhat similar to the Nymboida specimen but has more lobes which are wider (11 mm). McLoughlin et al. (2018) suggested *W. ipsvicensis* may be a whorl of *Heidiphyllum elongatum* leaves but this is unlikely since *Heidiphyllum* leaves attached to a stem were described by Anderson and Anderson (2003, p. 90, figs 2, 3) from the Molteno Flora.

***Weltrichia* sp. B**  
Figure 12A–F

**Material**

AMF 159205a, b (5804a, b) Reserve Quarry, collected by Phil Bell.

**Description**

A minimum of four visible lobes attached to a short stalk. The stalk is c. 1.5 mm wide for 4 mm and widens to c. 10 mm to form a basal cup-like structure. A few small scale-like bracts occur on the stalk and at the base of the lobes. The four lobes are at least 60 mm long, tips not preserved, and c. 8 mm wide. The lobes have fine parallel veins.

**Discussion**

This *Weltrichia* specimen (Figs 12A–F) has a minimum of four lobes showing fine parallel striations assumed to be veins especially near the base of the lobes (Figs 12C, F). The lobes arise from a cup-like structure with several small bracts (Fig 12E, position 1) attached to a short stalk, c. 4 mm long and 1.5 mm wide of irregular outline and possibly consisting of tiny bracts (Fig 12E, position 2). Whether this stalk is

joined to a small portion of a woody stem (Fig 12E, position 3), which shows some evidence of leaf or stalk scars, is not clear. Unfortunately the fossil slab does not preserve more of this stem. The lobes appear to have been a thin structure as when compressed in fossilisation they display other impressions such as the diagonal lines crossing the lobes and reaching beyond (as shown in Fig 12B).

The general shape is similar to a *Williamsonia* “flower” however as there is no evidence of any interseminal scales or seeds it is identified as belonging to the male *Weltrichia*. The possible spherical depressions (Fig 12E, position 4) may indicate the presence of resiniferous organs as found in other *Weltrichia* species. The elliptical scars may be insect damage (Fig 12F, see arrow) in the form of oviposition scars as have been recorded on Bennettitalean leaves by Popa and Zaharia (2011) and occur elsewhere in Gondwana (McLoughlin et al., 2015; Anderson and Anderson, 2018). As the lobes are twice as large as *Weltrichia* sp. A., described above, it is considered as probably distinct. For further comparisons elsewhere see discussion under sp. A.

CLASS GNETOPSIDA

The order Gnetopsida has three living representatives, *Gnetum*, *Ephedra* and *Welwitschia*, all of which have rather different vegetative morphology but united by similarities in their fertile structures. *Ephedra* and *Welwitschia* have been recorded as early as the Cretaceous whereas *Gnetum* has no megafossil record. The earliest representatives are extinct families from the Triassic (Anderson et al 2007) which include Fraxinopsiaceae (Anderson and Anderson 2003). Previously, a possible *Yabeiella* leaf was described by Holmes and Anderson (2013a) from the Nymboida Flora but this is the first record of the associated fertile organ (*Fraxinopsis*). from this flora.

**Order Fraxinopsiales**  
**Family Fraxinopsiaceae**  
***Fraxinopsis* sp. A**  
Figures 10 G–L

**Material**

AMF 159206a, b (4387a, b), Coal Mine Quarry.

**Description**

Lamina (wing) broad-elliptic, at base width is 3 mm increasing to 6 mm and somewhat constricted at

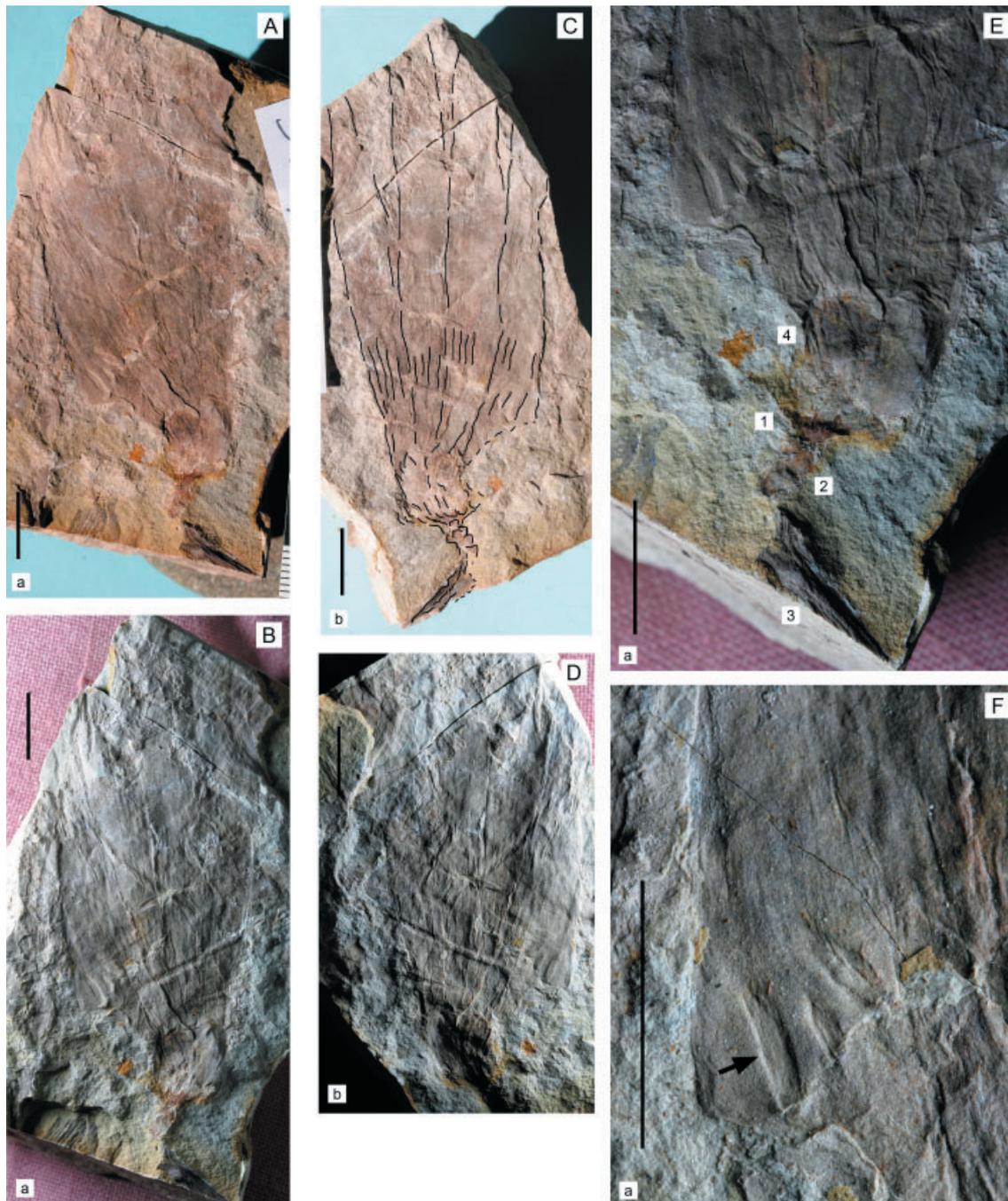


Figure 12. [A–F] *Weltrichia* sp. B, AMF 159205a, b; [A–B] side a; [C–D] side b (counterpart); [C] with black outline to show lobes and stalk at base; [E] enlargement of fig. A to show the cup-like structure with bracts ‘1’, and the short stalk ‘2’, alongside a woody stem ‘3’, and a possible spherical depression ‘4’; [F] enlargement of fig. A, possible oviposition by insects has resulted in the elongate scars on lower part of lobe (see arrow) and above that are fine vein lines; (scale bar = 10 mm).

the apex, length c. 21 mm; the longitudinal veins are slightly closer at the base and then run parallel till near the apex where they converge slightly.

#### Discussion

The lamina (wing) (Figs 10G–L) has four longitudinal veins and marginal veins (Fig. 10H). This single specimen cannot be specifically identified

with other known species of *Fraxinopsis* due to the absence of the basal ovule. Based on the lamina (wing) of similar size and with parallel veins it is best placed in this genus. However, it has fewer veins than previously described species which have 6–16 veins with rare anastomoses e.g. the type species *F. minor* (Weiland, 1929) from the Cacheuta Basin, Argentina. A single anastomosis is evident in the *Nymboidea* specimen on the lower side to the marginal vein (Fig. 10L).

*Fraxinopsis* seeds have been recorded from South America (Weiland, 1929; Oishi, 1931; Jain and Delevoryas, 1967); from the Molteno Formation of South Africa (Anderson and Anderson, 1989, 2003) and the Ipswich Coal Measures of Queensland (Jones and De Jersey 1947). At all of these localities *Fraxinopsis* is associated with the leaf *Yabeiella*. The most comprehensive evidence for the affiliation was provided by Anderson and Anderson (1989, 2003). Some rather unusual, narrow leaves from *Nymboidea* (Holmes and Anderson, 2013a) were provisionally identified as ?*Yabeiella brackebushiana* and these are possibly affiliated with the *Fraxinopsis* described here.

The possibility that this specimen belongs to some other genus was considered but it is unlike any other leaf so far described from the *Nymboidea* Flora. It could be an isolated leaflet of a cycad frond but among the 15 taxa described by Holmes and Anderson (2008) only two genera have small short leaflets: *Pseudoctenis* and *Ctenis*. These differ from the above in the following characters: *Pseudoctenis nettiana* has leaflets up to twice as large and numerous parallel veins (more than 24 in a 10 mm area), whereas *Ctenis marianana* has similar sized-leaflets but numerous anastomosing veins.

#### CONCLUSIONS

This paper is a further contribution to the knowledge of the *Nymboidea* Flora which is important in being the most diverse Ladinian (Middle Triassic) flora in Gondwana with a total of 60 genera and 121 species of vegetative macroplants and provides a window to the humid climate of the time. In a recent summary of Triassic climates (Preto, Kustatscher and Wignall, 2010) information from such Gondwana floras was largely omitted. It is here demonstrated that the lycopods so common in the warm arid Lower Triassic have persisted into the warm humid Middle Triassic alongside a flora dominated by ferns, *Dicroidium*, ginkgos, cycads, conifers that were more akin to the Late Triassic Carnian floras of Gondwana

(Anderson et al., 1999). Furthermore, the *Nymboidea* Coal Measures (Holmes and Anderson 2013b) are highly significant as they are probably the oldest commercial coal seams in the world following the ‘coal gap’ of the Early Triassic. This fossil flora is of global importance in highlighting the re-establishment of peat-forming plant communities some 10 million years after the end-Permian extinction event, which saw the collapse of mire communities across Gondwana and Cathaysia (Mays et al., 2020).

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