

## A “Mystery Fossil” is Evidence for Massive Devonian Trees in Australia

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**ABSTRACT.** In 1991 a Late Devonian sandstone block was found in a gravel quarry in Griffith, New South Wales with a fragment of a deep, repetitive impression within it. It was determined to be a genuine fossil but the impressing organism could not be identified. Within the Australian Museum it became known as the “mystery fossil”. New digital techniques have now been used to create a three dimensional image of the impressed surface which could be rotated through 360°. This revealed the shape of the impressing object. Digital matching of sections of the impressing surface created an expanded image with a structure similar to arborescent lycopsid leaf cushions. If this fossil was produced by an impression of lycopsid leaf cushions, the cushions would be some of the largest so far described. In order to place this fossil in context, the history and structure of Australian lycopsid fossils is reviewed together with that of arborescent lycopsids worldwide. A possible taphonomic process is postulated for the “mystery fossil”, and the effect of tectonic movements in the Late Devonian/Early Carboniferous on Australian forest structure is discussed. If further corroborating evidence of large arborescent lycopsids is found in Australia it will indicate that Australian Late Devonian/Early Carboniferous forests were of much higher profile than previously supposed.

**KEYWORDS.** Lycopsid; lycopod; leaf cushion; lycopsid forest ecosystems.

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In 1991 the Australian Museum received a specimen from the NSW National Parks and Wildlife Service in Griffith. The hand specimen was a sandstone rock from a gravel quarry near Griffith with a deep repetitive impression within it. The quarry was sited on loose gravel and processed scree material from a bedrock of pebbly sandstone with thin conglomerate bands, sandstone and lithic sandstone of Late Devonian age.

This specimen was shown to a number of palaeontologists who were all puzzled as to its origins. A fossil animal print was ruled out, as was the impression of a modern digging tool. All agreed it was a genuine fossil, and a natural mould of something organic. But what that “something organic” was, no-one could suggest. This specimen became the “Mystery Fossil”.



Figure 1. AM F.124805—the Griffith specimen. Scale bar 30 mm.

## Methods and overview

### Abbreviations

The specimens examined during this study are from the Australian Museum, Sydney (*AM*) or the Queensland Museum, Brisbane (*QMB*). They are *hand specimens* (*AM F*, *QMB F*) or *thin sections* (*AM FT*) made from hand specimens.

### Description of specimen

Sourced from a gravel quarry northwest of Griffith, New South Wales, Australia. Collected by Mrs Billie Wright. Submitted 28 October 1991 to the Australian Museum by The NSW National Parks and Wildlife Service. Registered AM F.124805, hereafter the *Griffith specimen*.

The Griffith specimen is a block of coarse sandstone approximately 20 cm long × 17 cm wide × 9 cm deep (Fig. 1). The sandstone block contains a number of waterworn pebbles embedded in the top surface which has a rough, weathered appearance. The block contains an impression comprising three tapering points widening out to the edge of the block. The perimeter walls of this impression are smooth and compacted (Fig. 2a). The central areas of each of the three sections of the impression are rough and weathered. At the point where the wall of one area merges with that of another there is a formed step (Fig. 2b). A small structure

crosses the top of the tapering peaks (Fig. 2c). It could possibly have been formed during the initial impressing by a straight groove across the impressing object.

### Provenance of specimen

The Griffith specimen was submitted to the Australian Museum in 1991 together with a marked up geological map (Geological Survey of New South Wales 1:250,000 Geological Map 1977 2nd edition) and a marked up topographical map (CMA 1:100,000 Kooroongal 8029) showing the collection site as a gravel quarry situated on a ridge composed of the Mailman Gap Conglomerate Member of the Cocopara Group of Late Devonian age.

To confirm the provenance of the specimen for this paper, the Griffith area was visited in October 2015. With the help of the National Parks and Wildlife Service the collection site as marked up by the original donor was located outside Griffith. A now disused gravel quarry was found at this map reference. The landowner confirmed that the quarry was in operation in 1991. The quarrying process consisted of sieving, washing and grading loose scree material and did not include crushing. The quarry was situated at the base of a low, rocky ridge elevated above extensive flat Quaternary sediments used for irrigated crops. The ridge corresponded to a Late Devonian outcrop shown on the above geological map. It was crowned with a conglomerate sandstone and the quarry was set above the base of the ridge on loose surface gravel in which were embedded

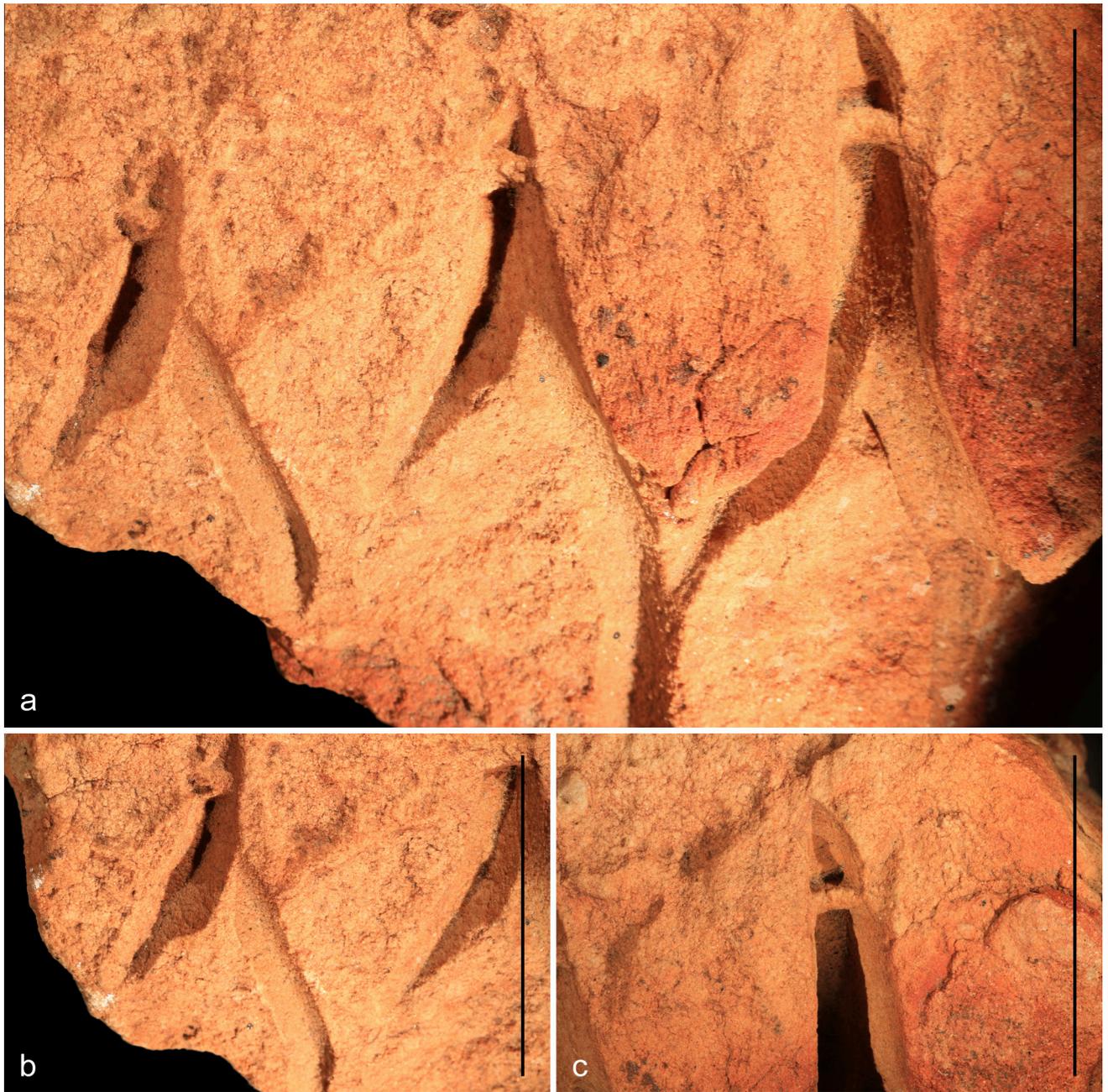


Figure 2. AM F.124805, the Griffith specimen (a) the compacted impression; (b) closeup showing the step at the junction of grooves; and (c) closeup showing the structure that crosses the tapering peaks of the impression. All scale bars 30 mm.

larger, loose rocks. The loose surface was derived from the ridge's underlying bedrock. An examination of many of the loose, larger rocks did not reveal any impressions similar to those on the Griffith specimen, but they were similar in the appearance of grain size and colour. Samples of the loose rocks and gravel were collected for further examination.

A thin section (AM FT.15356) was made from the Griffith specimen, two thin sections were made from two loose rock samples (AM FT.15357, AM FT.15358). The three thin sections were examined under a polarising microscope. Based on crystalline roundness, sphericity, grainsize, matrix and composition, the three fine-grained sandstone thin sections showed properties that indicated a high probability of similarity.

Examination of *Geological Survey of New South Wales* data showed that all sandstone outcrops within a 50 km radius of Griffith are of Late Devonian age.

The correspondence of the reported collection site with the observed gravel quarry, the probable similarity of the microcrystalline structure of the Griffith specimen with collected rock samples, and absence of sandstone outcrops of other ages within 50 km of Griffith indicates there is a high probability that the Griffith specimen is of Late Devonian origin.

### Digital reconstruction

The impression in the Griffith specimen appears to be a fragment of a repetitive pattern which could be expanded both in width and length. It is now possible to use computing power to image and manipulate surfaces in three dimensions. The use of this technology can provide clues to the identification of an object which has formed an original

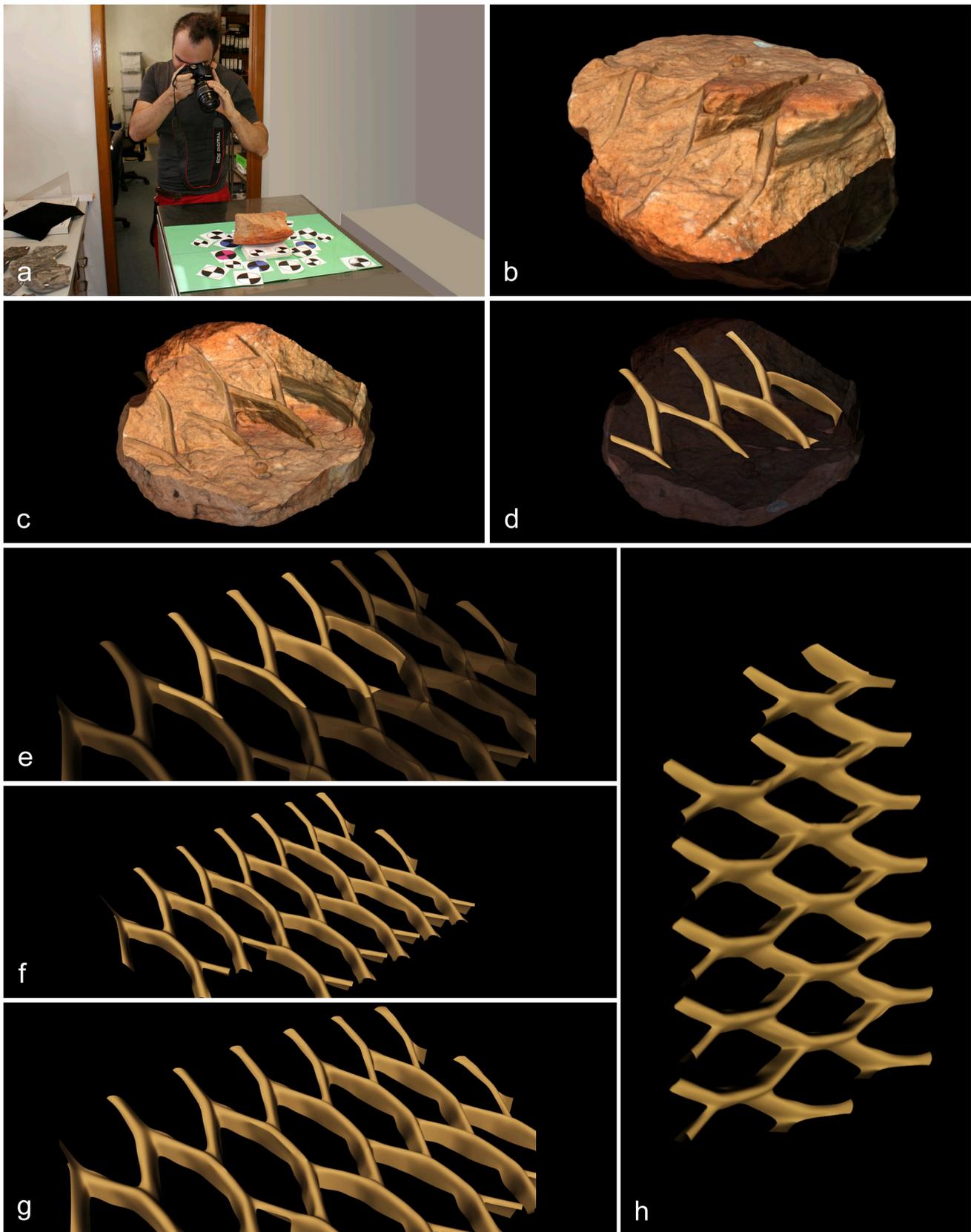


Figure 3. Process of digital reconstruction. (a) Step 1, the specimen was photographed from multiple angles; (b) step 2, a three dimensional image of the specimen surface was constructed; (c) step 3, the three dimensional surface was rotated through  $180^\circ$ , revealing the impressing object surfaces; (d) step 4, the unimpressed surfaces were removed, leaving only an image of the impressing object surfaces; (e) step 5, sections of the image were copied and matched to other sections of the repetitive image, creating a repetitive grid; (f, g, h) the final image was rotated through various angles to aid identification. See also 360-degree video (McLean, 2017).



Figure 4. Possible juxtaposition of a Griffith specimen impression pattern with a typical lycosid leaf cushion specimen (AM F.60491, *Lepidodendron undulatum* from Belgium). (Scale of the Griffith specimen is greater than that of AM F.60491).

impression in a surface.

The specimen was photographed multiple times from many angles in high resolution (Fig. 3a). These images were fed into a computer program which determined the position of every pixel on the surface of the specimen in three dimensional space, effectively producing an image of the “skin” of the specimen which can be rotated at any angle through three dimensions (Fig. 3b). The surface “skin” was then rotated through 180° which has the same effect digitally as taking a physical mould of the surface. This view revealed the shape of the object that made the impression (Fig. 3c). As there were still rough surface areas not impressed by the object these were deleted, leaving only an image of the surfaces of the object which actually made the impression (Fig. 3d).

The next stage was to build up a comprehensive image of the impressing object using selected sections of the surfaces of the object. As the initial impressing object image was a fragment of a repetitive structure, it was possible to select certain sections of this fragmentary image, copy them and place them with overlap at the extremities of other sections of the image. An accurate fit of the overlap was ensured using a colour contour facility—when the fit was exact the overlapping colour was uniform. By this method an image of a large section of the impressing object was built up. The end result was a repetitive grid of sub-rhombic sections (Fig. 3e).

It was then possible to rotate the expanded structure to

observe it from different viewpoints (Figs 3f,g,h). Each sub-rhombic section was slightly flattened on its long side, with the flattened part on one side higher than the adjacent section of the neighbouring sub-rhombic section. This gave the appearance of an overlap and an imbricating effect across the whole structure (Fig. 3h). Each sub-rhomboid measured 75 mm long and 34 mm wide, making the ratio of the length to the width of each sub-rhomboid 2.2 : 1. A 360-degree video was produced and published online (McLean, 2017).

### Initial hypothesis

The smooth, compacted surfaces of the impression and the small structure at the tapering peaks (Fig. 2c) preclude the origin of the impression being that caused by mechanical machinery such as a toothed backhoe. The size and shape of this digitally developed object does not match any animal or part of an animal known to the author. Therefore the next most likely place to look for a match was in the Plantae. Repetitive structures of this nature are found on the trunks of plants that progressively shed leaves or branches. Willis & McElwain (2014) provided an excellent survey of Middle to Late Devonian and Carboniferous arborescent plants. These include the seed-producing pteridosperms (seed ferns) and *Cordaites*, as well as the spore-producing Progymnosperms, Pseudosprochnales, sphenopsids (giant horsetails), filicopsids (ferns), and lycosids (giant clubmosses).

The earliest pteridosperm fossil found so far dates back to the Fammenian, but arborescent seed ferns radiated and diversified in the Carboniferous. The pteridosperm *Medullosa* grew to 10 m with a 0.5 m diameter trunk and shed branches containing fern-like leaves. However, the branch bases formed a spiral line around the trunk (Willis & McElwain, 2014), unlike the rhombic pattern of the Griffith specimen. *Cordaites* were present from the Late Carboniferous to the Permian with trunks up to 30 m tall and 1 m in diameter (Willis & McElwain, 2014). Single branches radiating near the top of the trunk did not leave a distinctive trunk pattern when shedding and their age period did not match that of the Griffith specimen. The Progymnosperms could grow up to 8 m high and 1.5 m diameter, and had a gymnosperm-like stem or trunk. Helically arranged, deciduous branches grew from the upper part of the main trunk (Willis & McElwain, 2014). Excised branches did not shed close to the trunk and did not leave a regular trunk pattern. In the Middle Devonian *Pseudosprochnus*, studied in Gilboa, New York State (Stein *et al.*, 2012), grew up to 8 m high with a crown of leafless, photosynthetic branches. They shed whole branches at the crown (Willis & McElwain, 2014), leaving a lumpy, irregular branch base pattern. Arborescent sphenopsids had a distinctive stem structure comprising regular horizontal nodes from which whorls of branches protruded. The trunk had a horizontally segmented appearance with segment traces completely unlike the Griffith specimen. Filicopsids were present in the early Carboniferous fossil record, some of which grew to 10 m in a growth habit similar to the modern tree ferns. When the fronds abscised from the crown of the plant they left a distinctive circular leaf scar with a “v” shaped vascular trace (Willis & McElwain, 2014). This circular trace cannot be compared to the rhombic shape of the Griffith specimen. Lycopoid (or lycopod) fossils from the Late Devonian and Carboniferous, however, did show that many of the specimens exhibited a similar pattern of sub-rhombic or rhombic structures on their trunks and limbs to that of the Griffith specimen (Fig. 3). These were produced by the formation of photosynthesising leaf cushions to which were attached leaves which grew from the trunks and limbs and were progressively shed during growth (Willis & McElwain, 2014). Re-enforcement of this concept was provided by the matching of the shape of the impression against a photo of a typical lycopoid stem (Fig. 4). The largest leaf cushion structure occurred on the upper trunk, and they grew progressively smaller as the branch diameter reduced (Eggert, 1961). The most likely plant candidate for producing the Griffith specimen was therefore a lycopoid.

The initial hypothesis is that the object which formed the impression in the Late Devonian sand near Griffith was the trunk or shed periderm of a large lycopoid that was first buried in sand and compressed, and which then slowly rotted away leaving an impressed void in the sandstone. The Griffith specimen is a fragment of this trunk impression.

It is worthwhile examining how this hypothesis matches past discoveries in Australia and the rest of the world, with particular reference to the size, shape and orientation of the leaf cushions as the primary diagnostics, and under what biogeographical and environmental conditions this specimen would have grown.

## History of lycopsid discoveries in eastern Australia

In the 19th and early 20th Centuries many fossil lycopsid specimens were collected from the eastern Australian states and identified in relation to the species already described from the northern hemisphere. Characteristic leaf cushions were the main diagnostic.

Sir Thomas Mitchell, the New South Wales Surveyor General and explorer, recorded the finding of *Lepidodendron* fossils at Wallamoul on the Peel River, near Tamworth, NSW, in 1835 (Clarke, 1861b). Clarke (1848) reported the occurrence of *Lepidodendron* at the Manilla, Namoi and Gwydir Rivers of NSW, as well as the Paterson and Allyn Rivers. In 1851 McCoy wrote to Clarke from Cambridge identifying an Australian fossil as very much like the northern hemisphere’s *Lepidodendron tetragonum*. In 1853 Stuchbury, the Government Geological Surveyor of NSW, recorded the finding of several specimens at Oakey Creek, near Cobbadah, NSW, with rectangular leaf cushions. Clarke (1861a) provided a list of lycopsid fossil discoveries he had made in New South Wales. These were found at Peel River, Goonoo Goonoo and Wellington. McCoy (1861) named specimens from the Upper Devonian rocks of the Avon River, Victoria as *Lepidodendron australe* (and elaborated on this classification in 1874). In 1870, Daintree, then the Government Geologist of Queensland, reported the collection of specimens of *Lepidodendron* from Mt Wyatt, Canoona and Broken River in Queensland. These specimens were subsequently identified as the Canadian Upper Devonian species *Leptophloem rhombicum* by Carruthers (1872). McCoy (1874) described in detail and figured a branched specimen from the Avon River, Victoria, naming it *Lepidodendron tetragonum* Sternberg var. *australe* after a European species. The stem was 2 inches (c. 5 cm) in diameter having rhombic leaf cushions with straight, thick boundaries (Fig. 5a). The specimen was found in micaceous Carboniferous sandstone. Tenison-Woods (1883) reported specimens identified as *Lepidodendron nothum* Unger by Carruthers (1872) being found at Mt Wyatt, Canoona and Broken River (Queensland) (e.g., Fig. 5h), and Cowra, Canowindra and Goonoo Goonoo Creek (New South Wales) (e.g., Fig. 5d). Leaf cushions were contiguous, rhombic with a single central vascular scar.

Kidston (1886) emended *Lepidodendron nothum* Unger from Queensland described by Carruthers (1872) to *Lepidodendron australe* McCoy. Kidston (1889) noted that specimens from Goonoo Goonoo (NSW) were probably referable to *Lepidodendron volkmannianum* Sternberg, comparing leaf scars (Fig. 6a). The specimens were obtained from a “Lower Carboniferous or Upper Devonian(?)” horizon (Kidston, 1889: 115). Feistmantel (1890) listed specimens found at Barrington River, Mt Lambie, Stroud and Rouchel River (all in New South Wales), Canoona River and Mt Wyatt (both in Queensland), as well as other previously known sites, and identified five species (*Lepidodendron australe*, *L. nothum*, *L. dichotomum*, *L. veltheimianum* [e.g., Figs 6b,c], *L. volkmannianum* [e.g., Fig. 6g]). He described the leaf cushions of *L. australe* as rhombic with thick boundaries and oval or rhombic vascular cicatrices. Etheridge (1891) disagreed with the earlier identification of the Victorian species *L. tetragonum* var. *australe* and the Queensland



Figure 5. Australian Late Devonian lycopsid specimens. Original taxonomic identifications are used. (a) AM F.68472, cast of holotype *Lepidodendron* (*Bergeria*) *tetragonum* Sternberg var. *australe* McCoy, 1874 from the Avon River, Victoria; (b) AM F.106082, *Lepidodendron* sp. from Cowra, NSW, showing distal extremity with microphyll leaves; (c) AM F.46924, *Leptophloem australe* compression from Hattons Corner, NSW; (d) AM F.6485, *Leptophloem australe* from Goonoo Goonoo, NSW, showing vascular scars; (e) AM F.38375, *Leptophloem australe* from Barraba, NSW, showing vascular scars; (f) AM F.14899, *Leptophloem australe* from Bingara, NSW; (g) AM F.58480, *Lepidosigillaria yalwalensis* from Bunga Head, NSW; (h) AM F.68538, *Lepidodendron nothum* from Drummond Ranges, Queensland (Tenison-Woods, 1883); (i) AM F.49870, *Lepidodendron volkmannianum* from Yetholme, NSW, showing imbricating effect. All scale bars 20 mm.



Figure 6. Australian Late Devonian and Early Carboniferous lycopod specimens. Original taxonomic identifications are used. (a) AM F.35636, *Lepidodendron volkmannianum* from Goonoo Goonoo, NSW (Kidston, 1889: fig. 1); (b) AM F.68489, decorticated *Lepidodendron veltheimianum* Sternberg from the Drummond Ranges, Queensland (Tenison-Woods, 1883); (c) AM F.49639, *Lepidodendron veltheimianum* Sternberg from the Upper Hunter Valley, NSW; (d) AM F.77988, *Stigmaria* sp. from Glenbawn Dam, NSW, showing rootlet scars; (e) AM F.2, *Leptophloem australe* from Cowra, NSW; (f) AM F.63707, *Lepidodendron* sp. from Stroud, NSW, showing vascular scars; (g) AM F.57266, *Lepidodendron volkmannianum* from Stroud, NSW; (h) AM F.63741, *Lepidosigillaria yalwalensis* from Bunga Head, NSW. All scale bars 20mm.

species *L. nothum*, classing them both as one separate Australian species—*Lepidodendron australe*. He compared many specimens in his collection and came to the conclusion that all belonged to one Australian species, and they all were of Early Carboniferous age (except for two doubtful cases at Mt Wyatt in Queensland and Mt Lambie in NSW). David & Pittman (1893) extensively researched the above papers and carried out their own field trips into many of the areas. In the Mt Lambie area they found *Lepidodendron* fossils at a geological horizon that convinced them this species occurred in Late Devonian rocks of Australia.

Smith & White (1905) concluded that the Carruthers (1872) and Etheridge (1891) specimens should be referred to the genus *Leptophloem*, emending the taxon to *Leptophloem australe* McCoy. Walton (1926) suggested that it was advisable to keep Australian species separate from American plants, although there were several points of agreement between them. He agreed with Smith & White (1905) that the correct name for Australian specimens identified as *Lepidodendron australe* and *L. nothum* should be *Leptophloem australe* McCoy (e.g., Figs 5c,e,f). The leaf cushions were described as rhombic (Walton, 1926). Barnard (1928) studied the cellular structure of a silicified stem specimen from Welshman's Creek, near Wallarobba, NSW, and found affinities to *Lepidodendron brevifolium*. The specimen was discovered nearby to outcropping beds of Lower Carboniferous cherty shale which contained abundant lepidodendroid impressions. Walkom (1928a) described some specimens found in 1901 by Andrews at Yalwal (NSW). Andrews (1901) had identified the lithography as Devonian. Walkom (1928a) placed two of the specimens in *Protolopidodendron*, *P. lineare* and *P. yalwalense*. The distinctive feature of *P. lineare* was the placement of leaf cushions on a series of vertical ridges. *Protolopidodendron yalwalense* had vertically elongate-rhomboidal leaf cushions about 7 mm long by 4.5 mm wide. He described a third specimen as (?) *Lepidodendron clarkei* and likened it to *L. australe* except for cushion size.

Interest in the Australian Late Devonian / Early Carboniferous lycopsid fossils waned early in the 20th century, possibly due to the realisation that, unlike the northern hemisphere, they were not associated with massive coal resources. By then, taxonomic identification had reached a stage where many specimens initially named as northern hemisphere species were reclassified as *Leptophloem australe* McCoy, a species with a regular, strictly rhombic leaf cushion pattern (e.g., Fig. 6e). Other described specimens, however, did exhibit sub-rhombic leaf cushion patterns with rounded and tapered corners, such as the specimens from Yalwal and Wallarobba.

Although study of Australian lycopsids dropped away in the early 1900's, sporadic interest was shown in the 1960's and the 1990's. McKay (1964) was the first author to identify an Australian lycopsid specimen as *Lepidophloios*. The specimen was an impression of a branch in fine quartzose sandstone from the Mt. Lambie region covered in rhomboidal, horizontally elongate, mildly imbricate leaf cushion impressions 11 mm wide and 7 mm high. Leaf scars were not preserved. He questioned the identification of *Leptophloem* ("*Lepidodendron*") *australe* specimens, saying many specimens could be of the *Lepidophloios* genus. Clifford (1996) used a natural cast of a *Leptophloem australe* collected by Leichhardt during his 1847 expedition

to Port Essington to determine a benchmark for the accurate calculation of the diameter of specimens prior to compression.

A search through the undescribed general collections of the Australian Museum and the Queensland Museum revealed that, although *Leptophloem australe* specimens were numerous and had been found at many sites other than those described, there were a range of specimens with sub-rhombic leaf cushions (e.g., Figs 5g, 6h). These general collections also included several examples of *Stigmara* root systems (e.g., Fig. 6d) and decorticated *Knorria* stems. The Late Devonian / Early Carboniferous collections also included psilophytes, rhacopterids, *Calamites* and tree ferns. The lycopsid forests of Australia were not monospecific. All lycopsid specimens were of small branches or twigs, and no sections of main stems (or trunks) of mature trees were evident. The sites ranged extensively along the east coast of Australia from present day northern Queensland (18°S) to eastern Victoria (37°S), a north/south distance of 1600 km (Fig. 7).

### Arborescent lycopsids worldwide

Because they were primarily responsible for the Euro-American coal deposits of the Carboniferous Period, the arborescent lycopsids have been comprehensively studied in the northern hemisphere. There was a rapid evolution and radiation of these plants in the Late Devonian and Early Carboniferous, culminating in their dominance of worldwide tropical swamps in the Westphalian Age, with a subsequent decline to extinction in the Permian Period, a time span of over 100 million years (Phillips & DiMichele, 1992).

The class Lycopsida contained two orders that included arborescent plants—the Lepidodendrales and the Isoetales. The Lepidodendrales (Devonian to Permian) had three arborescent families—Lepidodendraceae, Diaphorodendraceae and Sigillariaceae (Taylor *et al.*, 2009). The Isoetales included the arborescent Leptophloeaceae. The Leptophloeaceae had been placed in Lepidodendrales by Li *et al.* (1986), but subsequently Wang *et al.* (2005) emended this classification to Isoetales. These two orders included arborescent genera that formed extensive world-wide tropical forests in the Late Devonian and Carboniferous Periods, with some trees that reached 35–40 m in height with a base diameter of 2 m (Thomas & Watson, 1976).

Of the Lepidodendraceae, the most commonly encountered genus is *Lepidodendron* (Fig. 8a) (Willis & McElwain, 2014), fossils of which have been found in North America, Europe, China and Australia. In fact, this classification has been used to "house" many stem specimens that are arborescent but difficult to assign to actual species and exhibit a basically rhombic leaf cushion morphology which forms a rising spiral up the trunk and along the branches (Cleal & Thomas, 2009). Another common genus in this family was *Lepidophloios* (Fig. 8b), which had a similar growth habit to *Lepidodendron*, but had a leaf cushion structure where the longer axis was horizontal (Taylor & Taylor, 1993).

A new genus *Diaphorodendron* (Fig. 8c) was established by Dimichele (1985) for some structurally preserved specimens previously placed in *Lepidodendron*. Later this genus was restructured again to recognise two genera (*Diaphorodendron* and *Synchysidendron*) and both were placed in a new family Diaphorodendraceae (Dimichele & Bateman, 1992).

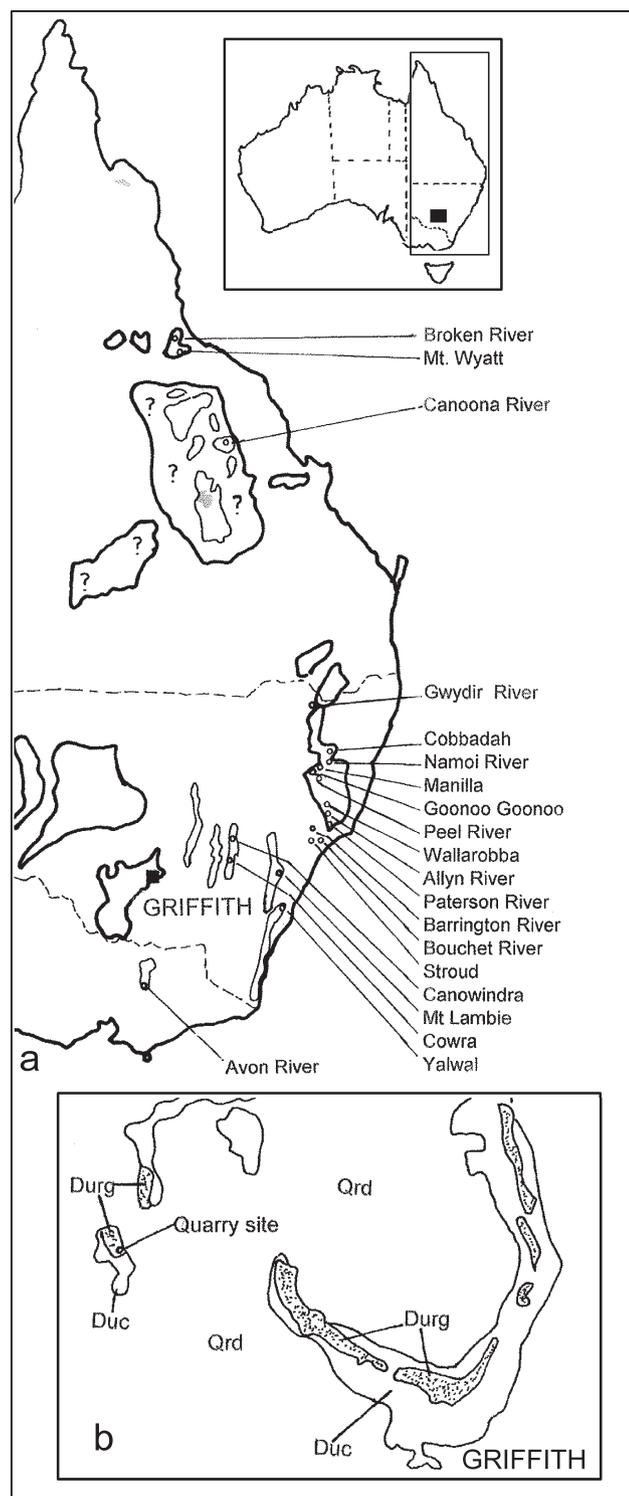


Figure 7. Map showing eastern Australian geological features. (a) Late Devonian–Early Carboniferous shallow marine and continental outcrops in eastern Australia showing positions of sites of described specimens (source of geological data: Day *et al.*, [1983], Scheibner [1998]). (b) Geological structure in Griffith locality showing the quarry site—Durg, Devonian pebbly sandstone with thin conglomerate bands, sandstone and lithic sandstone; Duc, Devonian Cocopara Group sediments mixed with residual deposits; Qrd, Quaternary deposits (source of geological data: Geological Survey of New South Wales map Narrandera 1:250,000 edn. 2, 1977).

Sigillariaceae contained *Sigillaria* (Fig. 8d), which was not as large as the Lepidodendraceae being only up to 20 m tall. Its leaf cushions were hexagonal in outline, and a large number of closely spaced leaves grew from the top of the trunk (Phillips & Dimichele, 1992).

Leptophloeaceae contains one other genus relevant to the study of Australian specimens. This is *Leptophloem*, a species of which was initially described by Dawson (1862) as *Leptophloem rhombicum*.

All genera exhibited leaf cushion structures covering the main stem and branches of the entire plant.

### Structure and growth patterns of arborescent lycosids

Eggert (1961) produced a paper generally accepted as a definitive description of the growth patterns and structure of a range of the most well-known North American *Lepidodendron* and *Lepidophlois* species. He placed particular importance on the question of changing morphology at various levels in the plant and the problem often faced in palaeobotany of merging isolated specimens into an overall plant structure. Eggert assembled a large number of representative specimens of four *Lepidodendron* species and three *Lepidophlois* species and studied their internal and morphological structures in an attempt to determine the ontogeny of this plant family, including the progressive development of primary and secondary xylem, cortical tissues and leaf cushions during growth.

A reconstruction of the mature plant was developed which showed a sub-aerial system of stigmarian axes with spirally placed rootlets from which a columnar trunk rose to a height of up to 20 m, a level at which the column branched dichotomously into smaller and smaller crown branches. Internally, the primary xylem expanded from a thin cross-section at the base to a maximum size just before the first dichotomous division. From then on the primary xylem decreased progressively as the branches divided. The girth of the entire trunk was expanded and maintained at an approximately equal cross-section by growth of secondary xylem and cortical tissue which formed the periderm. The periderm had on its surface photosynthetic leaf cushions which formed a spiral pattern from which protruded straplike leaves. The apex comprised branches covered in smaller and smaller spirally placed leaf cushions from which protruded microphyll leaves. The distal ends of branches carried sporophylls with male and female sporangia (Eggert, 1961, text fig. 75).

Although early studies of arborescent lycosid morphology figured the trees of most species with dichotomously branching crowns and no early side branches, later studies have determined that some genera produced lateral branches before crowning. These genera include *Leptophloem*, which Wang *et al.* (2005) indicated took a pseudomonopodial architectural form with a trunk up to 25 m tall and a base diameter of up to 0.4 m. Sparse, lateral branching of the trunk occurred rather than equally dichotomous branching as previously thought. Other genera were *Diaphorodendron* (Fig. 8c) and *Synchysidendron* which DiMichele *et al.* (2013) reported as having closely spaced, deciduous lateral branches.

The leaf cushions that spiralled up the trunks and along the branches of these lycopsids comprised a photosynthetic cushion surface containing stomata from which thin straplike leaves protruded. The leaf was supported by a vascular bundle, paracnos, and a ligule connection from the tree stem via the leaf cushion. These structures show up as scars on the fossilised leaf cushion (Fig. 9), although frequently they are not preserved. Expansive secondary growth of the dense, resinous periderm often separated the leaf cushions as the main stem grew and expanded (Thomas, 1970) (Fig. 9c,d). Lycopsid genera exhibited various leaf cushion morphologies. *Lepidodendron* leaf cushions had their longest dimension vertical (Fig. 9a,b,c), as compared to *Lepidophloios* on which the leaf cushions were oriented with the longer axis horizontal (Fig. 9e) (Taylor & Taylor, 1993). Each leaf cushion of *Lepidophloios* was directed downwards on the stem and overlapped the cushion below, forming an imbricated pattern similar to shingles on a roof (Taylor *et al.*, 2009). Other leaf cushions formed rhombic and sub-rhombic shapes with varying dimensional ratios (e.g., Fig. 9f,g), depending on the genus. Leaf cushion morphologies have been extensively used to identify families and genera of lycopsids, particularly when the specimen is an impression such as the Griffith object. The initial hypothesis identifying the Griffith specimen as a lycopsid is based on the repetitive shape of the impression being produced by secondary periderm which had separated the large leaf cushions on the primary stem (or trunk).

As the size of leaf cushions (or bases) is of particular interest in the study of the Griffith specimen it is important to note Eggert found that “in general, branches with greater diameters have larger leaf bases, and numerous specimens figured in the literature show that this phenomenon was of general occurrence in species of *Lepidodendron* and *Lepidophloios*” (Eggert, 1961: 67). One *Lepidophloios* specimen he studied (specimen LP-5), whose diameter exceeded 10 cm, had “leaf bases of very large dimensions (about 12–13 mm wide at their point of attachment to the underlying cortical tissues), while the laterally expanded portion of the leaf base, which overlaps lower leaf bases, reached 3.5 cm in width” (Eggert, 1961: 67). In a summary of the morphology of the *Lepidodendron* and *Lepidophloios* specimens he studied, Eggert stated that “the various parts of the primary body reached their maximum mature dimensions just below the level of the first dichotomy”, and “leaf base dimensions probably increased during the early development of the plant, reaching maximum size on the trunk at the levels where other components of the primary body reached maximum size. With successive branchings the leaf bases were smaller, and the number of rows decreased on the branches” (Eggert, 1961: 77). The occurrence of the largest leaf cushions just below the first dichotomous branching of *Lepidodendron* species is supported by Thomas & Watson (1976) who described a *Lepidodendron* trunk 114 ft (34.7 m) long to the first branching found near Bolton, UK. The leaf cushions at the 114 ft mark measured 55 × 16 mm, whereas the leaf cushions at the 120 ft (36.6 m) mark after the first branching measured 37 × 13 mm.

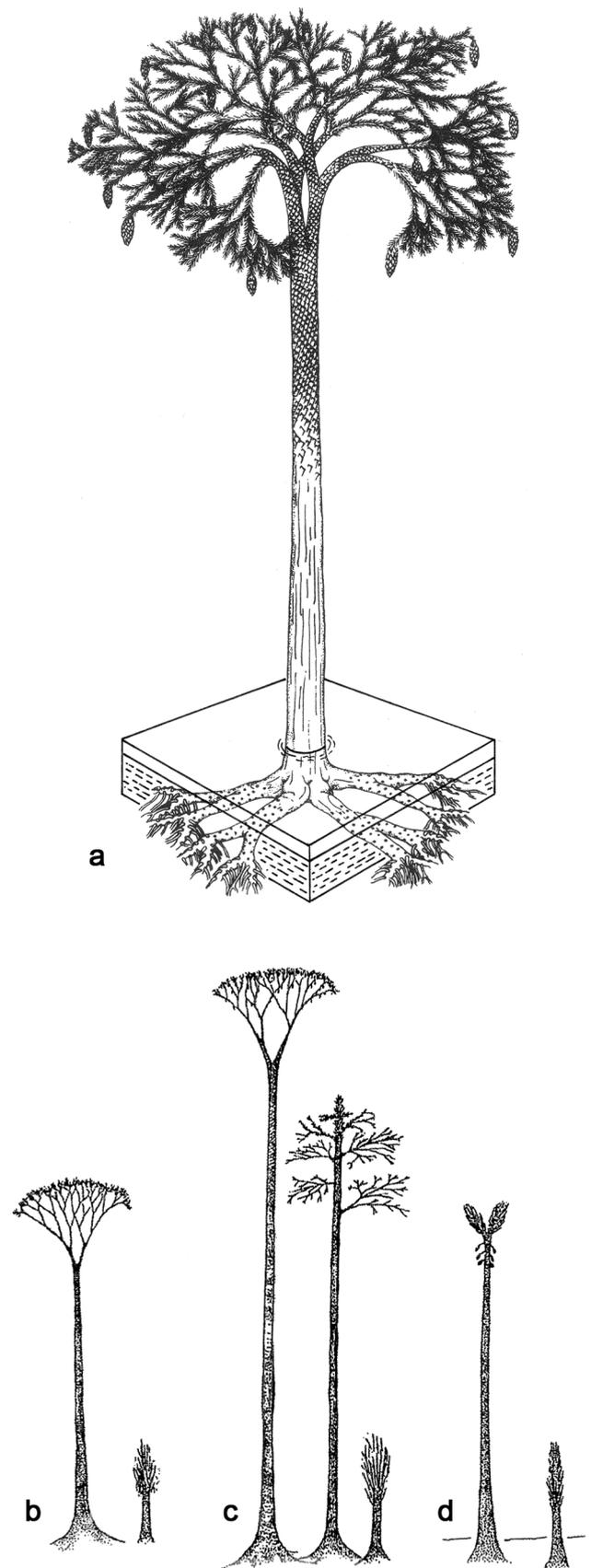


Figure 8. Growth habits of arborescent lycopsids: (a) *Lepidodendron* reconstruction (after D. A. Eggert, as cited in Taylor, Taylor & Krings, 2014); (b) *Lepidophloios*; (c) *Diaphorodendron*; (d) *Sigillaria* (b, c, d after Phillips & DiMichele, 1992).

**Table 1.** Comparison of the known dimensions of representative Australian lycopsid specimens and the Griffith specimen (F.124805). Certain measures are indeterminate (indet.) or unknown (—); all measures are in millimetres (mm). It is evident that this representative selection of Australian specimens shows a range of *leaf cushion dimensions* much smaller than that of the Griffith specimen. Where branch diameters can be determined, the range is between 40 and 100 mm. Eggert (1961) noted that leaf cushions reached maximum size on the trunk of *Lepidodendraceae* just below the apical branching, then the size reduced as further branching reduced branch diameter. These specimens are probably crown branches.

Museum Specimen	AM F.124805 <sup>a</sup>	AM F.68472	AM F.46924	AM F.49870	AM F.6485	AM F.2	QMB F3275 <sup>b</sup>
Leaf cushion dimensions	75 × 34	8 × 5	5 × 5	8 × 5	15 × 9	10 × 8	13.4 × 13.4
Thickness of intercushion periderm	9	1	< 1	< 1	< 1	< 1	< 1
Ligule and vascular scars	absent	absent	present	absent	present	absent	present
Apparent branch diameter	—	c. 40	c. 40	indet.	indet.	indet.	c. 100
See figure	—	Fig. 5a	Fig. 5c	Fig. 5i	Fig. 6d	Fig. 6e	—

<sup>a</sup> The Griffith specimen.

<sup>b</sup> after Clifford, 1996, tables 1, 2.

### Comparison of the impressing Griffith plant with others

The two studies summarized in Table 2 record main trunk leaf cushions of significantly greater dimensions than those of the representative Australian specimens (Table 1).

It is reasonable to conclude from its size that the leaf cushion of the Griffith specimen occurred towards the top of the main trunk of a large tree, just below the point where crown branching began.

### Taphonomy of lycopsid components

Plant material can be preserved in a number of ways - by compression when buried in sediments which often left carbonised residue, by impression when material was pushed into a substrate and was subsequently removed physically or by organic degradation, by permineralisation, or by inclusion in mineralised nodules such as coal balls. In the case of impression, depending on the coarseness and chemical qualities of the substrate, fine surface details can be preserved even though no organic material remains. However, a substrate of fine grained mud preserves more details than coarse sand (Schopf, 1975).

Study of trunk compressions of *Lepidodendraceae* have indicated that the trunk diameter expanded during growth by the development of thick secondary cortical growth which

produced the periderm (DiMichele, 1979), on the outside of which grew the leaf cushions. This periderm was thick, dense and wood-like. It was the main support tissue for the stem and probably quite rigid. Periderm tissues were living and quite different from traditional bark (Phillips & DiMichele, 1992) (although some authors refer to this tissue as bark). The periderm was regularly shed from trees (Cleal & Thomas, 2005), and was resinous and considered highly resistant to decay as an adaptation to habitats prone to frequent flooding (Phillips & DiMichele, 1992).

In the particular case of the Griffith specimen it is possible to use this information to speculate on the taphonomic process of its formation (Fig. 10). A mature tree growing in a swamp by a flowing channel fell, shedding a section of periderm just below its first branching (Fig. 10a). This periderm was carried downstream in a fast flowing current and was deposited on a sand bank (Fig. 10b). More sand rapidly built up and buried the fragment. The periderm, being resinous and resistant to decay, remained entrapped while more sand was deposited from the fast flowing channel. The substrate hardened under compression forming sandstone, but the resinous periderm, being resistant to decay, remained, consolidating its impression in the now hardened substrate. Finally, decay did occur and a slow removal of the organic material occurred via infiltration of the porous sandstone by water (Fig. 10c). A void was created, but infill did not occur

**Table 2.** Comparison of the main trunks of two large lycopsid specimens from Britain (*Lepidodendron*) and North America (*Lepidophloios*). These two examples have leaf cushion dimensions significantly greater than representative Australian specimens (Table 1). While large they are still less than the dimensions of the Griffith specimen. This comparison supports the contention that the Griffith specimen is an impression formed by the periderm of the main upper trunk of a very large arborescent lycopsid.

	<i>Lepidodendron</i>	<i>Lepidophloios</i> <sup>d</sup>
Source	Thomas & Watson, 1976	Eggert, 1961: 67
Leaf cushion dimensions	55 × 16 mm (max)	35 × 13 mm
Thickness of intercushion periderm	4 mm	2 <sup>c</sup> mm
Ligule and vascular scars	present	absent
Trunk diameter	760 <sup>c</sup> mm (2.5 ft)	> 100 mm
Trunk height to first branching	34.75 m (114 ft)	—

<sup>c</sup> estimated measures only

<sup>d</sup> Eggert's (1961) specimen LP-5

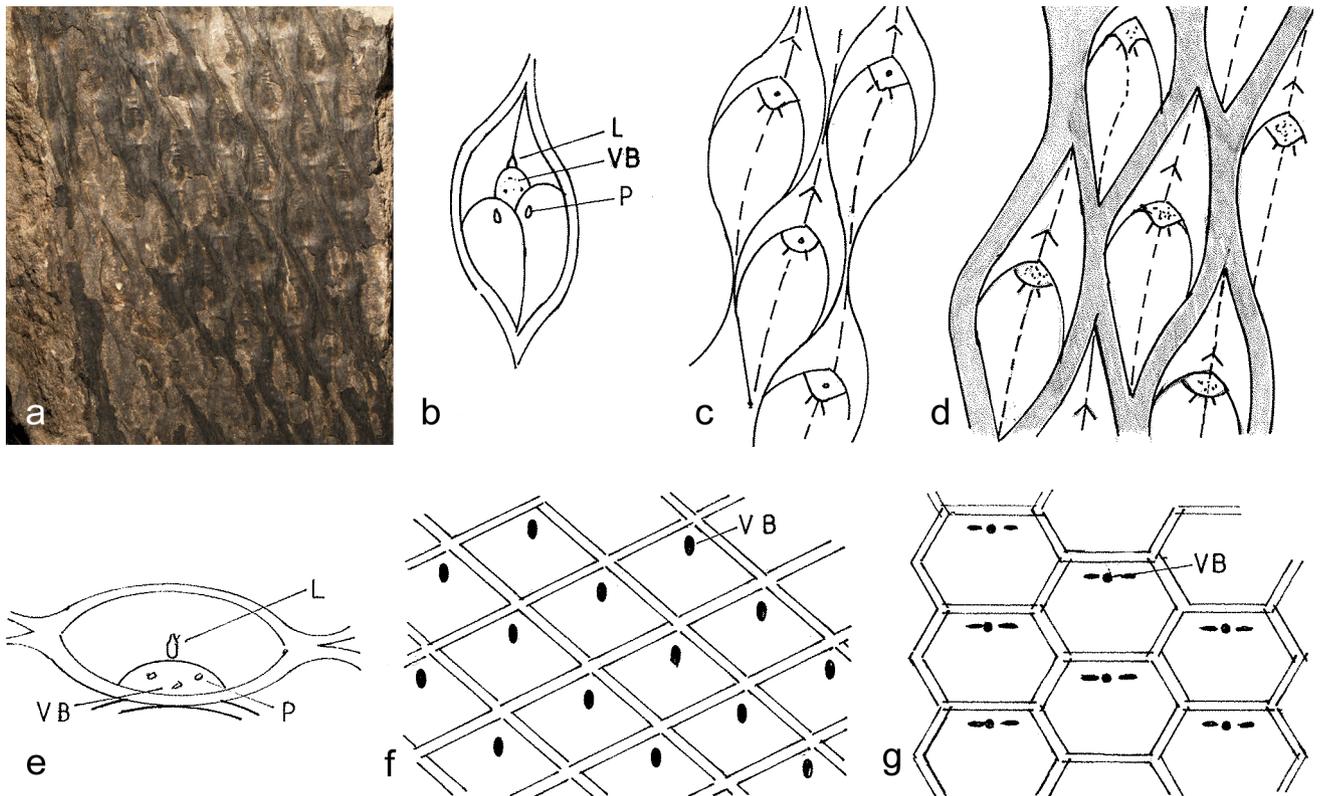


Figure 9. Various generic leaf cushion morphologies. *L*, ligule scar; *p*, parichnos scar; *VB*, vascular bundle scar. (a) *Lepidodendron* sp. from Scotland (AM F.17751); (b) *Lepidodendron* (after Taylor & Taylor, 1993); (c) *Lepidodendron aculeatum* before secondary expansion (after Thomas, 1970); (d) *L. aculeatum* after secondary expansion (after Thomas, 1970); (e) *Lepidophloios* (after Taylor & Taylor, 1993); (f) *Leptophloem australe*; and (g) *Sigillaria*.

as the bulky sandstone deposit filtered out fine sediment. 370 million years later erosion exposed the void (Fig. 10d). The impression of the outer surface of the void containing the secondary cortical growth outlining the leaf cushions was thus exposed on the surface of the bedrock (Fig. 10e). The bedrock surface progressively broke down into loose rocks and pebbles forming scree against the lowering bedrock ridge (Fig. 10f). One of these rocks contained a fragment of the periderm impression. The quarrying process collected the scree material which was fed through primary and secondary screens before being washed. This rock was exposed during the primary screening stage and separated from the gravel production. The sandstone preserved the major structure of the leaf cushion borders, but not the fine detail of the ligule and vascular bundle scars.

### The lycopsid forest ecosystem

From the Late Devonian, arborescent lycopsids evolved and radiated rapidly within the tropical swamps of Pangea (Phillips & DiMichele, 1992), and by the Early Carboniferous the Lepidodendrales had established themselves as forests in peaty, coal forming (organic) and clastic (inorganic) swampy substrates (Phillips & DiMichele, 1992). Five genera dominated this ecosystem—*Paralycopodites*, *Sigillaria*, *Diaphorodendron*, *Lepidodendron* and *Lepidophloios*—although a number of others, including *Leptophloem*, found

their place. Each genus dominated a particular elevation within this ecosystem. For example, *Lepidophloios* evolved to favour flooded swamps, while *Sigillaria* favoured the stream margins (Phillips & DiMichele, 1992).

The Lepidodendrales relied on leaf bases on trunks and branches as well as leaves for photosynthesis. They were determinant species with short lifespans of approximately 15 years. Their pole growth habit coupled with a short, final sparse crown formation meant that there was a high level of light penetration through the canopy to ground level, allowing efficient photosynthesis within the leaf bases on the forest trunks and in the sporelings, and possibly in the *Stigmaria* (Phillips & DiMichele, 1992). Thus the Lepidodendrales evolved a community forest strategy that supported the growth pattern of the individual tree from sporeling onwards, in contra-distinction to our modern rainforests where photosynthesis occurs in the dense forest canopy, and young seedlings must wait for a break in this canopy to allow in light for growth. The Lepidodendrales were therefore able to dominate the equatorial wetlands of Pangea during the first half of the Carboniferous Period before a drying, oscillatory climate at the end of the Westphalian drove many species to extinction in the North American and European equatorial basins (and later, in the Permian, on the Chinese microcontinents) (DiMichele *et al.*, 2009).

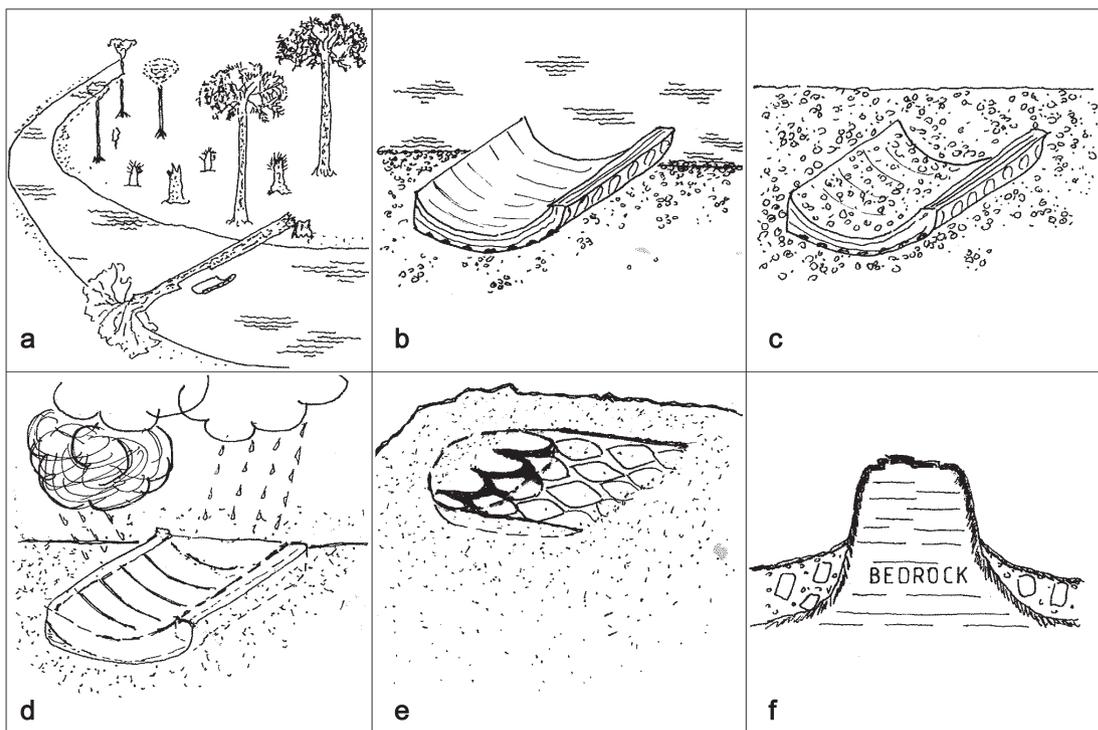


Figure 10. A possible taphonomic process experienced by the Griffith specimen. (a) A section of trunk periderm dislodged and carried down a fast flowing stream; (b) the periderm stranded on a coarse sandbank and buried; (c) the sand compacted into rock, entrapping the resinous, long-lasting periderm, which eventually rotted and leached away, leaving an impressed void; (d) the rock eroded; (e) the impression of the outer surface of the periderm exposed on the bedrock surface; (f) bedrock broke down into gravel and loose rocks deposited in scree, one of which contained the impression.

### Australian palaeogeography and global vegetation distribution in the Late Devonian/Early Carboniferous

Scotese (2002) has plotted the tectonic positions of continental land masses over the Phanerozoic Eon. These maps show Protoaustralia (as part of Gondwana) straddling the equator in the Early Devonian, then travelling progressively south from the tropics through the southern arid zone in the Late Devonian as Pangea assembled. By the Early Carboniferous the east coast of Protoaustralia was in the southern warm temperate zone. During this time tectonic activity produced north/south oriented orogeny with related basins. These included the Thomson Orogen and Burdekin Basin and Drummond Basin in Queensland (Day *et al.*, 1983), and the New England Orogenic Province and associated Tamworth Forearc Basin and the Texas-Coffs Harbour Slope and Basin in New South Wales (Scheibner, 1998). Regular continental sedimentation occurred in these coastal basins with brief marine incursions (Day *et al.*, 1983; Scheibner, 1998).

The diversity and structure of the Late Devonian forests has been well studied, but it is not until the Early Carboniferous that an adequate range of fossil evidence has been assembled to define global distributions (Willis & McElwain, 2014). By the Early Carboniferous five biogeographical regions, or biomes, can be identified. The Tropical Everwet Biome on the equator included the China micro-continents, Scandanavia, Greenland and North America. The Summerwet (tropical) Biome included the remainder of Euramerica and Kazakhstan. The Subtropical

Desert Biome covered western Protoaustralia and part of Saudi Arabia and did not preserve plant fossils. The southern Warm Temperate Biome included the eastern Gondwanan region, whose vegetation was dominated by similar vegetation of arborescent lycopsids, sphenopsids and seed ferns to that in lower latitudes, but apparently of less diversity. The fifth biome was the Cool-Cold Biome encompassing cool temperate, polar and glacial areas (Willis & McElwain, 2014).

Fossil flora of the Tropical Everwet Biome was dominated by arborescent lycopsids, sphenopsids and pteridosperms. These everwet swamps produced an abundance of coal deposits, as did the lycopsids and pteridosperms of the summerwet marshes (Willis & McElwain, 2014). However, Willis & McElwain (2014) stated that vegetation in the southern Warm Temperate Biome where Protoaustralia resided at this time contained lycopsids that were shorter in stature than those of the everwet and summerwet regions as they lacked *Stigmaria* rooting structures, which indicated cooler temperatures.

Climatic conditions favouring the lycopsid dominated swamp forests of Euramerica persisted until the Middle-Late Pennsylvanian (306 Ma). Change occurred during a dynamic planetary cooling period when glacial/interglacial oscillations, possibly driven by orbital variations similar to the Pleistocene, produced regular sea level and climate changes in the tropics. Wetland vegetation dominated by arborescent lycopsids, pteridosperms and tree ferns changed to one dominated by tree ferns and subdominant seed ferns (DiMichele *et al.*, 2009). This change did not occur at this time in the Chinese micro-continents which maintained lycopsid dominated vegetation in their wetland



Figure 11. The extant Australian herbaceous lycopsid *Lycopodium*, photographed in the Cathedral Rocks National Park, New South Wales. (a) Plant growth habit; (b) plant with fertile organs on distal extremities of branches. Scale bars 10 cm.

basins until well into the Permian (DiMichele *et al.*, 2009). No fossil evidence of arborescent lycopsids after the Early Carboniferous has yet been found in Australia, so it is currently assumed that the Australian lycopsid forests also gave way to the new forest structure at this time.

As a postscript to this story, lycopsid species are still endemic in recent time in Australia. They are small, herbaceous plants, but still retain some basic features of the arborescent lycopsids, including dichotomous branching, spiral microphyll leaf placement along stems and sporophylls on the distal ends of branches (Fig. 11a,b).

## Discussion

A large body of knowledge on arborescent lycopsids has been developed over the last 150 years. Initially the taxonomy was structured on morphological features, particularly the leaf cushion patterns and their leaf connection and vascular scars. The majority of specimens collected were of compressions or impressions of small branches or even twigs. These typically contained small rhombic and sub-rhombic leaf cushions ranging in size from about 2 mm to 10 mm long. Later, permineralised specimens of trunks were obtained that allowed internal structures to be studied and a picture of the ontogeny of these large plants was developed. This growth pattern revealed that the developing main stem (or trunk) of an arborescent lycopsid was covered in photosynthetic

leaf cushions which reached maximum size just before the first dichotomous branching of the crown (Eggert, 1961). Very few specimens of these large leaf bases have been discovered, but Eggert (1961) reported one  $35 \times 12\text{--}13$  mm and Thomas & Watson (1976) reported one  $55 \times 16$  mm. The Griffith specimen “leaf cushion” dimensions are  $75 \times 34$  mm, larger again than those reported by Eggert, and Thomas & Watson. If the Griffith specimen is indeed that of a lycopsid impression it ranks as one of the largest so far described.

Another diagnostic used for identification of arborescent lycopsids is that of the leaf connection ligule and vascular bundle scars (Fig. 9). These are not always preserved, but often are observable in fine grained fossils formed in silty shales (Figs 5d,e). The lack of these leaf connection scars in the Griffith specimen does throw doubt on its origins. However, the Griffith specimen was formed in Devonian sandstone which does not retain fine impressed detail. As well, the internal sections of the fossil appear to have been subject to erosion, and any delicate or faint impressions would have been destroyed.

Thomas (1970) described the secondary growth of the periderm which formed expanding raised barriers around the existing leaf cushions, pushing them apart. The periderm material was dense and resinous to resist rot in a swampy environment. Figure 4 shows how the shape of the Griffith impression can match that of the borders of a leaf cushion fossil. If the Griffith specimen is that of a lycopsid periderm,

it is this dense, resinous secondary barrier tissue that made the impression.

A close inspection of the Griffith specimen revealed a repetitive “step” at the point where two impressed “walls” joined (Fig. 2b). The digital reconstruction of the impressing object showed that this was produced by each element of the object overlapping the next, thus creating an imbricating effect (Fig. 3h). A number of authors describing lycopsid leaf cushion patterns mention an imbricating structure. Taylor *et al.* (2009: 283) stated that *Lepidophloios* leaf bases are “... wider than they are tall. They are directed downward on the stem and overlap the bases below, much like shingles on a roof”. Eggert (1961: 67), describing his *Lepidophloios* specimen LP-5, stated “... while the laterally expanded portion of the leaf base, which overlaps lower leaf bases, reached 3.5 cm in width”. DiMichele (1979: 64) stated that small leaf cushions of *Lepidophloios* species protrude only slightly but intermediate leaf cushions are “much more imbricate”, and leaf cushions of *L. kansanus* “are highly imbricate”. This imbricating tendency can be seen on Fig. 5i.

It is difficult to identify a digital construct down to the level of genus. However, it is interesting to note that the *Lepidophloios* had leaf cushions oriented on its trunk with the longest dimension horizontal and directed downwards on the stem overlapping the bases below (Taylor & Taylor, 1993) (Fig. 9e). Also, the large leaf cushion specimen LP-5 described by Eggert (1961) is a *Lepidophloios* and has its largest dimension horizontal and overlapping the lower leaf base. The digital construct of the Griffith specimen also has its “leaf cushions” overlapping. If its structure is oriented so that the overlaps are directed downwards, its longest dimension is horizontal and each “leaf cushion” has an imbricating effect, like shingles on a roof (Fig. 3h).

On the premise that the Griffith specimen is a fragment of a *Lepidophloios*, it is possible to speculate on the structure of the complete plant. The leaf bases were larger than those described by Eggert (1961) and Thomas & Watson (1976). Their specimens had trunk diameters of greater than 100 mm and 760 mm respectively. Also, the trunk of the specimen described by Thomas & Watson (1976) was 34.75 m high. The Griffith specimen exhibited secondary growth of intercushion periderm, indicating trunk expansion (Thomas, 1970). So the main trunk could have been one meter in diameter and 30 m high with leaf cushions spiralling upwards on the upper half. Leaf cushions would have been oriented with their longer dimension horizontal and they would have overlapped the leaf cushion beneath. A straplike leaf would have hung from each leaf cushion. Dichotomous branching would have started at 30 m and continued as branches and leaf cushions became progressively smaller to the distal ends (Eggert, 1961), forming the crown. Spore bearing cones would have hung from the branch ends. This entire structure would have been anchored by dichotomous branching subaerial *Stigmaria*. This is a much larger

Australian Devonian tree than was expected from previous Australian fossil evidence.

Although the structure and composition of the Late Devonian/Early Carboniferous forest communities in Euramerica have been extensively documented (e.g., Phillips & DiMichele, 1992), this level of study has not been applied to the Protoaustralian forests of the same age. From the Early Devonian, tectonic plate movement carried Protoaustralia (within Gondwana) from the tropics south across the arid Subtropical Desert Biome and into the Warm Temperate Biome by the Early Carboniferous. This raises the question “By what process did the arborescent lycopsid forests of the tropics survive this transition across the arid band to the warm temperate conditions of the Early Carboniferous?”. We have fossil evidence that these forests did survive (although of lower diversity and apparently lower profile), so we can only speculate that the tropical forests that developed while Protoaustralia was in the tropics were protected in coastal refugia where the environment remained wet due to a coastal climate, perhaps augmented by a nearby mountainous topography. Independent geological evidence showed orogenic activity along the east coast of Protoaustralia through this period with the formation of continental sediment basins that could harbour swampland forests (Day *et al.*, 1983; Scheibner 1998). These conditions maintained our modern eastern Australian rainforests in the nominally sub-tropical arid band.

There are no Carboniferous coal deposits in Australia (White, 1988) (Australia’s extensive black coal deposits were laid down in the Permian by *Glossopteris* forests). This has been interpreted as the result of Protoaustralia being outside the everwet and summerwet biomes during the age of the lycopsid swamp forests that produced the northern hemisphere coal deposits. The apparent lower plant diversity and lack of fossil evidence for large arborescent lycopsids in Protoaustralia at this time has led to assumptions that the Protoaustralian lycopsid forests were sparser and of lower profile than the Euramerican forests of the same age (Willis & McElwain, 2014). Northern hemisphere authors failed to note that *Stigmaria* root systems had been described by Australian authors (e.g., Walkom 1928b), and assumed no *Stigmaria* were evident in Australian collections. They took this “absence” of *Stigmaria* as evidence of forests of small stature which did not require the stabilising support of a large underground structure (Willis & McElwain, 2014). However, this assumption was incorrect, as specimens existed (e.g., Fig. 6d). If the presence of *Stigmaria* is evidence of tall lycopsids, then this assessment of warm temperate forest structure being of low profile should be revisited. If the Griffith specimen is confirmed to be part of a large arborescent lycopsid, this will be further evidence of tall Devonian forests in the nominally arid and warm temperate conditions of Protoaustralia.

## Conclusions

Undoubtedly, the identification of the Griffith specimen as a partial impression of a lycopsid trunk is speculative. The only direct evidence available is a fragment of a repetitive pattern in a piece of Devonian sandstone. However, the digital tools now available allow the development of an initial idea to a point where corroborative data can be applied to the task of identification. There is little doubt that, whatever the origin of the impressing object, its shape was that of the digital reconstruction.

The arguments for the identification of the Griffith specimen as a lycopsid impression rest on the shape of each unit, its regular repetition, and its imbricating structure. The doubts about this interpretation are produced by the large size of each “leaf cushion”, larger than any other yet found, and the lack of ligule and vascular scars. These doubts can be partially countered by the fact that large leaf cushions have been found (although not reaching the dimensions of the Griffith specimen), and that the substrate is sandstone which would not preserve the fine detail of ligule and vascular scars.

If further evidence is found for the presence of lycopsid leaf cushions in Australia of the size found in Griffith, it would corroborate the contention that forests of very large lycopsids existed not only on the tropical everwet continental plates now making up Europe and North America, but at the extremes of warm temperate Pangaea, where the future Australia resided.

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