

GEOMETRICAL STUDY OF A CAST OF *LEPTOPHLOEUM AUSTRALE* (McCoy) WALTON FROM QUEENSLAND

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Clifford, H.T. 1996 07 20: A geometrical study of a cast of *Leptophloeum australe* (McCoy) Walton from Queensland. *Memoirs of the Queensland Museum* 39(2): 227-230. Brisbane. ISSN 0079-8835.

Geometrical study of a cast of *Leptophloeum australe* (McCoy) Walton confirms that during its compression there has been no increase in diameter. □ *Leptophloeum*, axis, cast, compression.

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Axial casts of the lepidophyte *Leptophloeum australe* (McCoy) Walton have been recorded in Australia from Queensland (Carruthers, 1872) and Victoria (McCoy, 1874). Herein an additional cast is described from Queensland. The specimen is of particular interest because over most of its surface the outlines of leaf-cushion bases are clearly defined, (Fig. 1) thereby enabling the length of its diameter, prior to compression, to be determined with reasonable accuracy. This length therefore provides a bench mark against which diameters as estimated by other methods may be evaluated.

All methods employed assume the cast to have been cylindrical prior to its compression, a viewpoint justified by the uniformity in size and shape of the leaf-cushions on its surface. Furthermore, the cast was assumed to be elliptical in transverse section which assumption has been confirmed by direct observation. Although casts are often reported to be elliptical in section (Pant & Srivastava, 1995) there appears to be no previous publication in which the contention has been confirmed by a direct comparison of the observed section shape with that of the ellipse calculated from the maximum and minimum widths of the cast.

MATERIAL

The cast (QMF3275) was collected by Leichhardt during his expedition from Moreton Bay to Port Essington and is the only specimen in the Queensland Museum known to have been collected by the explorer whose misfortune it was to lose, by misadventure or necessary abandonment, most of his collections when near to his journey's end (Leichhardt, 1847). The specimen is labelled 'Clarke River' and so most probably has its Provenance in the Clarke River Basin (Draper *et*

al., 1993). Because the cast was collected as a surficial boulder its precise age is not determinable. However, the taxon is well represented by impressions in the Ruxton Formation whose age, based on conodonts, is Late Devonian to Early Carboniferous.

Two available casts (Table 1) are entirely mineral in composition and a thin section of QMF3204 revealed it to be a fine sediment dominated by rock fragments and quartz. Other minerals present are muscovite, orthoclase, plagioclase, sericite and undifferentiated iron oxides. The unabraded condition of the grains and their composition indicates the cast formed in young sediments with a proximal igneous and metamorphic provenance. The cement is dominated by silica and clay with subordinate iron oxides (Alex Cook per. comm.).

RESULTS

From measurements of the specimen (Table 1) it is possible to make several independent estimates of the diameter of the cast before its compression. That the outline of the cast in transverse section approximates closely to an ellipse may be confirmed by reference to Fig. 2 where the ellipse calculated on the basis of the maximum and min-

TABLE 1. Five attributes of two casts of *Leptophloeum australe*.

ATTRIBUTE	DIMENSIONS (mm)	
	QMF3275	QMF3204
Perimeter	283	194
Maximum width	117	75
Minimum width	51	47
Leaf-cushion width	13.4	12
No. leaf-cushions encircling axis	25	n.a.

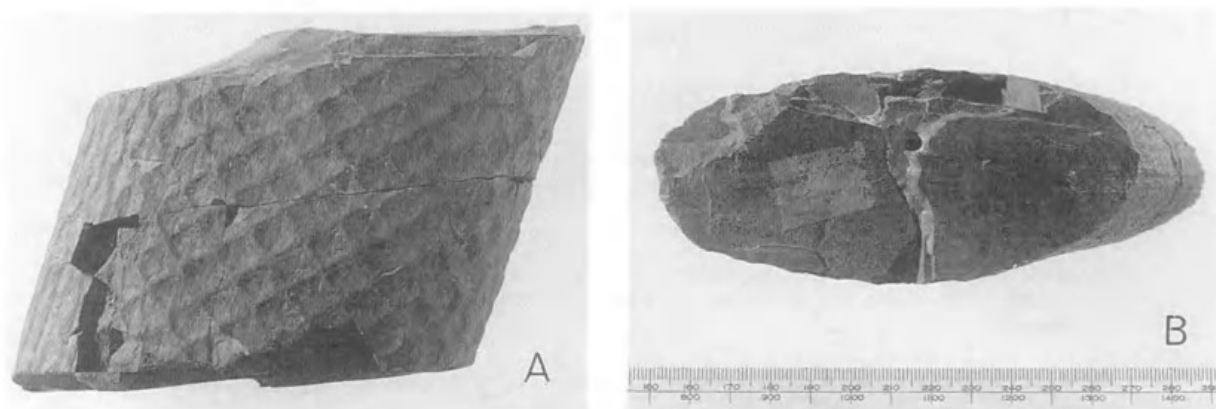


FIG.1. Cast of *Leptophloeum australe* (QMF3275). A, Lateral view. B, End view.

imum widths of the cast is superimposed upon its original outline.

Four approaches to the estimation of the diameter of the cast prior to its compression will now be considered:

1. Perimeter of Cast. If it is assumed that during compression the perimeter of the cast is unchanged the diameter of a circle with the same perimeter is readily calculated (Table 2).

2. Cross Sectional Area of Cast. If the cross sectional area of the cast is unaffected by compression the areas of the elliptical section of the cast and that of its precompression circular section will be the same. Accepting the maximum and minimum width of the cast as axis-lengths the area of the elliptical section may be calculated and from this the diameter of a circle of similar area determined (Table 2).

3. Maximum Width of Cast. Assuming that the vertical compression of a horizontal cylindrical cast may occur without any lateral expansion the maximum width of the cast is the same as the diameter of the uncompressed cast (Table 2).

4. Leaf-cushion number x Leaf-cushion width.

TABLE 2. Four estimates of the diameter of a presumed cylindrical cast of *Leptophloeum australe* as determined from certain attributes of its compressed cast (QMF3275).

BASIS OF ESTIMATE	ESTIMATED CAST DIAMETER (mm)
1. Perimeter	90
2. Cross sectional area	77
3. Maximum width	117
4. Cushion number x cushion width	107

The number of leaf-cushions encircling the cast is half the number of the vertical rows in which they are arranged (Fig. 3). The recognition of these rows is more reliable than that of adjacent leaf-cushion boundaries wherever the surface of the cast is irregular or the leaf-cushions are strongly compressed as in regions of maximum curvature. Therefore, the number of leaf-cushions encircling the cast was determined as half the number of vertical rows of leaf-cushions on the surface of the cast. Multiplication of leaf-cushion number by leaf-cushion width provided a perimeter for the uncompressed cast from which its diameter was calculated (Table 2).

DISCUSSION OF RESULTS

Each of the 4 methods employed provided a different estimate of the diameter of the original cast (Table 2). These differences are readily accounted for if it is assumed that during compression a cylindrical cast was deformed into one elliptical in transverse section, with the major axis of the ellipse being of the same length as the diameter of the cylinder.

Such a situation is illustrated in Fig. 4 where sections of a theoretical cast, prior to and subsequent to its compression, are superimposed. The ellipse is similar to that of Fig. 2 because the lengths of the major and minor axes of the two are the same. Along the perimeter of both the circle and ellipse solid circles mark the positions of leaf-cushion margins. The number of leaf-cushions is the same as that on the cast being studied and their positions on the ellipse are vertical projections of those on the circle. Therefore

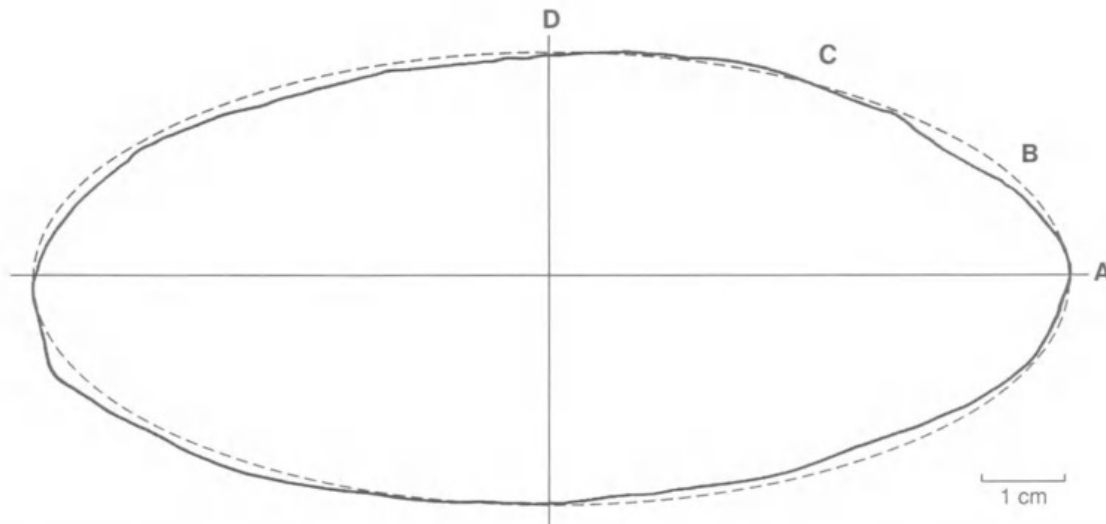


FIG. 2. Outline of cast of *Leptophloeum australe* (QMF3275) with the perimeter of theoretical ellipse superimposed. A-D are places on cast surface at which leaf-cushion widths (Table 3) were measured.

the ellipse may be regarded as a compression of the circle without a change of its diameter.

Both the perimeter and the area of the ellipse will provide measurements which will lead to underestimates of the diameter of the circumscribing circle, and the shorter the minor axis of the ellipse the poorer will be the estimate. Furthermore, of the two parameters under discussion the perimeter of the ellipse will always

provide a closer estimate of the perimeter of the inscribing circle than will the area of the ellipse. This statement is especially true of strongly compressed casts. Towards the limit of compression, as the length of its minor axis approaches zero, the perimeter of an ellipse approaches a value of twice the length of its major axis but the area of the ellipse approaches zero. Hence it is clear that ellipses whose minor axes are short in com-

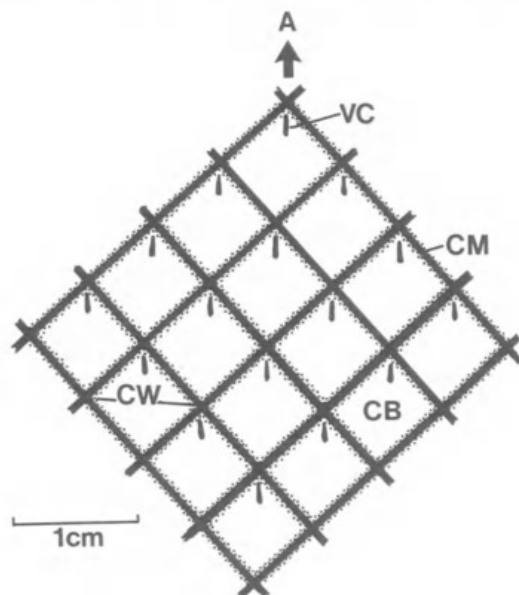


FIG. 3. Semidiagrammatic drawing of the disposition of leaf-cushion outlines on the surface of cast of *Leptophloeum australe* (QMF3275). A=direction of stem apex; CB=leaf-cushion base; CM=leaf-cushion margin; CW=leaf-cushion width; VC=vascular cicatrix..

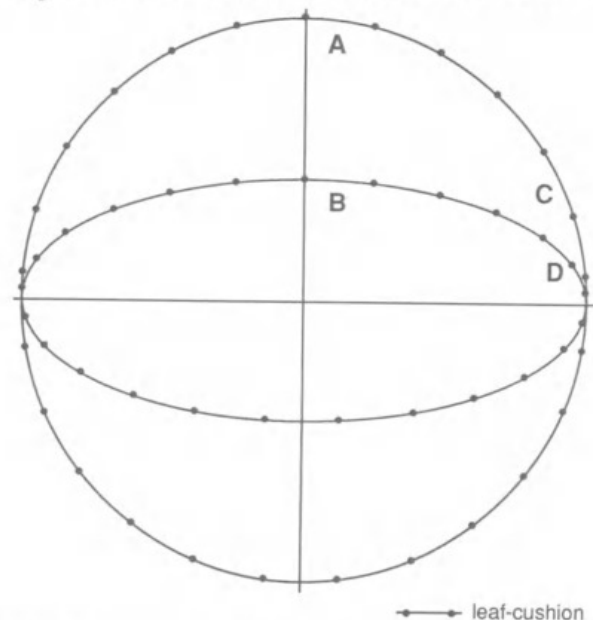


FIG. 4. Transverse sections of 2 theoretical casts on whose perimeters the margins of the leaf-cushion outlines have been marked by solid circles - circle, before compression; ellipse, after compression. The major and minor axes of the ellipse are the same length as in Fig. 2.

TABLE 3. The areas and perimeters of an ellipse with different minor and major axis ratios expressed as proportions of its circumscribing circle.

Length of minor axis Length of major axis	Ellipse as proportion if its circumscribing circle	
	Area	Perimeter
1.0	1.00	1.00
0.9	0.90	0.94
0.8	0.80	0.88
0.7	0.70	0.82
0.6	0.60	0.76
0.5	0.50	0.70

parison to their major axes provide poor information for predicting the diameter of the circumscribing circle.

However, the situation is different if the length of the minor axis of the ellipse equals or exceeds half the length of the major axis. Over this range of values both the area (exactly) and the perimeter (closely) of the ellipse are linearly related to the area of the circumscribing circle. Whereas for high values of the ratio of the lengths of the minor and major axes, both the perimeter and the area of the ellipse are useful predictors of the diameter of the circumscribing circle, for low values of the ratios neither is useful but the perimeter is the better estimator (Table 3). This observation is confirmed by the estimates of diameter (Table 2).

It is also clear (Fig. 4) that whereas the leaf-cushion bases around the perimeter of the circle are all of the same width their projections on to the ellipse vary in width. Whereas leaf-cushion B (Fig. 4) is almost the same width as that of A, the width of leaf-cushion D is much less than that of C. If the leaf-cushion is bisected by the minor axis of the ellipse its width will be almost exactly that of its width before projection from the circle. Therefore, provided the leaf-cushions measured are situated close to where the minor axis of the ellipse meets its surface their widths combined with their number provide an accurate basis for estimating the diameter of the uncompressed cast.

Because only one cast is available it is not possible to determine whether the diameters of the uncompressed cast as estimated from the maximum width of the compressed cast (117mm) and by the leaf-cushion number x width method (107mm), are statistically different. However, the data indicate that if there has been any lateral spread of the cast during compression the extension has been slight for the ratio of the former to the latter is 1.09 which value is close to unity.

Further support for the view that the width of

TABLE 4. The widths of leaf-cushion at 4 positions on the surface of a cast of *Leptophloeum australe* (QMF3275) as measured directly and as determined by projection from a circular cast onto one elliptical in transverse section with a major axis the same length as the diameter of the circular cast.

Place on surface (Fig. 2)	Leaf-cushion width (mm)	
	Measured	Predicted
A	4.0±0.3	5.5
B	7.2±0.4	8.0
C	11.9±0.2	11.5
D	13.4±0.8	13.5

the cast has not increased as a result of compression comes from a comparison of the measured and predicted widths of leaf-cushions. Measurements were made on four areas of the cast surface and the predicted widths were taken from similar positions on the ellipse (Fig. 2; Table 4). Standard errors can be attached to the means of the measurements because there are several leaf-cushions available on similar areas of the cast but there is only one predicted value for corresponding parts of the ellipse. Only on the surface of greatest curvature does the predicted value of leaf-cushion width differ significantly from that measured. Such close agreement between the two sets of values is further support for the hypothesis that compression of the cast has occurred without any lateral extension.

Although casts of *Leptophloeum australe* are rare, impressions of their axes are abundant. Most are flat and irregular in outline, but a few are parallel-sided thereby resembling impressions of complete axes. However, it is not reasonable to assume that the impression revealed on a flat surface derives from a whole axis. It may represent any portion of the surface, the remainder of which may be buried in the rock on either side of the plane (along which the rock split) to reveal the impression. Cleavage across a cast near to its surface and parallel to its length would expose impressions with parallel sides but whose widths are much less than the diameter of the cast. That this situation is common is suggested by the many impressions whose leaf-cushion bases have widths typical of casts whose diameters are greater than the width of the impression.

CONCLUSION

Although it has been widely accepted that compression of plant tissues and casts usually occurs, without a concomitant increase in their width at

right angles to the force applied, the process has been subject to little theoretical or experimental study.

Using a series of projections similar to that employed above, Walton (1936) compared the shapes of some solids pre- and post-compression. His approach was qualitative and non-experimental. However, according to Harris (1974: 144) Walton's observations were underpinned by a series of experiments in which he had compressed 'various solid plant organs - plant stems, apples and the like in wet sand in a power press so constructed as to allow surplus water to drain away'. Apples so compressed were converted into hemispheres filled with sand but with their diameters unchanged.

The pioneering study of Walton (1936) has been extended by Harris (1974), Niklas (1978) and Rex & Chaloner (1983). Harris (1974) embedded hollow balls of wax or plastic, in a variety of matrices which were then compressed. After compression the balls were approximately hemispherical and circular in outline. None of the compressions showed any obvious evidence of horizontal extension. Simulated compression studies of Niklas (1978) were quite extensive but, unfortunately, the procedures adopted were not adequately described. However, he demonstrated that whereas hollow and solid, but dehydrated stems compress without lateral extension hydrated solid stems 'show a maximum increase of 10% diameter'. Experimental procedures adopted by Rex & Chaloner (1983) are fully explained and so their results can be critically assessed. Foam rubber was used to represent plant material and saw dust the embedding matrix. Pressure was applied either with a single piston or a parallel system of independent pistons each of which was spring loaded, but with the whole set controlled by a single screw mechanism. After compression, transverse sections of the original cylinders (stems), differed in shape according to the piston system employed. Nonetheless in both systems and for several cylinder diameters the maximum width of the stem following compression was equal to or slightly less than the original diameter. That is, the results are in accord with the predictions of Walton (1936).

It is not possible to compare with certainty the results obtained from the several experimental studies because of the diversity of materials employed and the differences in procedures adopted. Furthermore, these results are not direct-

ly comparable with the observational data reported above for none of the experimenters included casts in their studies. Nonetheless, the application of pressure to embedded material did not result in its lateral extension except for one report by Niklas (1978). The similarity of the pre- and post-compressional diameters of the Leichhardt cast (QMF3275) suggest that even when subjected to pressures much greater than those employed in the laboratory plant axes do not expand lateral to the force applied.

ACKNOWLEDGEMENTS

Thanks are extended to Mary Wade, Alex Cook and Vincent Hart for helpful discussions during the preparation of this paper and to Natalie Camilleri and Maryanne Venables for assistance in preparing the diagrams. The photographs were taken by Gary Cranitch.

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POSSIBLE AFFINITIES BETWEEN *VARANUS GIGANTEUS* AND *MEGALANIA PRISCA*. *Memoirs of the Queensland Museum* 39(2):232. 1996:- Molnar (1990) described two frontals, and a parietal, of a giant Pleistocene varanid at King Creek, eastern Darling Downs. The material was assigned to *Megalania prisca*, the only varanid of comparable size. This identification is probably correct since undoubted remains of *Megalania* occur in the same deposits.

Molnar (1990) noted that the frontals and parietal of the King Creek varanid exhibited many unusual features, which could not be found in any varanid skulls examined, and were thus presumably derived within varanids. Among these features were the prominent sagittal crest along the median suture between the frontals, and the parallel transverse ridges extending at right angles to this crest. Both these features are also found in *Varanus giganteus* (Fig. 1) and are absent in other species of *Varanus* (Molnar, 1990) and in the nearest outgroup taxa, *Lanthanotus* and *Heloderma* (Rieppel, 1980; Pregill et al., 1986; Estes et al., 1988). They are thus derived within *Varanus* suggesting affinities between the King Creek varanid and *V. giganteus*. Molnar (1990) noted that, in the King Creek varanid as in *V. giganteus* (Fig.1), the sagittal crest and parallel transverse ridges were confined to the frontals, and did not extend onto the parietals. This phylogeny is based on very incomplete material and only two characters.

Megalania prisca, *Varanus giganteus*, *V. salvadori* and *V. komodoensis* are the 4 largest known varanids (Pianka, 1995). Despite the latter two not being Australian natives, all 4 belong to a discrete radiation of Australian monitors, the 'gouldii species group' (Baverstock et al., 1993). If *Megalania prisca* has affinities with *V. giganteus* and thus belongs within the 'gouldii species group' *Megalania* will have to be synonymised with *Varanus*. Relationships within the 'gouldii species group' are not yet well established (Baverstock et al. 1993): there is a distinct possibility that, when relationships within this radiation are resolved, *V. giganteus*, *V. salvadori*, *V. komodoensis*, and *Megalania prisca* will form a clade. If so, this would mean that the four largest varanid species represent a single discrete radiation of giant predatory lizards.

I thank the Australian Research Council for funding, Jenny Clack and Ray Symonds for loan of the figured specimen, and Malcom Ricketts for photography.

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FIG. 1. Skull of *Varanus giganteus* (University Museum of Zoology, Cambridge R9586) in (A) dorsal, and (B) right laterodorsal view, showing the sagittal crest and dermal sculpture on the frontals between the orbits. Scale bar = 3cm.



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