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Foliar physiognomic climate estimates for the Late Cretaceous (Cenomanian–Turonian) Lark Quarry fossil flora, central-western Queensland, Australia

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Abstract. Although there is a broad knowledge of Cretaceous climate on a global scale, quantitative climate estimates for terrestrial localities are limited. One source of terrestrial palaeoproxies is foliar physiognomy. The use of foliar physiognomy to explore Cretaceous assemblages has been limited, and some of its potential sources of error have not been fully explored. Although museum collections house a wealth of material, collection bias toward particular taxa or preservation qualities of specimens further magnifies existing taphonomic bias to cold temperatures. As a result, specific collection for foliar physiognomy can be necessary. Here, we conduct three foliar physiognomic analyses on the early Late Cretaceous Lark Quarry flora and assess the results in the context of other proxies from the same formation. Our results suggest that the climate at the Cenomanian–Turonian boundary in central western Queensland was warm and had high precipitation (leaf-area analysis: 1321 mm + 413 mm – 315 mm mean annual precipitation; leaf-margin analysis: 16.4°C mean annual temperature, 5.3°C binomial sample error; climate leaf-analysis multivariate program: 16 ± 2°C for mean annual temperature, 9-month growth season, 1073 ± 483 mm growth-season precipitation). Our analysis also gave higher mean annual temperature estimates than did a previous analysis by climate leaf-analysis multivariate program, based on museum collections for the Winton Formation.

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Introduction

Global-scale patterns of climate during the Cretaceous are broadly known. The general consensus is that the 'mid'-Cretaceous (Albian–Cenomanian) was warm and equable (Barron 1983; Ufnar *et al*. 2008; Hay 2011). For Australia, Dettmann and Playford (1969) postulated a warm temperate environment for the Cenomanian, with cooling later in the Cretaceous. Although global palaeoclimate estimates are broadly in keeping with preliminary observations of the Australian palaeoclimate, and palaeolatitude, higher temporal and geographic resolution of the change in climate, and correlations with changes in the floral and faunal components of the palaeoenvironment, are needed to capture the complexity of the Australian palaeoclimate during the Cretaceous, and to understand how climate affected floral and faunal turnover.

Methods used for investigating Cretaceous palaeoclimates are numerous. The most commonly used approaches include foliar physiognomic methods (Upchurch and Wolfe 1987; Miller *et al*. 2006; Fletcher *et al*. in press), mutual climate-range (MCR) methods such as bioclimatic analysis (Greenwood *et al*. 2003, 2005; Fletcher *et al*. in press), wood growth-ring indices (McLoughlin 1996), isotopic analysis both on sediment deposits (Gregory *et al*. 1989) and on a range of marine-animal hard parts, including belemnites (Stevens and Clayton 1971; Pirrie *et al*. 1995; Price *et al*. 2012) and foraminifera (Huber 1998), and the identification of various geological features such as glendonites (De Lurio and Frakes 1999) and lonestones (Frakes and Krassay 1992). By comparing the results of multiple methods at localities where that is possible, our understanding of the relationships between various climatic proxies and the palaeoenvironment can be improved.

The Winton Formation of central-western Queensland, which spans the Early to Late Cretaceous, has produced a significant palaeobotanical assemblage. Many studies have been conducted on the flora, including Bose (1955), White (1966, 1974), Peters and Christophel (1978), Peters (1985), Dettmann *et al*. (1992, 2009), McLoughlin *et al*. (1995, 2010), Pole (1999*a*, 1999*b*, 2000*a*, 2000*b*), Pole and Douglas (1999), Dettmann and Clifford (2000) and Clifford and Dettmann (2005). At least 50 macrofossil taxa are present, from 10 orders, showing a co-dominance of conifers and angiosperms (McLoughlin *et al*. 2010). Despite this wealth of material and its significance, comments on the likely climate that existed at the time are limited, and quantitative analyses have not yet been conducted. In the present study, we used the angiosperm morphotypes of McLoughlin *et al.* (1995, 2010) to categorise the leaf impressions found at The University of Queensland Lark Quarry localities, so as to conduct foliar physiognomic method-based analyses. This type of analysis is based on the premise that characters of leaves, such as leaf size, shape, margin type and the ratio of leaf width to leaf length, represent adaptive strategies to a plant's evolutionary environment (Wolfe 1993), and that the mean phenotype approximates the optimal phenotype for that environment (Jordan 1997). Of the various analyses that are available, we used leaf-area analysis (LAA; Wilf *et al.* 1998), leaf-margin analysis (LMA; Wing and Greenwood 1993; Yang *et al.* 2011) and climate leaf-analysis multivariate program (CLAMP; Wolfe 1993). We chose to conduct the analyses on new material from Lark Quarry for two reasons. The first is that the existing Queensland Museum collections have been collected from several sites that, although broadly coeval, were not necessarily deposited at the same time. In contrast, the Lark Quarry materials appear to derive from a single sedimentary layer, which is likely to have been deposited quite quickly because of the three-dimensional preservation of the leaves and the lithological characteristics of the horizon. Second, museum collections are likely to be biased toward completeness of specimens such that the sample contains smaller size classes than one representing true proportions in the assemblage. This is because larger leaves are more likely to be damaged, broken or incomplete. As a consequence, museum collections tend to magnify the effect of one of the common taphonomic biases, namely, the bias toward smaller leaves.

The current understanding of the effect of taphonomic bias is that it generally leads to a 'lower than true' estimation of mean annual temperature (MAT). Spicer *et al.* (2011) noted that microclimate effects can result in lower MAT estimations than modern data calibrations suggest. Kowalski and Dilcher (2003) reported the effect of wet soils, causing a 2.5–10°C underestimation of MAT compared with that recorded. Peppe *et al.* (2011) did not find evidence to support that extreme an effect but did support the maximum underestimation of 4°C reported by Burnham *et al.* (2001). Other authors have noted that within streambed assemblages, estimates will be systematically skewed toward lower MAT rather than the true MAT (Greenwood 2005), perhaps because of increased occurrence of toothed-margin species on stream banks (Burnham *et al.* 2001), transport of toothed-margin leaves from cooler sites upstream (Steart *et al.* 2002), or reduced transportation of larger leaf classes (Greenwood 1992, 2007).

Unresolved criticism of foliar physiognomy includes taphonomic (as above), phylogenetic (e.g. Little *et al.* 2010) and methodological (e.g. Jordan 2011; Milla and Reich 2011) concerns. However, we believe there is great potential for the continued development and investigation of foliar physiognomic methods, and for the use of these methods as part of multiproxy approaches. Following previous studies (Greenwood *et al.* 2003, 2005; Uhl *et al.* 2003; Grein *et al.* 2011), we use multiple botanical climate proxies, and compare the results. However, we note that the three techniques are not independent, and interpret them in the context of palaeoclimate studies based on museum collections of leaf impressions and palynological surveys from the whole Winton Formation (Fletcher *et al.* in press), recent models of global Cretaceous palaeoclimate (Hay 2011), and the known fauna of the Winton Formation.

Materials and methods

Localities

The present study focused on material from the following two University of Queensland field localities within the Lark Quarry Conservation Area (approximately –23′01S, 142′40E), 95 km south-west of Winton, central-western Queensland, Australia: UQL-LQ-II and UQL-LQ-III (Fig. 1).

The sediment at UQL-LQ-II and UQL-LQ-III derives from the Winton Formation. The Winton Formation extends over a large geographic area of western Queensland, north-eastern South Australia and north-western New South Wales (Gray *et al.* 2002; Fig. 1). It is the uppermost unit of the Manuka Subgroup within the Rolling Downs Group, and the youngest Cretaceous strata of the Eromanga Basin, conformably overlying the sediments of the Makunda Formation (Gray *et al.* 2002).

The Winton Formation was deposited from the latest Albian to approximately the Cenomanian–Turonian boundary (Tucker *et al.* 2013). It is at this upper boundary that many of the important plant and vertebrate fossil sites are found (Tucker *et al.* 2013), including the Lark Quarry localities used in the present study. The plant remains in the study were found in lag deposits in abandoned channels or flood levees (R. Tucker, pers. comm., 2012), and have been dated to 92 (±1.2) million years ago to 94.5 (±1.3) million years ago, using laser ablation of detrital zircons, placing them at the Cenomanian–Turonian boundary (Tucker *et al.* 2013). At that time, Lark Quarry Conservation Area would have been at ~50′S (Li and Powell 2001).

Collection

To conduct an initial comparison of the proportions of plant groups found at UQL-LQ-II and UQL-LQ-III, rocks were split at random and scored for presence/absence of non-ginkgophyte gymnosperms, angiosperms, ginkgos and ferns, until 100 blocks with at least one plant fossil present were recorded at each site. Specific collection of angiosperms for the LAA, LMA and CLAMP analyses was also conducted. To reduce bias in the sampling, all leaf fragments large enough to be tentatively identified to morphotype were kept.

Leaf-area analysis

Leaf-area analysis (LAA) is based on the relationship between the size of woody dicotyledonous angiosperm leaves and precipitation; leaves tend to be larger in wetter environments. It is a univariate technique that correlates the natural log of the mean area of the leaf types at a locality, to the mean annual precipitation (MAP; Wilf *et al.* 1998). The mean area was calculated for the eight of the nine types as described in McLoughlin *et al.* (1995, 2010) that matched the impressions found at the Lark Quarry field localities (no sufficiently complete specimen of 'Morphotype F' has been found at Lark Quarry for inclusion in the analysis; see Table 1). Samples chosen were those that were sufficiently complete to estimate the leaf area, as per the rule 2/3 × length × width (Cain and Castro 1959), and thus, were required to be complete or discernibly near complete in length

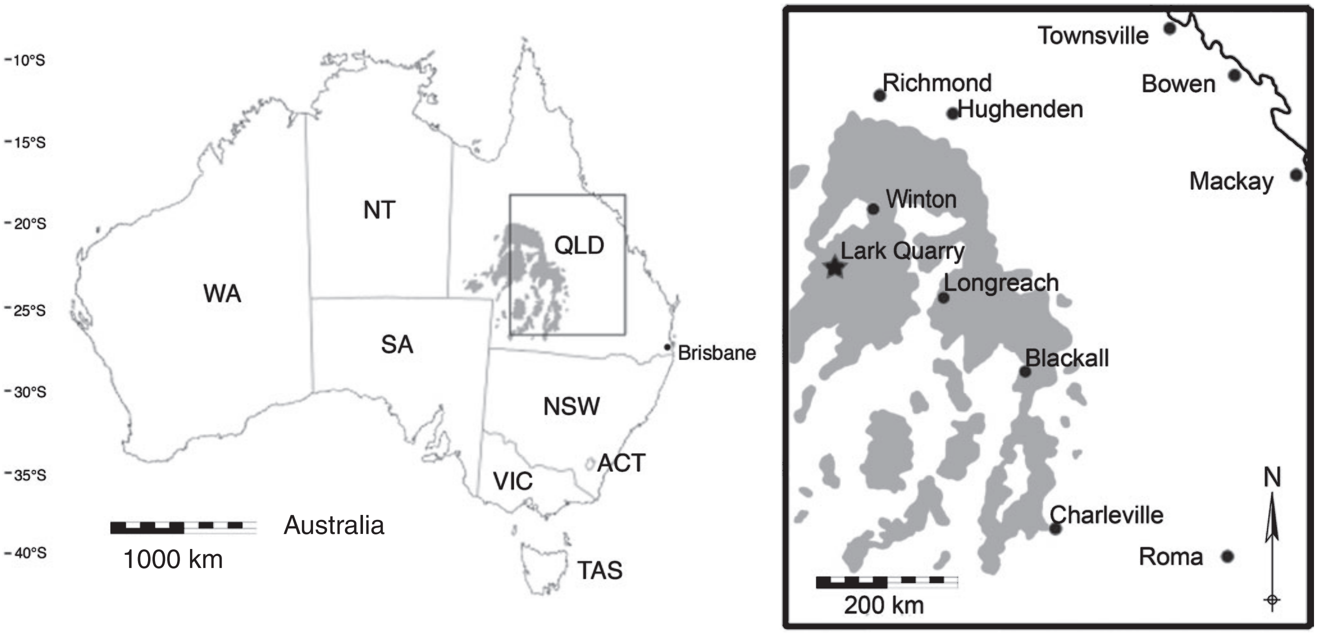

Fig. 1. A map of Australia, indicating the location of Lark Quarry Conservation Area, which includes UQL-LQ-II and UQL-LQ-III. Area marked in grey indicates the extent of outcrop of the Winton Formation in Queensland. NT, Northern Territory; Qld, Queensland; NSW, New South Wales; ACT, Australian Capital Territory; Vic., Victoria; Tas., Tasmania; SA, South Australia; and WA, Western Australia.

(Fig. 2), and were preserved from edge to mid-vein on at least one side (Fig. 3).

This calculated mean of the natural logarithm of the leaf areas was then used in the formula from Wilf *et al*. (1998) to estimate MAP, as follows:

$$\ln(\mathrm{MAP}) = 0.548\ \mathrm{MlnA} + 0.768,\ r^2 = 0.760.$$

The MAP s.e. was calculated as the difference between the mean MAP estimate and MAP estimates derived using mean leaf area ± s.e.; because these estimates are calculated from natural logarithms, they are asymmetrical.

Leaf-margin analysis

Leaf-margin analysis is based on the relationship between woody dicot leaf margin and temperature, namely, that the proportion of toothed leaf margins decreases with increasing MAT. The first regression of that relationship was established in the 1990s (Wing and Greenwood 1993), and others for different regions have followed (Gregory-Wodzicki 2000; Kowalski 2002; Greenwood *et al*. 2004; Traiser *et al*. 2005; Miller *et al*. 2006; Steart *et al*. 2010). Although the majority of studies using LMA has focussed on the Palaeogene and Neogene, Upchurch and Wolfe (1987) suggested that this relationship was already established by the Cenomanian, and it has since been applied to other Early–Late Cretaceous localities (e.g. Miller *et al*. 2006).

For LMA, the proportion of 'entire' to 'toothed' specimens of leaf impressions was calculated. The cause of the difference between regression equations for different regions is not completely understood. Although many of the regressions are similar within the tropical to cool-temperate regions, the Australian equation has a similar slope but a higher intercept (Greenwood *et al*. 2004; Fig. 3). An interesting hypothesis that explains the difference between the Australian regression and other southern and northern hemisphere equations is the high number of myrtaceous taxa in Australian forests, which are predominantly 'untoothed' regardless of temperature (Jordan 1997); however, other hypotheses have been proposed (Greenwood *et al*. 2004). To confirm the Myrtaceae bias hypothesis, a comparison of the Australian regression with and without myrtaceous taxa should be made. As we believe Myrtaceae is the most likely cause of the higher intercept, and because the Australian dominance of Myrtaceae appears to not extend to the Cretaceous, we used the original regression equation (Wolfe 1979; Wing and Greenwood 1993) to determine MAT as follows:

$$\mathrm{MAT}_{\mathrm{LMA}} = 30.6 \times \mathrm{P}_{\mathrm{margin}} + 1.141,$$

where $\mathrm{P}_{\mathrm{margin}}$ is the proportion of dicot species or morphospecies in which the margin is entire.

Climate leaf-analysis multivariate program

Unlike the univariate methodology of LAA and LMA, CLAMP uses a suite of 31 morphological characters of woody dicotyledonous plants, and the correlative relationship of these characters to particular climate variables to estimate the climatic conditions at a given locality (Wolfe 1995). The physiognomic characters correlate with climate variables such as MAT, growth season (in months), growth-season precipitation and enthalpy, by using the ordination technique canonical correspondence analysis.

To conduct the CLAMP analysis, we used CLAMP Online (Yang *et al*. 2011), a form-based web facility, and the scoresheets available on the associated website (http://clamp.ibcas.ac.cn/Clampset2.html, accessed 17 September 2013). We used the

Table 1. Data for calculating the mean annual precipitation from woody dicot leaf area of the eight morphotypes identified at Lark Quarry

Morphotype	Length (mm)	Width (mm)	Area (mm^2)	Ln (area)	Mean ln(area) per morphotype
A	125	12	1000	6.907755	6.907755279
B	145	70	6766.666	8.819763	
B	78	45	2340	7.757906	
B	87	60	3480	8.154787	
B	180	78	9360	9.144200	
B	75	72	3600	8.188689	
B	114	63	4788	8.473868	
B	130	76	6586.666	8.792802	8.476002586
C	95	46	2913.333	7.97705	
C	125	62	5166.666	8.549983	
C	61.2	41.7	1701.36	7.43918	
C	85.5	42.5	2422.5	7.792555	
C	100	77	5133.333	8.5435	
C	90	55	3300	8.101677	
C	95	52	3293.333	8.099655	8.0719455
D	52	45	1560	7.3524	7.3524411
E	80	60	3200	8.070906	
E	55	52	1906.666	7.553111	
E	50	47	1566.666	7.356705	
E	49.5	41.4	1366.2	7.219788	
E	48.5	40	1293.333	7.164978	
E	38	20	506.666	6.227853	
E	45.5	27	819	6.708084	7.185918197
G	75	45	2250	7.718685	
G	80	70	3733.333	8.225056	
G	38	42	1064	6.96979	7.637844311
H	20	20	266.666	5.585999	5.585999439
McLoughlin *et al.* 2010	107	72	5136	8.544029	
McLoughlin *et al.* 2010	130	96	8320	9.026417	
McLoughlin *et al.* 2010	110	84	6160	8.725832	
McLoughlin *et al.* 2010	170	92	10426.666	9.252121	
McLoughlin *et al.* 2010	120	78	6240	8.738735	
McLoughlin *et al.* 2010	140	88	8213.333	9.013514	
McLoughlin *et al.* 2010	120	80	6400	8.764053	8.866386314
				Total MLnA	7.510536591
				Ln(MAP)	4.883774052
				MAP	1321 mm

settings ‘Physg3brc’ because it is the most precise calibration dataset for warm (above 0°C) localities, which was hypothesised for our locality, and ‘MET3BR’, the corresponding meteorological data array (Spicer *et al.* 2009). The diversity of our assemblage was low, including nine morphotypes, which is below the recommended number of morphotypes for this analysis; thus, the completeness of the data for the morphotypes represented is especially important. The CLAMP completeness index for the Lark Quarry Flora was 0.82, which is above the recommended 0.66 (Yang *et al.* 2011).

Results

The palaeoflora of The Lark Quarry Conservation Area is co-dominated by angiosperms and gymnosperms (araucarians and podocarps), with a minor representation of ginkgos and ferns. The following are the scores for the frequency of specimens of each group in the sample: UQL-LQ-II scored 61 gymnosperms, 79 angiosperms, zero ginkgophytes and six pteridophytes, and UQL-LQ-III scored 83 gymnosperms, 73 angiosperms, four ginkgophytes and nine pteridophyte specimens.

Leaf-area analysis

The LLA yielded a MAP estimate of 1321 mm + 413 mm – 315 mm; however, we note that because of the low number of morphotypes, the error may be as much as twice that amount. Also potentially increasing the error, these are likely underestimates compared with approximations of error of Wilf *et al.* (1998), because some morphotypes were only represented by one specimen. As a result, we were unable to calculate estimates of uncertainty for the variation of leaf size in these morphotypes in the MAP-error calculations.

Leaf-margin analysis

The proportion of morphotypes with entire-margined leaves at the Lark Quarry sites was 0.5, on the basis of the specimens present of recognised morphotypes from McLoughlin *et al.* (1995, 2010).

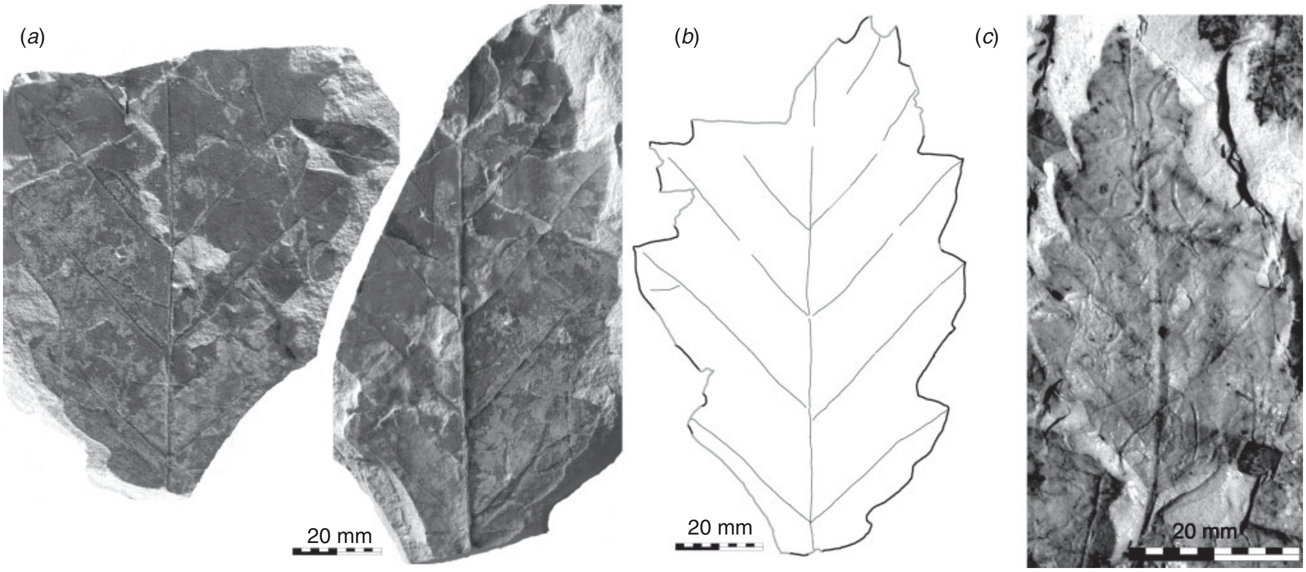

Fig. 2. An example of a specimen from UQL-LQ-III suitable for leaf-area analysis, with near full length and width preserved. A, part and counterpart; B, schematic of the combined part and counterpart; C, comparable material, Winton Formation Leaf morphotype C (QMF32510). All scale bars = 20 mm.

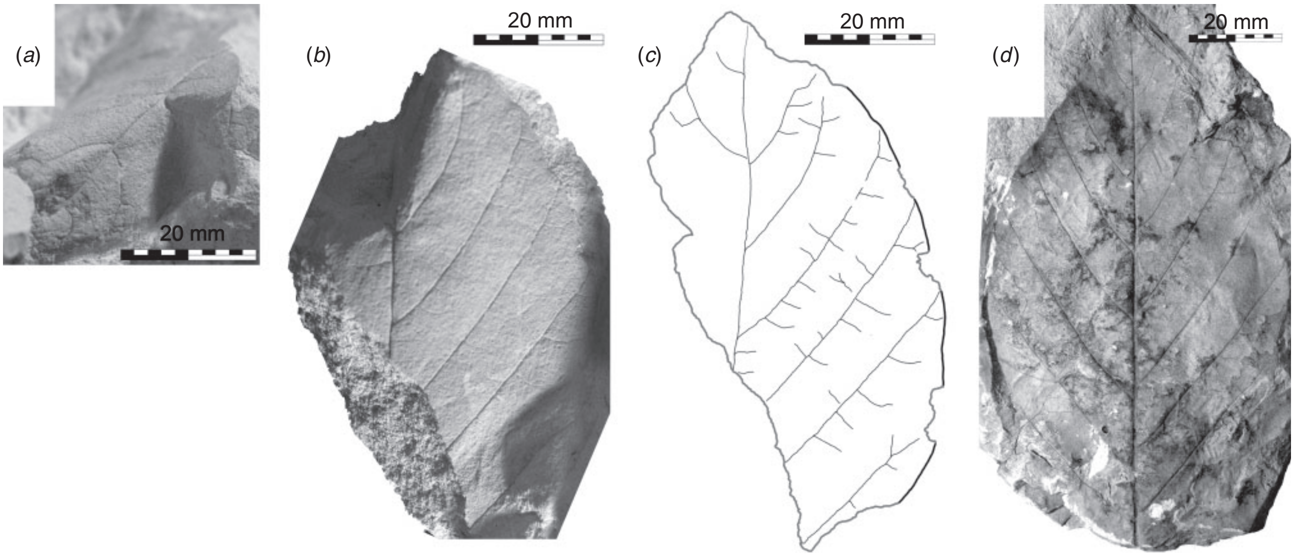

Fig. 3. An example of a specimen from UQL-LQ-II suitable for leaf-area analysis, folded in the matrix, with near full length, and the leaf edge to past the mid-vein preserved. A, folded distal end; B, main plane of preservation; C, schematic of the leaf 'flattened'; and D, comparable material, Winton Formation Leaf morphotype B (QMF32459). All scale bars = 20 mm.

The regression equation resulted in a MAT estimation of 16.4°C and a binomial sample error of 5.3°C, as per Wilf (1997), which is quite high as a result of a low sample size.

Climate leaf-analysis multivariate program

The CLAMP analysis estimated ~16 ± 2°C (true error would have been higher because of a low sample size, as per LAA) for MAT, a suggested growth season of 9 months, and resulted in a growth-season precipitation of 1073 ± 483 mm. Other CLAMP outputs are not reported because these could not be compared with results from LAA or LMA.

Discussion

The results of the present study indicated that UQL-LQ-II and UQL-LQ-III were mesothermal, with high precipitation and a long growth season. Because of the low diversity of morphospecies represented at these localities, and the low number of those that were adequately preserved to be informative in the analyses, it is especially important to compare and interpret them in the context of all other available palaeoclimatic data for the period. The Lark Quarry estimates are very similar to, although slightly warmer than, those derived from museum collections from throughout the Winton Formation

(Fletcher *et al*. in press), as tested with CLAMP and bioclimatic analysis of non-angiosperms, a somewhat independent dataset. The CLAMP analysis estimated 13.6 ± 2°C for MAT for the museum collections, compared with 16 ± 2°C from the present sample, a growth season of 7.8 ± 1.1 months compared with 9 months, and growth-season precipitation of 1289 ± 483 mm compared with 1073 ± 483 mm herein. The major difference between the two CLAMP datasets was that representatives of some morphotypes were larger in the Lark Quarry material, and thus were classed one category larger than those in the type collection. The bioclimatic analysis yielded similar estimates of 15.9 ± 1.2°C for MAT and 1646 ± 370 mm for MAP. Unfortunately, the Lark Quarry sediment did not yield palynological material suitable for a comparable palynologically derived bioclimatic analysis. However, our estimates of LMA of 16.4°C and LAA of 1321 mm + 413 mm – 315 mm are within the error for the estimates of museum collection-based study, with temperature being higher than in the museum collection-based study of the Winton Formation flora. This supports our hypothesis that collections from museums magnify the existing taphonomic cold-temperature bias; we consider it unlikely to represent a true change in temperature, because the sediments from which the museum collections were taken are approximately coeval with those from Lark Quarry (Tucker *et al*. 2013).

Although the Lark Quarry angiosperm material is not diverse or numerous, and comes from a time early in the diversification of eudicot angiosperms, once the likely minimum 2.5–4°C wet-soil bias of Kowalski and Dilcher (2003; see Introduction) is accounted for, the palaeoclimatic estimates produced are in keeping with other measures of climate. The results of the present study are consistent with the 17–19°C MAT for the approximate latitude and time of the global climate estimates from Hay (2011). Our results broadly agree with sea-surface temperatures estimated from oxygen isotopes in calcareous sediments (17.9°C) from an approximately coeval and similar-latitude locality in Western Australia (Clarke and Jenkyns 1999). In comparison to estimates from other floral studies in the southern hemisphere, they are warmer than those for the older Albian–Cenomanian of the New Zealand Clarence Valley (MAT ~10°C; Parrish *et al*. 1998), which is expected considering its much higher palaeolatitude at the time (70–85°), and are in broad agreement with the results of other studies of the palaeoclimate of the Winton Formation (Fletcher *et al.* in press). Although other Gondwanan angiosperm assemblages of this time are more diverse than the Winton Formation flora, such as the Cenomanian–Conician Mata Formation (~50°; Iglesias *et al.* 2007), palaeoclimate estimates are not yet available for comparison. A direct comparison with the results of a physiognomic analysis of the Mata Formation flora may prove informative in the future.

In addition to floral methods, the diverse fauna of the Winton Formation also offers climate information. The occurrence of the basal eusuchian crocodyliform, *Isisfordia duncani* (Salisbury *et al.* 2006), limits MAT to >16°C if eusuchians are accepted as paleothermometers (Markwick 1994, 1998). Similarly, freshwater turtles from the Winton Formation (Molnar 1991; Salisbury *et al.* 2006) support our climate estimates, because even cold-adapted modern freshwater turtles require warmest mean monthly temperatures over 17.5°C (Tarduno *et al.* 1998). Finally, the lungfish *Metaceratodus ellioti* is known from the Winton Formation (Kemp 1997), and its modern descendants have a distribution limited to the tropics and subtropics of Australia, South America and Africa, also indicating MAT of >16°C.

By comparing the results of the present study with those from other types of analysis, and knowing what we can discern as limits for the fauna that occurred in the area, as well as comparing this locality to others and global estimates, we are beginning to test whether foliar physiognomy has potential at low-diversity sites near the beginning of the Eudicot radiation. Our results support previous studies (Upchurch and Wolfe 1987; Miller *et al*. 2006; Fletcher *et al.* in press), indicating that foliar physiognomic methods may be useful for estimating palaeoclimates from the early Late Cretaceous. They also suggest that foliar physiognomy may have some utility across poorly preserved assemblages and low-diversity localities, when used with caution. Low-diversity localities are likely to give broad indications of climate at best, and should not be taken as precise estimates, especially if used in the absence of other climate proxies.

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