PALEOCLIMATE OF THE LATE CRETACEOUS (CENOMANIAN–TURONIAN) PORTION OF THE WINTON FORMATION, CENTRAL-WESTERN QUEENSLAND, AUSTRALIA: NEW OBSERVATIONS BASED ON CLAMP AND BIOCLIMATIC ANALYSIS

Author(s): TAMARA L. FLETCHER, DAVID R. GREENWOOD, PATRICK T. MOSS, and STEVEN W. SALISBURY

Source: PALAIOS, 29(3):121-128. 2014.
Published By: Society for Sedimentary Geology
URL: http://www.bioone.org/doi/full/10.2110/palo.2013.080

PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2014, v. 29, 121–128
Research Article
DOI: http://dx.doi.org/10.2110/palo.2013.080

1926 SEPM Society for Sedimentary Geology

PALEOCLIMATE OF THE LATE CRETACEOUS (CENOMANIAN–TURONIAN) PORTION OF THE WINTON FORMATION, CENTRAL-WESTERN QUEENSLAND, AUSTRALIA: NEW OBSERVATIONS BASED ON CLAMP AND BIOCLIMATIC ANALYSIS

TAMARA L. FLETCHER,[1,2] DAVID R. GREENWOOD,[3,4] PATRICK T. MOSS,[2] AND STEVEN W. SALISBURY[1]
[1]*School of Biological Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia*
[2]*Climate Research Group, School of Geography, Planning and Environmental Management, The University of Queensland, Brisbane, Queensland 4072, Australia*
[3]*Department of Biology, Brandon University, Brandon, Manitoba R7A 6A9, Canada*
[4]*Barbara Hardy Institute, University of South Australia, Mawson Lakes, South Australia 5095, Australia*
e-mail: t.fletcher1@uq.edu.au

ABSTRACT: **Although there is an emerging consensus about global climate patterns during the Cretaceous, details about the climate in Australia at this time are poorly resolved, and estimates for terrestrial climate are scarce. Using Climate Leaf Analysis Multivariate Program (CLAMP) and Bioclimatic Analysis (BA) on plant fossils from the mid- to Upper Cretaceous Winton Formation, central-western Queensland, and working within the context of global paleoclimatic reconstructions and the vertebrate fauna from this unit, we have improved the temporal and geographic resolution of Australia's Cretaceous climate. During the time that the Cenomanian–Turonian portion of the Winton Formation was deposited, the climate in central-western Queensland was warm, wet, and relatively equable. Frost would have been extremely uncommon, if it occurred at all, and much of the year would have been favorable for plant growth. These results are consistent with both previous isotope records for northern Australia, and the fauna of the Winton Formation, and are in keeping with current reconstructions of global Cretaceous climates.**

INTRODUCTION

Global-scale patterns of climate during the Cretaceous are broadly known. The general consensus is that the mid- to Late Cretaceous (Albian–Turonian) was warm and equable (Barron 1983; Ufnar et al. 2008), with dramatic temperature increases through the Albian (Hay 2008, 2011; Fig. 1A) following the Aptian–Albian cold snap (Mutterlose et al. 2009). However, there are significantly fewer sites and greater temporal restriction for terrestrial climate reconstructions than for oceanic ones (Fig. 1B), which indicate that the warming period may have commenced as early as the Barremian, slowly increasing to a peak in the Albian, then a cooling period, followed by an even higher temperature peak in the late Cenomanian.

Currently, the most widely recognized terrestrial proxies for Cretaceous climate in Australia are based on a series of lower Aptian–lower Albian fossil-bearing localities in southern Victoria (Wagstaff and McEwan Mason 1989; Rich and Vickers-Rich 2000; Rich et al. 2002; Seegets-Villiers 2012). However, there are a number of other studies that have contributed to our understanding of Australia and New Zealand's Cretaceous environments, and their resulting estimates regarding the paleotemperature are summarized here (Table 1). Although Hay's (2011) global climate estimates for the Cretaceous are broadly in keeping with these observations of the Australian paleoclimate, higher temporal and geographic resolution of the climate, and correlations with changes in the floral and faunal components of the paleoenvironment, are needed for terrestrial localities globally and for Australian sites specifically. This more complete dataset will facilitate and increase the resolution of our modeling and enable application of the climate data to other fields, such as studies of the physiology and evolution of ancient flora and fauna.

Although often considered a period of high humidity and precipitation, Albian to Turonian climate reconstructions do not preclude the occurrence of wildfires as an important part of the paleoecology of various floral assemblages. Charcoal deposits are found throughout the Albian to Turonian, from middle to high latitudes at a number of sites. Charcoal is widespread at some sites including the Winton Formation (Pole and Douglas 1999), and Waihere Beach and Tupuangi Bay on Pitt Island in the Chatham Archipelago, New Zealand (Pole and Philippe 2010). In contrast, charcoal is reported as scarce and indicative of rare events (Falcon-Lang et al. 2001) in the Albian sediments of Alexander Island, Antarctic Peninsula (Falcon-Lang et al. 2001), in the Gippsland–Otway basins, Australia (Seegets-Villiers 2012), and in the Albian–Cenomanian of Patagonia (Passalia 2007).

Based on these studies, and those listed in Table 1, it is clear that the complexity of the Australian Cretaceous paleoenvironment is not accurately captured by our current paleoclimatic overviews. Here we attempt to improve the temporal and geographic resolution of both Australian and global terrestrial climate patterns from the Cenomanian–Turonian. Following previous studies (e.g., Uhl et al. 2003; Greenwood et al. 2003, 2005; Grein et al. 2011; Reichgelt et al. 2013) that use multiple paleobotanical climate proxies, we use two techniques, with independent data sets, angiosperm and nonangiosperm, to overcome uncertainty inherent in very ancient plant fossil assemblages. We applied Climate Leaf Analysis Multivariate Program (CLAMP) to the Winton Formation angiosperm morphotypes identified by McLoughlin et al. (1995, 2010), and we applied Bioclimatic Analysis (BA) to the known flora from the youngest portion of the Winton Formation, excluding angiosperms.

Geology

The Winton Formation extends over a large geographic area of western Queensland, northeastern South Australia and northwestern New South Wales (Fig. 2; Gray et al. 2002). It is the uppermost unit of the Manuka

Published Online: June 2014
 0883-1351/14/029-121/$03.00

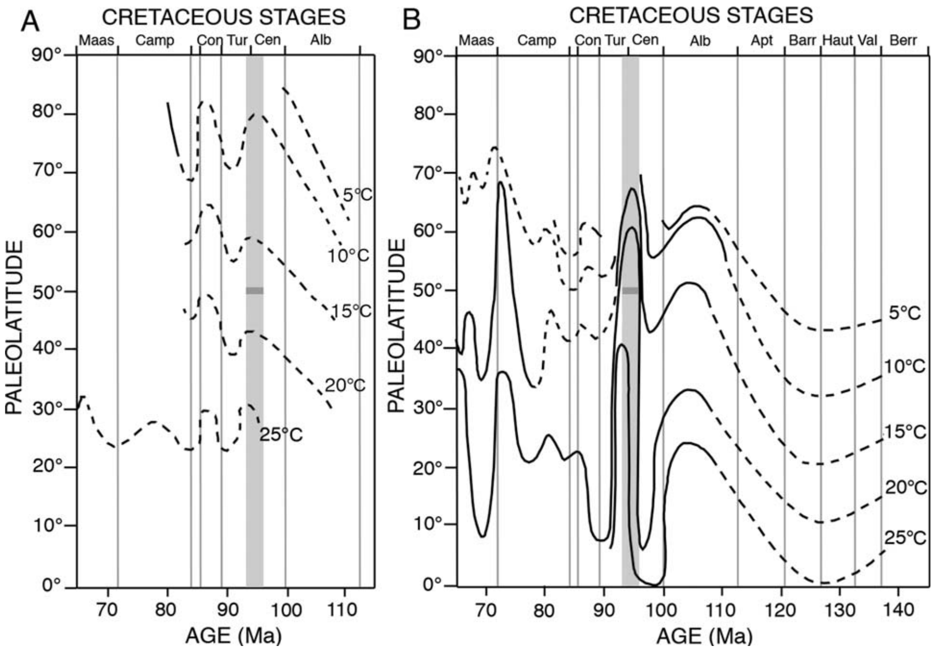

FIG. 1.—5–25 °C isotherm paleolatitudes through the Cretaceous, for **A)** terrestrial and **B)** oceanic environments. The approximate age of our localities in light gray, and the approximate paleolatitude crosses this as a dark-gray line. Dashed lines represent the more uncertain estimates. This figure is modified from the global paleotemperature reconstruction by Hay (2011).

TABLE 1.—*Summary table of the paleoclimate of the Australian region during the Cretaceous with notably few mid- to Upper Cretaceous localities represented.*

Epoch	Age	Approximate paleolatitude	MAT estimate	Location	Proxy	Citation
Early Cretaceous	early Aptian–early Albian	70° south	0°C	Terrestrial southern Victoria	Oxygen isotopes from carbonate concretions	Gregory et al. 1989
Early Cretaceous	Aptian–Albian	70° south	Warm to cool temperate	Terrestrial southern Victoria	Palaeobotanical	Douglas and Williams 1982
Early Cretaceous	late Aptian	65–70° south	1.9–7°C	Bottom water of shallow seaway eastern Australia	Glendonites	De Lurio and Frakes 1999
Early Cretaceous	Probable late Aptian	55–65° south	Indicates presence of freezing	Sea surface eastern Australia	Lonestones	Frakes and Krassay 1992
Early Cretaceous	Neocomian–Albian	70° south	Cool, warming into the Albian	Terrestrial southern Victoria	Broad assessment of flora and fauna	McLoughlin et al. 2002
Early Cretaceous	late Aptian–early Cenomanian	40° south	10°C	Sea Surface western Australia	Oxygen isotopes in belemnites	Price et al. 2012
Early Cretaceous	Albian	40° south	15°C	Sea Surface western Australia	Oxygen isotopes in belemnites	Price et al. 2012
Early Cretaceous	Aptian–Albian	40–55° south	10°C	Sea Surface northern Queensland	Oxygen isotopes in belemnites	Price et al. 2012
Early Cretaceous	Albian	70° south	10°C	Terrestrial southern Victoria	Leaf physiognomy, cuticle thickness, and the proportion of deciduous plants	Parrish et al. 1991
Early Cretaceous	Neocomian to Early Cretaceous Barremian	45–55° south	Mesothermal (and humid)	Terrestrial West Australia	Growth indices from fossil wood, plant presence	McLoughlin 1996
Early Cretaceous	Albian	45–55° south	10°C	Sea surface western Australia	Oxygen isotopes in belemnites	Pirrie et al. 1995
Early Cretaceous	late Albian	45–60° south	11.9°C (northeast) 16.3°C (southwest)	Eromanga sea surface eastern Australia	Oxygen isotopes in belemnites	Stevens and Clayton 1971
Early Cretaceous	Study includes Aptian–Santonian	54–47° south	12.3°C Aptian	Sea surface western Australia	Oxygen isotope temperatures from calcareous sediments	Clarke and Jenkyns 1999
Late Cretaceous	Study includes Aptian–Santonian	54–47° south	17.9°C Cenomanian Turonian boundary	Sea surface western Australia	Oxygen isotope temperatures from calcareous sediments	Clarke and Jenkyns 1999
Early–Late Cretaceous	late Albian–Cenomanian	80° south	10°C	Terrestrial New Zealand	Leaf physiognomy	Parrish et al. 1998
Late Cretaceous	Turonian	75° south	Cool	New Zealand	Conifer leaf size, and large leaf size of the deciduous angiosperm taxa	Pole and Philippe 2010

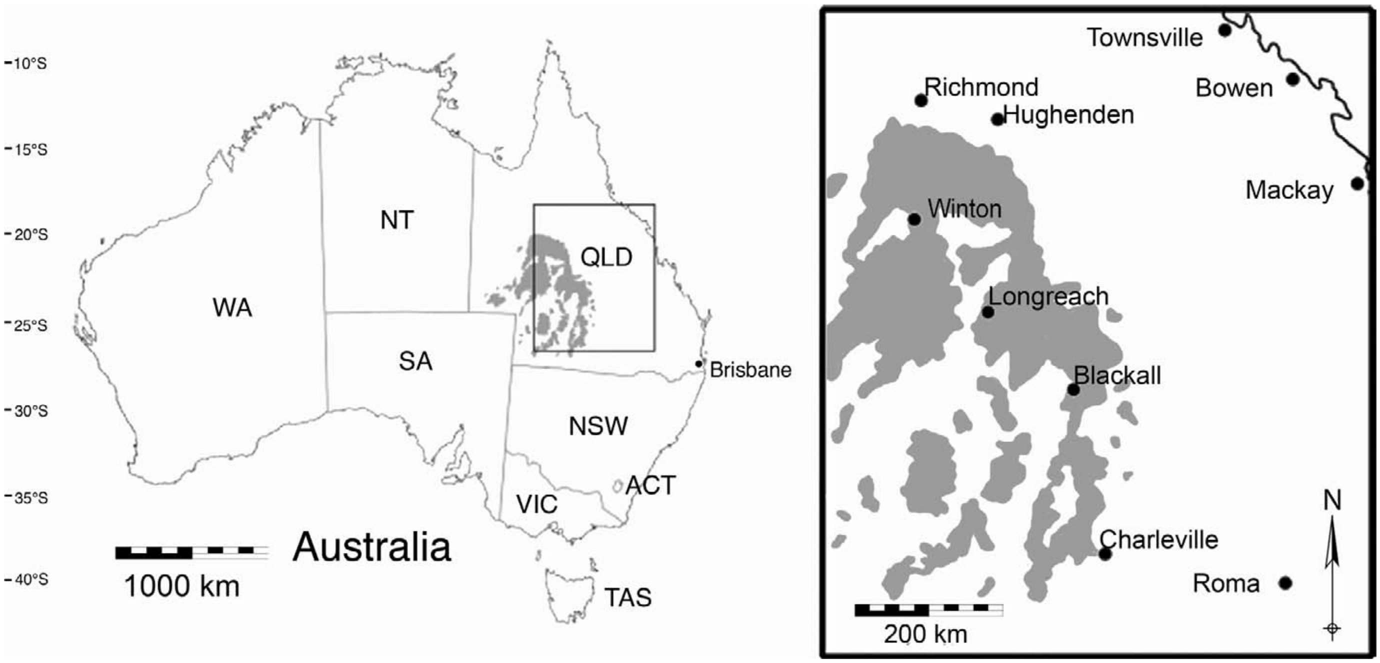

FIG. 2.—A map of Australia. Area marked in gray indicates the extent of the outcropping of the Winton Formation in Queensland. State abbreviations: NT, Northern Territory; QLD, Queensland; NSW, New South Wales; ACT, Australian Capital Territory; VIC, Victoria; TAS, Tasmania; SA, South Australia; WA, Western Australia.

Subgroup within the Rolling Downs Group, and the youngest Cretaceous strata of the Eromanga Basin (Gray et al. 2002). The Winton Formation has until recently been regarded as mid-Cretaceous (latest Albian–Cenomanian) in age based on palynology, corresponding to the upper *Phimopollenites pannosus* and *Appendicisporites distocarinatus* spore-pollen zones (Dettmann et al. 1992). A new study (Tucker et al. 2013), using U-Pb isotope dating of detrital zircons by laser ablation, places initial deposition of the Winton Formation in the late Albian, while most of the important vertebrate and plant fossil-bearing localities are close to the Cenomanian–Turonian boundary. At this time, these localities would have been at approximately 50°S (Li and Powell 2001).

The Winton Formation consists of repeated facies that represent major channels, flood basins, and mires, all signifying a freshwater fluvial–lacustrine environment deposited on a broad coastal plain as the epicontinental Eromanga Sea withdrew (Exon and Senior 1976; McLoughlin et al. 1995; Tucker et al. 2013). They are complex and repetitive including fine- to medium-grained feldspatholithic or lithofeldspathic arenite, siltstone, mudstone, and claystone (Fielding 1992; Romilio and Salisbury 2011; Tucker et al. 2011, 2013; Romilio et al. 2013) with very minor coal seams (Senior et al. 1978). Vertebrate fossils and associated plant remains in the Winton Formation are often found in point bar deposits, crevasse splay from flood events, and ox-bow lakes (Salisbury et al. 2006a, 2006b; Tucker et al. 2011). The Winton Formation conformably overlies the shallow marine and paralic sediments of the Makunda Formation (Gray et al. 2002).

MATERIALS AND METHODS

Climate Leaf Analysis Multivariate Program

Foliar physiognomy is based on the premise that the morphological characters of leaves correlate with climate constantly through time, perhaps because the morphological characters of leaves represent adaptive strategies to a plant's evolutionary environment, and that the mean phenotype approximates the optimal phenotype for that environment (Wolfe 1993; Jordan 1997; Greenwood 2007; Peppe et al. 2011; Royer 2012). CLAMP is one example of multivariate foliar physiognomy. It uses the correlative relationship of a suite of 31 morphological characters of dicotyledonous plants to a particular climate from a global survey of modern localities to estimate the climatic conditions at a fossil locality using Canonical Correspondence Analysis (Wolfe 1995; Spicer et al. 2009). Peppe et al. (2011) reported a global survey of leaf physiognomy and climate across 92 sites, and provided a digital calibration for estimating paleoclimate based on scanning leaf fossils for digital scoring of continuous morphological characters. This method, however, is impractical to apply to leaf floras dominated by incomplete leaves preserved as low contrast impressions and compressions that often occur as curled laminae. As this is the condition of the Winton flora, Digital Leaf Physiognomy was not attempted as part of the present analysis.

To conduct the CLAMP analysis we used CLAMP Online (http://clamp.ibcas.ac.cn/Clampset2.html), and a dataset comprising the nine known Winton Formation angiosperm morphotypes as described by McLoughlin et al. (1995, 2010; Scoresheet available: Supplementary file 1, see Acknowledgments). We used the settings Physg3brc, as it is the most precise calibration data set for warm (above 0 °C) localities, which was hypothesized for our locality, and MET3BR, the corresponding meteorological data array (Spicer et al. 2009). As the completeness score for the character coded was 0.87, above the 0.66 limit considered to increase error significantly above the calibration data set (Yang et al. 2011), the errors quoted are the passive uncertainties for Physg3brc + MET, ±1 standard deviation, as supplied at CLAMP online. However, it should be noted that there are a wide range of uncertainties that are difficult or impossible to account for (see Green 2006; Greenwood 2007), as well as lingering concerns regarding spatial autocorrelation or regional signals (e.g., Greenwood et al. 2004; Adams et al. 2008; Peppe et al. 2011), in addition to the very low diversity of leaf morphotypes at this locality from early in the eudicot radiation. Thus results should not be considered as precise estimates, with accuracy for mean annual temperature (MAT) likely no better than ± 3 °C (Greenwood 2007).

TABLE 2.—*The nonangiosperm plant taxa from the Winton Formation (modified from McLoughlin et al. 2010), with the addition of microflora where groups were not otherwise represented, or their age within the Winton Formation was uncertain. Modern relatives listed were used in the Bioclimatic Analysis.*

Plant group	Representative taxa and authorities	Publication	Modern relative
Hepaticales	*Marchantites marguerita* Dettmann and Clifford 2000	Dettmann and Clifford (2000)	Unknown affiliation
Equisetales	Equisetalean rhizomes and nodal diaphragms	McLoughlin et al. (2010)	*Equisetum* - Uninformative
Pterophyta	Aff. Schizaeaceae: *Lygodium*?	Peters and Christophel (1978)	*Lygodium*
	Osmundaceae: *Phyllopteroides macclymontae* McLoughlin et al. 1995	McLoughlin et al. (1995, 2010)	*Osmunda*
	?Osmundaceae: *Cladophlebis* sp.	McLoughlin et al. (1995)	*Osmunda*
	Gleicheniaceae: *Microphyllopteris* sp. cf. *M.gleichenoides* (Oldham and Morris) Walkom 1919	McLoughlin et al. (1995)	*Gleichenia*
	Family uncertain: *Sphenopteris* sp. cf. *S. warragulensis* McCoy in Stirling 1892	McLoughlin et al. (1995)	Extinct and no close affiliation
	Family uncertain: *Sphenopteris* sp.	McLoughlin et al. (1995)	Extinct and no close affiliation
	Indeterminate fern pinnule	McLoughlin et al. (1995)	Unknown affiliation
	Tempskyaceae: *Tempskya judithae* Clifford and Dettmann 2005	Clifford and Dettmann (2005)	Extinct and no close affiliation
	Dicksoniaceae: *Trilobosporites tribotrys* Dettmann 1963, *T. trioreticulosus* Cookson and Dettmann 1958	Martin (1998)	*Dicksonia*
	Cyatheaceae: *Cyathidites australis*, *C. minor* Couper 1953	Martin (1998)	*Cyathea*
Cycadales	*Pterostoma* spp.	Pole and Douglas (1999)	*Macrozamia*, *Lepidozamia*, *Cycas*, *Stangeriaceae*
Ginkgoales	*Ginkgo wintonensis* McLoughlin et al. 1995	McLoughlin et al. (1995)	*Ginkgo* (not used due to restricted, uncertain modern range)
	Up to four *Ginkgo* spp.	Pole and Douglas (1999)	*Ginkgo* (as above)
Pinophyta	Cupressaceae: *Austrosequoia wintonensis* Peters and Christophel 1978 and comparable forms	Peters and Christophel (1978), McLoughlin et al. (1995, 2010)	*Athrotaxis*, *Metasequoia*, *Glyptostrobus*, *Cryptomeria*, *Callitris*, *Sequoia*, *Libocedrus*, *Taxodium*
	Araucariaceae: at least three species of strap-, scale-, and awl-leafed shoots, together with pollen cones and ovuliferous cone scales, a foliage bearing twig and cluster of cone scales	Pole (2000), Dettmann et al. (1992), Mcloughlin et al. (2010)	*Agathis atropurpurea*, *A. microstachya*, *A. australis*, *Araucaria bidwilii*, *A. cuninghamii*, *A. araucana*
	?Podocarpaceae: *Elatocladus plana* (Feistmantel) Seward 1918, and five cuticle types	McLoughlin et al. (1995), Pole (2000)	*Dacrycarpus*, *Dacrydium*, *Halocarpus*, *Lagarostrobos*, *Lepidothamnus*, *Phyllocladus*, *Podocarpus*, *Prumnopitys*
	Cheirolepidaceae: four taxa, Classopilis	Pole (2000), Martin (1998)	Extinct and no close affiliation
	12 conifer species of uncertain familial affiliation	Pole (2000)	Unknown affiliation
Pentoxylales	*Taeniopteris* sp.	McLoughlin et al. (1995)	Unknown affiliation
Bennettitales	*Ptilophyllum fasciatum* Douglas 1969	Pole and Douglas (1999)	Extinct and no close affiliation
	Unidentified bennettitaleans	Pole and Douglas (1999)	Extinct and no close affiliation
	Otozamites sp. cf. *O. bengalensis* Oldham and Morris 1863	McLoughlin et al. (2010)	Extinct and no close affiliation
	Ptilophyllum sp.	McLoughlin et al. (2010)	Extinct and no close affiliation

Bioclimatic Analysis

Bioclimatic Analysis (Greenwood et al. 2003, 2005; Reichgelt et al. 2013) is a mutual climate range (MCR) method, similar to the Coexistence Approach (Kershaw 1997; Mosbrugger and Utescher 1997) and the Mutual Climatic Range Technique (Thompson et al. 2012), all of which use the climate envelope of the nearest living relatives of a fossil assemblage to estimate its likely climate. Bioclimatic Analysis defines the zone of overlap as between the 10th and 90th percentiles as an objective, statistical method of removing outliers (Reichgelt et al. 2013).

To conduct the Bioclimatic Analysis (as per Greenwood et al. 2005), we collated a taxonomic list of nonangiosperms for the Winton Formation (see Table 2). We used the reported affinities of the taxa known for the Winton Formation to identify modern analogues. The 27 (26 for CMMT and WMMT) modern taxa were chosen on the basis of their representation of the total climatic range of the related taxonomic group at the generic level where possible. We used the library of climate profiles for MAT and mean annual precipitation (MAP) developed by Greenwood et al. (2003, 2005) and Pross et al. (2012), with the addition of data from Mitchell (1991), Duarte et al. (2012), Mundo et al. (2012), and Reichgelt et al. (2013). The resultant estimates are taken as the mid-range of the data with extremes removed (10th to 90th percentiles, Appendix 1, see Acknowledgments).

RESULTS

The Winton CLAMP analysis (Fig. 3) shows the Winton site clearly within the calibration data space, addressing concerns in some analyses that Australian floras may not fall within the global climate-leaf physiognomy calibration (e.g., Greenwood et al. 2004; Green 2006). The CLAMP analysis estimates a MAT of 13.6 ± 2 °C. The growing season (GS) was 7.8 ± 1.1 months, with a growing season precipitation (GSP) of 1289 ± 483 mm and relative humidity (RH) of 73.9 ± 11.1%. The three wettest months' precipitation was 630 ± 206 mm (3-WET) and the three driest, 268 ± 137 mm (3-DRY). Cold month mean temperature (CMMT) and warmest mean monthly temperature (WMMT) were estimated, using

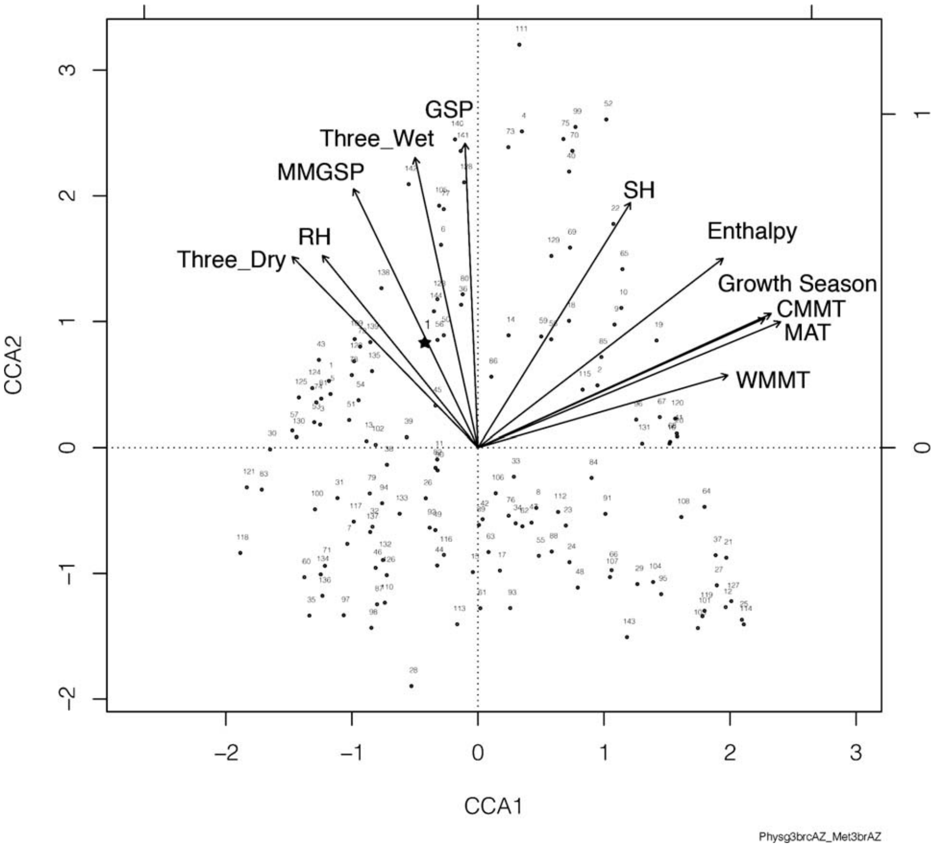

FIG. 3.—The CCA1 vs. CCA2 plot showing the spread of the modern sites (circles) that define physiognomic space for the Physg3brc calibration dataset, and the position of the Winton fossil flora (star), clearly within the calibration space. The climate vectors are defined by the black arrows. This graph is a reproduction of the PDF plot file produced by CLAMP Online. The identities of the calibration sites are shown as numbers relating to the order in which they are listed in the Physg3brcAZ file provided on the CLAMP website.

CLAMP, as 6.7 ± 3.4 °C and 21.2 ± 2.7 °C respectively. The Bioclimatic Analysis yielded a MAT estimate of 15.9 ± 1.2 °C, WMMT of 20.3 ± 2 °C, CMMT of 10.3 ± 1 °C and a MAP estimate of 1646 ± 370 mm. The estimates of MAT, WMMT, and CMMT from CLAMP and BA overlap within the errors of the estimates providing corroborating proxy climate data for the Cretaceous climate of the Winton Formation.

DISCUSSION

The results of this study indicate a humid (~ 74% RH), high (~ 1600 mm MAP) but seasonal rainfall (630 ± 206 mm 3-WET to 268 ± 137 mm 3-DRY), warm to hot summer (~ 21 °C WMMT, but with error that could class it as either), mesothermal climate (~ 9 °C CMMT to above −3 °C) for the mid-Cretaceous Winton Formation of central-western Queensland. Frost would have been extremely uncommon, if it occurred at all, and the seasons would have been favorable for plant growth for two thirds of the year (7.8 ± 1.1 months GS) with minimum day length at this latitude rarely below 8 hours. Thus the growing season was likely September to April, (i.e., the southern hemisphere summer) and limited by precipitation rather than temperature. These results are consistent with both previous isotope records for northern Australia, and the described fauna of the Winton Formation. The fauna known to have occurred within the Winton Formation includes a basal eusuchian crocodyliform, *Isisfordia duncani* (Salisbury et al. 2006a), which limits MAT to >16 °C if eusuchians are accepted as paleothermometers (Markwick 1994, 1998). It also has yielded freshwater turtles (Molnar 1991; Salisbury et al. 2006a), with even cold-adapted modern turtles requiring WMMTs over 17.5 °C (Tarduno et al. 1998), and the lungfish *Metaceratodus ellioti* (Kemp 1997), for which modern descendants have a distribution limited to the tropics and subtropics of Australia, South America, and Africa.

Miller et al. (2006) and Upchurch and Wolfe (1987) suggest that the relationship between foliar characters and climate measured in modern calibration datasets was established by the Cenomanian. The results of our CLAMP and BA support this supposition; however, in stating this there are several caveats that need to be taken into account. Although it has been demonstrated that CLAMP provides results for fossil assemblages that are not significantly affected by taphonomic information loss, provided the completeness score is above 0.66 (see Spicer et al. 2011), the effects of microclimate can result in lower MAT estimations than modern data calibrations suggest. Other authors have noted that within streambed assemblages, estimates will be systematically skewed towards lower MAT than the true MAT (Greenwood 2005), perhaps due to increased representation 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). Kowalski and Dilcher (2003) reported the effect of wet soils, causing a 2.5 to 10 °C underestimation of MAT compared to 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). Spicer et al. (2011) found that humid, warm climates with seasonal wet/dry seasons were likely to be the most impacted. As the Winton Formation paleoclimate appears to have each of these features, it was expected that the results of the CLAMP for the Winton Formation sample would underestimate the MAT by a minimum of 2.5–4 °C compared with BA. When the minimum wet soil bias to cooler MAT is accounted for, the results of the BA and CLAMP are concordant, and are reasonable estimates for the fauna, reinforcing the current paradigm of warm temperatures in the Cenomanian–early Turonian for central-western Queensland.

That global temperatures were comparatively isothermal during the mid-Cretaceous, as suggested by Barron (1983) and Ufnar et al. (2008), can be investigated by reviewing previous independent studies, with the addition of our estimates for the Winton Formation. Parrish et al. (1998) established a MAT of 10 °C for coeval localities in New Zealand at a latitude within the polar circle (70–85°S). Also for the mid-Cretaceous, and at approximate equivalent high latitude in northern Alaska, a similar MAT (within a few degrees of 10 °C) was found by Spicer and Parrish (1986) based on Leaf Margin Analysis. More recently, Spicer and Herman's (2010, their fig. 10) CLAMP values from the Cretaceous arctic, estimate a MAT of around 10 °C at 80°N, at the Cenomanian–Turonian boundary. Miller et al. (2006) investigated several North American mid-Cretaceous sites of varying latitudes. When temperature estimates from the mid-Cretaceous are compared with modern temperatures, the difference in temperature between the equator and comparable near-polar latitudes is 15.6 °C for the mid-Cretaceous and 33.3 °C for the present. This supports the claim of a more isothermal climate, from the equator to the poles, for the mid-Cretaceous.

Although Hay's (2011) modeling of terrestrial Cretaceous global temperatures was considered tentative, the temperature and precipitation estimates generated by the methods used herein support his reconstructions; namely, that the mid-Cretaceous generally had greenhouse conditions (warm, humid, and equable) that peaked toward the end of the Cenomanian to the very early Turonian. In many respects, this climate was similar to that during the Paleocene–Eocene Thermal Maximum (PETM; McInerney and Wing 2011).

CONCLUSIONS

This study examines the climate in central-western Queensland, Australia, with no other coeval estimates, indicating a humid and mesothermal environment. For these reasons it expands our knowledge of the Australian Cretaceous climates, and confirms that Australian climate patterns were at least broadly following the current global paleoclimate models. Due to the range of error in this analysis, the low diversity and the time over which the samples were deposited, more specific estimates cannot be made with confidence.

The Winton Formation is situated at a time of rapid floral change and significant diversification of the angiosperms. Better knowledge of the conditions under which angiosperms diversified may increase our understanding of their evolutionary history. Our results support CLAMP as a viable method for mid- to Late Cretaceous floras, with the noted caveats, and we have supported the theory that the modern correlations between climate and leaf physiognomy were established very early in angiosperm evolution.

Further studies of Cretaceous climates globally, particularly from terrestrial localities, are needed to increase the resolution of our modeling to be able to apply the climate data to other fields, such as studies of the physiology and evolution of ancient flora and fauna.

ACKNOWLEDGMENTS

We would like to thank Dr. Andrew Rozefeld and Professor Emeritus Trevor Clifford for early advice and comments. Dr. Peter Kershaw and an anonymous reviewer also provided constructive and insightful comments on earlier versions of our manuscript. Dr. John-Paul Zonneveld and the anonymous reviewers of this journal are thanked for their valuable input. For assistance and access to the type specimens, we would like to acknowledge the Geosciences staff of the Queensland Museum. This research was funded in part by the Australian Research Council (LP0347332 and LP0776851) and The University of Queensland (to SWS), in association with Isisford Shire Council, Longreach Regional Council, Winton Shire Council, Land Rover Australia, the Queensland Museum, and Carnegie Museum of Natural History. DRG's contribution was funded by prior funding from both the Australian Research Council (A39802019) and the Natural Sciences and Engineering Research Council of Canada (DG 311934). Supplemental material is available from the PALAIOS Data Archive: http://www.sepm.org/Page.aspx?pageID=332.

REFERENCES

Adams, J.M., Green, W.A., and Zhang, Y., 2008, Leaf margins and temperature in the North American flora: recalibrating the paleoclimatic thermometer: Global and Planetary Change, v. 60, p. 523–534.

Barron, E.J., 1983, A warm, equable Cretaceous: the nature of the problem: Earth-Science Reviews, v. 19, p. 305–338.

Burnham, R.J., Pitman, N.C.A., Johnson, K.R., and Wilf, P., 2001, Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest: American Journal of Botany, v. 88, p. 1096–1102.

Clarke, L.J., and Jenkyns, H.C., 1999, New oxygen isotope evidence for long-term Cretaceous climatic change in the Southern Hemisphere: Geology, v. 27, p. 699–702.

Clifford, H.T., and Dettmann, M.E., 2005, First record from Australia of the Cretaceous fern genus *Tempskya* and the description of a new species, *T. judithae*: Review of Palaeobotany and Palynology, v. 134, p. 71–84.

De Lurio, J.L., and Frakes, L.A., 1999, Glendonites as a paleoenvironmental tool: implications for Early Cretaceous high latitude climates in Australia: Geochimica et Cosmochimica Acta, v. 63, p. 1039–1048.

Dettmann, M.E., and Clifford, H.T., 2000, Gemmae of the Marchantiales from the Winton Formation (mid-Cretaceous), Eromanga Basin, Queensland: Memoirs of the Queensland Museum, v. 45, p. 285–292.

Dettmann, M.E., Molnar, R.E., Douglas, J.G., Burger, D., Fielding, C., Clifford, H.T., Francis, J., Jell, P., Rich, T., Wade, M., Rich, P.V., Pledge, N., Kemp, A., and Rozefelds, A., 1992, Australian cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications: Cretaceous Research, v. 13, p. 207–262.

Douglas, J.G., and Williams, G.E., 1982, Southern polar forests: the Early Cretaceous floras of Victoria and their palaeoclimatic significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 39, p. 171–185.

Duarte, L.D.S., Prieto, P.V., and Pillar, V.D., 2012, Assessing spatial and environmental drivers of phylogenetic structure in Brazilian *Araucaria* forests: Ecography, v. 35, p. 952–960.

Exon, N.F., and Senior, B.R., 1976, The Cretaceous geology of the Eromanga and Surat Basins: Bureau of Mineral Resources, Journal of Australian Geology and Geophysics, v. 1, p. 33–50.

Falcon-Lang, H.J., Cantrill, D.J., and Nichols, G.J., 2001, Biodiversity and terrestrial ecology of a mid-Cretaceous, high-latitude floodplain, Alexander Island, Antarctica: Geological Society of London, Journal, v. 158, p. 709–724.

Fielding, C.R., 1992, A review of Cretaceous coal-bearing sequences in Australia: Geological Society of America, Special Paper, v. 267, p. 303–324.

Frakes, L.A., and Krassay, A.A., 1992, Discovery of probably ice-rifting in the late Mesozoic of the Northern Territory and Queensland: Australian Journal of Earth Sciences, v. 39, p. 115–119.

Gray, A.R.G., McKillop, M., and McKellar, J.L., 2002, Eromanga Basin stratigraphy, *in* Draper, J.J., ed., Geology of the Cooper and Eromanga Basins, Queensland, Volume 1: Brisbane, Department of Natural Resources and Mines, 94 p.

Green, W.A., 2006, Loosening the clamp: an exploratory graphical approach to the Climate Leaf Analysis Multivariate Program: Palaeontologia Electronica, v. 9, p. 17 PE Article no. 9.2.9A.

Greenwood, D.R., 1992, Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates: Review of Palaeobotany and Palynology, v. 71, p. 149–190.

Greenwood, D.R., 2005, Leaf margin analysis: taphonomic constraints: PALAIOS, v. 20, p. 498–505.

Greenwood, D.R., 2007, North American Eocene leaves and climates: From Wolfe and Dilcher to Burnham and Wilf: Courier Forschungsinstitut Senckenberg, v. 258, p. 95–108.

Greenwood, D.R., Moss, P.T., Rowett, A.I., Vadala, A.J., and Keefe, R.L., 2003, Plant communities and climate change in southeastern Australia during the early Paleogene: Geological Society of America, Special Paper, v. 369, p. 365–380.

Greenwood, D.R., Wilf, P., Wing, S.L., and Christophel, D.C., 2004, Paleotemperature estimation using leaf-margin analysis: Is Australia different?: PALAIOS, v. 19, p. 129–142.

Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T., 2005, Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape: Canadian Journal of Earth Science, v. 42, p. 167–185.

Gregory, R.T., Douthitt, C.B., Duddy, I.R., Rich, P.V., and Rich, T.H., 1989, Oxygen isotopic composition of carbonate concretions from the Lower Cretaceous of Victoria, Australia: implications for the evolution of meteoric waters on the Australian continent in a paleopolar environment: Earth and Planetary Science Letters, v. 92, p. 27–42.

Grein, M., Utescher, T., Wilde, V., and Roth-Nebelsick, A., 2011, Reconstruction of the middle Eocene climate of Messel using palaeobotanical data: Neues Jahrbuch für Geologie und Paläontologie, v. 260, p. 305–318.

Hay, W.W., 2008, Evolving ideas about the Cretaceous climate and ocean circulation: Cretaceous Research, v. 29, p. 725–753.

Hay, W.W., 2011, Can humans force a return to a "Cretaceous" climate?: Sedimentary Geology, v. 235, p. 5–26.
Jordan, G.J., 1997, Uncertainty in palaeoclimatic reconstructions based on leaf physiognomy: Australian Journal of Botany, v. 45, p. 527–547.
Kemp, A., 1997, Four species of *Metaceratodus* (Osteichthyes: Dipnoi, Family Ceratodontidae) from Australian Mesozoic and Cenozoic deposits: Journal of Vertebrate Paleontology, v. 17, p. 26–33.
Kershaw, A.P., 1997, A bioclimatic analysis of early to Middle Miocene brown coal floras, Latrobe Valley, south-eastern Australia: Australian Journal of Botany, v. 45, p. 373–387.
Kowalski, E.A., and Dilcher, D.L., 2003, Warmer paleotemperatures for terrestrial ecosystems: Proceedings of the National Academy of Science U.S.A., v. 100, p. 167–170.
Li, Z.X., and Powell, C.M., 2001, An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic: Earth-Science Reviews, v. 53, p. 237–277.
Markwick, P.J., 1994, "Equability," continentality, and Tertiary "climate": The crocodilian perspective: Geology, v. 22. p. 613–616.
Markwick, P.J., 1998, Fossil crocodillians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 137, p. 205–271.
Martin, H.A., 1998, Late Cretaceous–Cainozoic palynology of the Poonarunna No. 1 well, central Australia: The Royal Society, South Australia, v. 122, p. 89–138.
McInerney, F.A., and Wing, S.L., 2011, The Paleocene–Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future: Annual Review of Earth and Planetary Science, v. 39, p. 489–516.
McLoughlin, S., 1996, Early Cretaceous macrofloras of Western Australia: Records of the West Australian Museum, v. 18, p. 19–65.
McLoughlin, S., Drinnan, A.N., and Rozefelds, A.C., 1995, A Cenomanian flora from the Winton Formation, Eromanga Basin, Queensland, Australia: Memoirs of the Queensland Museum, v. 38, p. 273–313.
McLoughlin, S., Tosolini, A.-M.P., Nagalingum, N.S., and Drinnan, A.N., 2002, The Early Cretaceous (Neocomian) flora and fauna of the lower Strzelecki Group, Gippsland Basin, Victoria, Australia: Association of Australian Palaeontologists, Memoir, v. 26, p. 1–144.
McLoughlin, S., Pott, C., and Elliot, D., 2010, The Winton Formation flora (Albian, Cenomanian, Eromanga Basin): implications for vascular plant diversification and decline in the Australian Cretaceous: Alcheringa, v. 34, p. 303–323.
Miller, I.M., Brandon, M.T., and Hickey, L.J., 2006, Using leaf margin analysis to estimate the mid–Cretaceous (Albian) paleolatitude of the Baja BC block: Earth and Planetary Science Letters, v. 245, p. 95–114.
Mitchell, N.D., 1991, The derivation of climate surfaces for New Zealand, and their application to the Bioclimatic Analysis of the distribution of Kauri (*Agathis australis*): Journal of the Royal Society of New Zealand, v. 21, p.13–24.
Molnar, R.E., 1991, Fossil reptiles in Australia, *in* Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H., eds., Vertebrate Palaeontology of Australasia: Pioneer Design Studio, Melbourne, p. 606–702.
Mosbrugger, V., and Utescher, T., 1997, The coexistence approach: a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 134, p. 61–86.
Mundo, I.A., Junent, F.A.R., Villalba, R., Kitzberger, T., and Barrera, M.D., 2012, *Araucaria araucana* tree-ring chronologies in Argentina: spatial growth variations and climate influences: Trees: Structure and Function, v. 26, p. 443–458.
Mutterlose, J., Bornemann, A., and Herrle, J., 2009, The Aptian–Albian cold snap: Evidence for "mid" Cretaceous icehouse interludes: Neues Jahrbuch für Geologie und Paläontologie, v. 252, p. 217–225.
Parrish, J.T., Spicer, R.A., Douglas, J.G., Rich, T.H., and Vickers-Rich, P., 1991, Continental climate near the Albian South Pole and comparison with climate near the North Pole [abstract]: Geological Society of America, Abstracts with Programs, v. 23, p. A302.
Parrish, J.T., Daniel, I.L., Kennedy, E.M., and Spicer, R.A., 1998, Paleoclimatic significance of mid-Cretaceous floras from the middle Clarence Valley, New Zealand: PALAIOS, v. 13, p. 149–159.
Passalia, M.G., 2007, A mid-Cretaceous flora from the Kachaike Formation, Patagonia, Argentina: Cretaceous Research, v. 28, p. 830–840.
Peppe, D., Royer, D., Cariglino, B., Oliver, S., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., and Adams, J., et al., 2011, Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications: New Phytologist, v. 190, p. 724–739, doi: 10.1111/j.1469-8137.2010.03615.x.
Peters, M.D., and Christophel, D.C., 1978, *Austrosequoia wintonensis*, a new taxodiaceous cone from Queensland, Australia: Canadian Journal of Botany, v. 56, p. 3119–3128.
Pirrie, D., Doyle, P., Marshall, J.D., and Ellis, G., 1995, Cool Cretaceous climates: new data from the Albian of Western Australia: Geologial Society of London, Journal, v. 152, p. 739–742.
Pole, M.S., 2000, Mid-Cretaceous conifers from the Eromanga Basin, Australia: Australian Systematic Botany, v.13, p. 153–197.
Pole, M.S., and Douglas, J.G., 1999, Bennettitales, Cycadales and Ginkgoales from the mid Cretaceous of the Eromanga Basin, Queensland, Australia: Cretaceous Research, v. 20, p. 523–538.
Pole, M., and Philippe, M., 2010, Cretaceous plant fossils of Pitt Island, the Chatham group, New Zealand: Alcheringa, v. 34, p. 231–263.
Price, G.D., Williamson, T., Henderson, R.A., and Gagan, M.K., 2012, Barremian–Cenomanian palaeotemperatures for Australian seas based on new oxygen-isotope data from belemnite rostra: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 358, p. 27–39.
Pross, J., Contreras, L., Bijl, P.K., Greenwood, D.R., Bohaty, S.M., Schouten, S., Bendle, J.A., Röhl, U., Tauxe, L., Raine, J.I., Huck, C.E., van De Flierdt T., Jamieson, S.S.R., Stickley, C.E., van De Schootbrugge B., Escutia, C., Brinkhuis, H., and 318 others, 2012, Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch: Nature, v. 488, p. 73–77, doi: 10.1038/nature11300.
Reichgelt, T., Kennedy, E.M., Mildenhall, D.C., Conran, J.G., Greenwood, D.R., and Lee, D.E., 2013, Quantitative palaeoclimate estimates for early Miocene southern New Zealand: evidence from Foulden Maar: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 378, p. 36–44.
Rich, T.H., and Vickers-Rich, P., 2000, Dinosaurs of Darkness: Bloomington, Indiana, Indiana University Press, 222 p.
Rich, T.H., Vickers-Rich, P., and Gangloff, R.A., 2002, Polar dinosaurs: Science, v. 295, p. 979–980.
Romilio, A., and Salisbury, S.W., 2011, A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity: Cretaceous Research, v. 32, p. 135–142.
Romilio, A., Tucker, R.T., and Salisbury, S.W., 2013, Re-evaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): No longer a stampede?: Journal of Vertebrate Paleontology, v. 33, p. 102–120.
Royer, D.L., 2012, Leaf shape responds to temperature but not CO_2 in *Acer rubrum*: PLoS ONE, v. 7, no. 11, e49559, doi: 10.1371/journal.pone.0049559.
Salisbury, S.W., Molnar, R.E., Frey, E., and Willis, P.M.A., 2006a, The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia: Proceedings of the Royal Society B, Biological Sciences, v. 273, p. 2439–2448.
Salisbury, S.W., Molnar, R.E., and Lamanna, M.C., 2006b, A new titanosauriform sauropod from the mid-Cretaceous (Albian–Cenomanian) Winton Formation of central-western Queensland, Australia: Journal of Vertebrate Paleontology, v. 26, 118A.
Seegets-Villiers, D., 2012, Palynology, taphonomy and geology of the Early Cretaceous Dinosaur Dreaming fossil site, Inverloch, Victoria, Australia [Unpublished Ph.D. thesis]: Monash University, Melbourne, 173 p.
Senior, B.R., Mond, A., and Harrison, P.L., 1978, Geology of the Eromanga Basin: Bureau of Mineral Resources, Bulletin, v. 167, p. 1–102.
Spicer, R.A., and Herman, A.B., 2010, The Late Cretaceous environment of the Arctic: a quantitative reassessment using plant fossils: Palaeogeography, Palaeoclimatolgy, Palaeoecology, v. 295, p. 423–442.
Spicer, R.A., and Parrish, J.T., 1986, Paleobotanical evidence for cool north polar climates in middle Cretaceous (Albian–Cenomanian) time: Geology, v. 14, p. 703–706.
Spicer, R.A., Valdes, P.J., Spicer, T.E.V., Craggs, H.J., Srivastava, G., Mehrotra, R.C., and Yang, J., 2009, New developments in CLAMP: calibration using global gridded meteorological data: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 283, p. 91–98.
Spicer, R.A., Bera, S., De Bera, S., Spicer, T.E.V., Srivastava, G., Mehrotra, R., Mehrotra, N., and Yang, J., 2011, Why do foliar physiognomic climate estimates sometimes differ from those observed? Insights from taphonomic information loss and a CLAMP case study from the Ganges Delta: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 302, p. 381–395.
Steart, D.C., Boon, P.I., Greenwood, D.R., and Diamond, N.T., 2002, Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in southeastern Australia: Archiv Für Hydrobiologie, v. 156, p. 43–61.
Stevens, G.R., and Clayton, R.N., 1971, Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance: New Zealand Journal of Geology and Geophysics, v. 14, p. 829–897.
Tarduno, J.A., Brinkman, D.B., Renne, P.R., Cottrell, R.D., Scher, H., and Castillo, P., 1998, Evidence for extreme climatic warmth from Late Cretaceous Arctic vertebrates: Science, v. 282, p. 2241–2243.
Thompson, R.S., Anderson, K.H., Pelltier, R.T., Strickland, L.E., Bartlein, P.J., and Shafer, S.L., 2012, Quantitative estimation of climatic parameters from vegetation data in North America by the mutual climatic range technique: Journal of Quaternary Science, v. 51, p. 18–39.
Tucker, R.T., Roberts, E.M., and Salisbury, S.W., 2011, New information on the stratigraphy, depositional environment and taphonomy of the mid-Cretaceous Winton Formation, central-western Queensland, Australia, *in* Trinajstic, K., Bunce, M., Warburton, N., Hadley, C., Baynes, A., and Siversson, M., eds., CAVEPS Perth 2011, 13th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, April 27th–30th, Geological Survey of Western Australia, Record 2011/9, p. 84.
Tucker, R.T., Roberts, E.M., and Salisbury, S.W., 2013, U-Pb detrital zircon constraints on the depositional age of the Winton Formation, western Queensland, Australia: Contextualizing Australia's Late Cretaceous dinosaur faunas: Gondwana Research, v. 24, p. 767–779.
Ufnar, D.F., Ludvigson, G.A., Gonzlez, L., and Grôcke, D.R., 2008, Precipitation rates and atmospheric heat transport during the Cenomanian greenhouse warming in North America: Estimates from a stable isotope mass-balance model: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 266, p. 28–38.

Uhl, D., Mosbrugger, V., Bruch, A., and Utescher, T., 2003, Reconstructing palaeotemperatures using leaf floras: case studies for a comparison of leaf margin analysis and the coexistence approach: Review of Palaeobotany and Palynology, v. 126, p. 49–64.

Upchurch, G.R.J., and Wolfe, J.A., 1987, Mid-Cretaceous to early Tertiary vegetation and climate evidence from fossil leaves and wood, *in* Friis, E.M., Chaloner, W.G., and Crane, P.R., eds., The Origins of Angiosperms and Their Biological Consequences: Cambridge, U.K., Cambridge University Press, p. 75–106.

Wagstaff, B.E., and McEwen Mason, J.R.C., 1989, Palynological dating of Lower Cretaceous coastal vertebrate localities, Victoria, Australia: National Geographic Research, v. 5, p. 54–63.

Wolfe, J.A., 1993, A method of obtaining climatic parameters from leaf assemblages: U.S. Geological Survey, Bulletin, v. 2040, p. 1–73.

Wolfe, J.A., 1995, Paleoclimatic estimates from Tertiary leaf assemblages: Annual Review of Earth and Planetary Science, v. 23, p. 119–142.

Yang, J., Spicer, R., Spicer, T., and Li, C.-S., 2011, CLAMP Online: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America: Palaeobiodiversity and Palaeoenvironments, p. 1–21.

Received 2 August 2013; accepted 6 November 2013.