

# Late Oligocene Kangaroo Well Local Fauna from the Ulta Limestone (new name), and climate of the Miocene oscillation across central Australia

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The Late Oligocene Kangaroo Well Local Fauna from the Ulta Limestone (new name), northwestern Lake Eyre Basin correlates best with vertebrate assemblages from the Etadunna, Namba and Wipajiri Formations of the central Lake Eyre Basin, and from the Carl Creek Limestone (Karumba Basin) of northwestern Queensland. The biochronologically informative marsupials, *Neohelos tirarensis* (Diprotodontidae, Zygomaturinae), *Marlu* sp. cf. *M. kutjamarpens* and *Pildra* sp. cf. *P. magnus* (Pseudocheiridae), and *Ektopodon ulta* sp. nov. (Ektopodontidae), indicate that the Kangaroo Well Local Fauna may be slightly older than the Kutjamarpu Local Fauna (Wipajiri Formation) and slightly younger than the Ngama Local Fauna (zone D of the Etadunna Formation) of Late Oligocene age. A new species of primitive ?Wynyardiidae, *Ayekaye jaredi* sp. nov., is described, and the nomenclature of two extinct gastropods, *Glyptophysa rodingae* (McMichael) and *Cupedora lloydi* (McMichael) (new combinations), the type localities of which are in the Ulta Limestone, is revised in line with current taxonomy. The Ulta Limestone, an alluvial calclithite composed primarily of caliche fabrics, and its correlatives were deposited during the Miocene oscillation climatic event. Palaeoclimatic modelling using sedimentological data, crocodilians and extant analogs of fossil terrestrial gastropods indicates that the average annual temperature at Kangaroo Well during the Late Oligocene was probably between 14 and 20°C, while mean annual rainfall was probably <600 mm. Similar associations from central parts of the Lake Eyre Basin, from Riversleigh, northwestern Queensland, and from Bullock Creek, north-central Northern Territory, indicate that such conditions were widespread during depositional phases of the Miocene oscillation. Palaeoclimatic indicators do not support the presence of widespread closed forests in northwestern Queensland and across the inland of the Northern Territory and South Australia during the Miocene oscillation.

**KEY WORDS:** calclithite, Kangaroo Well Local Fauna, Lake Eyre Basin, Miocene oscillation, Oligocene, palaeoclimate, Ulta Limestone.

## INTRODUCTION

The purpose of this communication is to provide an overview of the Kangaroo Well Local Fauna (Table 1) from the Ulta Limestone (new name), and to discuss the palaeo-environmental significance of the fossil assemblage and its host formation.

In 1963, sparse vertebrate fossils associated with gastropods and ostracods were discovered in limestone near Kangaroo Well on Deep Well pastoral station, Northern Territory (Figure 1), during the course of regional geological mapping by the Bureau of Mineral Resources (now Geoscience Australia). In the initial reports of the discovery, McMichael (1968) named three new species of gastropods, and Lloyd (1968a) reported crocodilians and turtles as the most common vertebrate remains. Bird bones were also collected, the whereabouts of which are now unknown, presumed lost (Rich 1991). However, the most significant find was a single, small, macropodid jaw, apparently similar to unspecified forms from the central Lake Eyre Basin of South Australia (Lloyd 1968a).

Stirton *et al.* (1968) named the assemblage the Kangaroo Well Fauna, now recognised as a Local Fauna, which is a biochronological unit based on a vertebrate assemblage from a particular geographical locality that is interpreted to represent an instant in geological time (Woodburne *et al.* 1985; Rich 1991; Megirian 1994) (Figure 2). [In contrast, in biochronology a Fauna has come to represent the maximum temporal and geographical limits of a group of animals sharing a suite of common species (Tedford 1970; Megirian 1994).] Stirton *et al.* (1968) likened the kangaroo jaw to apparently similar but undescribed forms from both South Australian and Queensland Local Faunas.

The kangaroo jaw [CPC 7349<sup>†</sup> (on next page)] came from a juvenile animal and is incomplete, the dentition represented only by an unerupted fourth molar. It was determined by Flannery *et al.* (1983) to be a *Balbaroo* sp. on the basis of its similarities to the genotypic species *Balbaroo camfieldensis* Flannery, Archer & Plane 1983, from the

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**Table 1** The Kangaroo Well Local Fauna, including some provisional determinations of material under study that will be described elsewhere.

	Genus and species	Family	sources
Gastropods	<i>Potamopyrgus</i> sp.	Hydrobiidae	McMichael (1968)
	<i>Bothriembryon praecursor</i>	Bulimulidae	McMichael (1968)
	<i>Cupedora lloydi</i>	Camaenidae	McMichael (1968); present paper (Figure 5e)
	<i>Glyptophysa rodingae</i>	Planorbidae	McMichael (1968); present paper (Figure 5e)
	<i>Syrioplanorbis hardmani</i>	Planorbidae	McMichael (1968)
	cf. <i>Cylindrovertilla</i> sp.	Pupillidae	Present paper, det. B. J. Smith 2003 (Figure 5d)
	Undetermined species	–	Present paper (Figure 5c)
Ostracods	Undetermined species	–	Present paper (Figure 5b)
Fish (teleosts)	Undetermined species	–	Rich (1991 p. 1027)
Frogs	<i>Australobatrachus ilius</i>	Myobatrachidae	Det. M. J. Tyler 2003
	<i>Australobatrachus</i> sp.	Myobatrachidae	Det. M. J. Tyler 2003
	cf. <i>Limnodynastes</i> sp.	Myobatrachidae	Det. M. J. Tyler 2003
	<i>Litoria</i> sp.	Hylidae	Det. M. J. Tyler 2003
Crocodyles	Undetermined species	–	Present paper (Figure 5h)
Turtles	Undetermined species	Chelidae	Gaffney (1981 p. 34)
	<i>Chelodina</i> sp.	Chelidae	Present paper (Figure 5g)
	cf. <i>Birlimarr</i> sp.	Chelidae	–
Lizards	Undetermined species	Scincidae	Det. M. Hutchinson 2003
Snakes	<i>Yurlunggur</i> sp. cf. <i>Y. camfieldensis</i>	Madtsoiidae	Present paper (Figure 5g)
Birds	Undetermined species	–	Rich (1991 p. 1027)
Marsupials	<i>Nimbacinus</i> sp. cf. <i>N. dicksoni</i>	Thylacinidae	Present paper (Figure 10)
	<i>Ayekaye jaredi</i> sp. nov.	?Wynyardiidae	Present paper (Figures 11 and 12)
	<i>Neohelos tirarensis</i>	Diprotodontidae	Present paper (Figure 13)
	<i>Ektopodon ulta</i> sp. nov.	Ektopodontidae	Present paper (Figure 14)
	<i>Pildra</i> sp. cf. <i>P. magnus</i>	Pseudocheiridae	Present paper (Figure 15)
	<i>Marlu</i> sp. cf. <i>M. kutjampensis</i>	Pseudocheiridae	Present paper (Figure 16)
	cf. <i>Wakiewakie lawsoni</i>	Potoroidae	Godthelp <i>et al.</i> (1989)
	<i>Balbaroo</i> sp.	Macropodidae	Flannery <i>et al.</i> (1983)
	<i>Nambaroo</i> sp.	Macropodidae	–
	‘genus D’	Peramelidae	Rich (1991 p. 1027)
	cf. <i>Yarala burchfieldi</i>	Yaralidae	–
	Undetermined species	Miralinidae	–
	Undetermined species	Pilkipildridae	–

Camfield beds (Bullock Creek Local Fauna) of the Northern Territory. Although smaller than *B. camfieldensis* and a congener, *B. gregoriensis* Flannery, Archer & Plane 1983, from the Carl Creek Limestone [Riversleigh (Local) Fauna of Tedford (1967) of northwestern Queensland], Flannery *et al.* (1983) refrained from erecting a third *Balbaroo* species because the Kangaroo Well form could not be compared dentally with *B. gregoriensis*. However, they postulated that the small size of the Kangaroo Well *Balbaroo* sp. represented a relatively primitive stage of balbarine evolution, and concluded that the Kangaroo Well Local Fauna might therefore be older than both the Riversleigh and Bullock Creek Local Faunas.

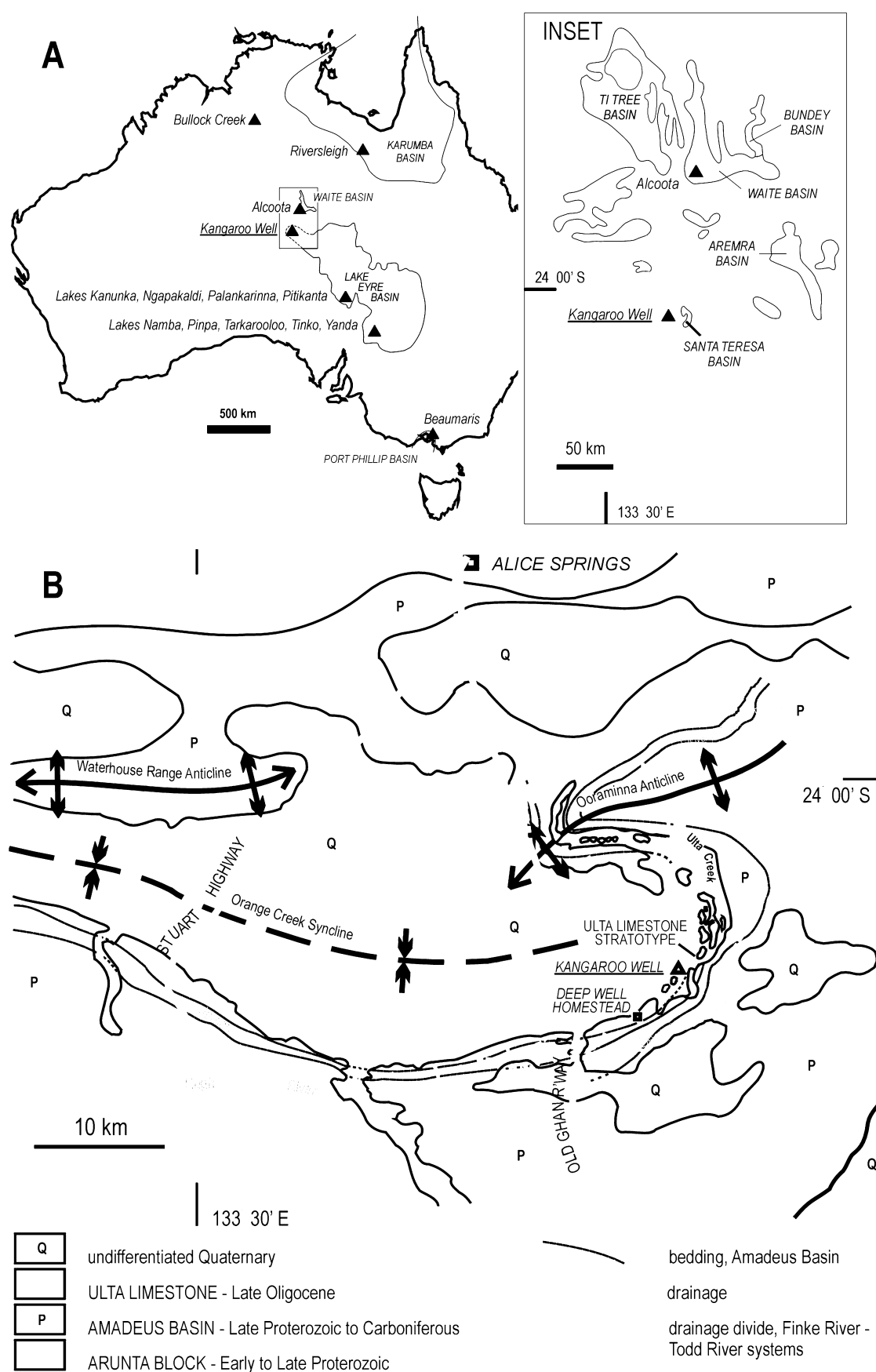
R. T. Wells (Flinders University) and M. O. Plane (BMR) visited Deep Well Station in *ca* 1978 to collect more fossiliferous limestone, but their collection site is uncertain. Wells' recollections (pers. comms 1989–2002) of where they collected do not correspond to published details of the original find-site, raising the possibility that two different sites were sampled. In 1988, Plane passed on to H. Godthelp, M. Archer and S. Hand (University of New South Wales) remaining unprocessed material from Kangaroo Well, but whether this was only limestone collected in *ca* 1978, or whether it included remainders of the original collection made in 1963, is also not known. Godthelp *et al.* (1989) extracted from this material of uncertain and possibly

mixed provenance a new potoroine genus and species cf. *Wakiewakie lawsoni* Woodburne 1985, from the Kutjamparpu Local Fauna, Wipajiri Formation of the Lake Eyre Basin. The species remains undescribed, but was characterised as being a plesiomorphic sister-taxon to *W. lawsoni*, implying that the Kangaroo Well Local Fauna might also pre-date the Kutjamparpu Local Fauna (Godthelp *et al.* 1989).

A 1988 survey by staff from the Museums and Art Galleries of the Northern Territory resulted in the discovery of another partial macropodoid jaw at Kangaroo Well. On a return visit in 1991, Wells was able to confirm that this find-site was not the same locality as that sampled in *ca* 1978.

The original (1963) find-site was relocated in 2000 (Figure 3f). Samples had been quarried from low in the succession, and turtle, crocodilian and macropodoid remains were still present. We distinguish this source of

\*Institutional abbreviations: BMR, Bureau of Mineral Resources (now Geoscience Australia), Canberra; CPC, Commonwealth Palaeontological Collection, Canberra; NTM, Museums and Art Galleries of the Northern Territory, Darwin; SAM, South Australian Museum, Adelaide; UCMP, University of California Museum of Palaeontology, Berkeley; UNSW, University of New South Wales, Sydney.



**Figure 1** (a) Sedimentary basins and Late Oligocene and Miocene vertebrate fossil localities mentioned in the text. Inset after Senior *et al.* (1995 figure 1). (b) Simplified geology of the Deep Well region (after Ranford *et al.* 1968) showing the extent of the Ulta Limestone and its relationship to structure in the underlying Amadeus Basin, and to present drainage, which is largely relict.

vertebrate fossils, which constitute the type assemblage of the Kangaroo Well Local Fauna, as the BMR Site in recognition of the staff of that institution who contributed to its discovery and initial interpretation. The section, which also serves as the stratotype of the Ulta Limestone, was logged, and samples for petrographic and palaeontological analysis were collected. The 1988 find site (NTM Site) was also logged and resampled. On a return visit in 2002 another productive site was found, which we distinguish as RTW Site in acknowledgement of R. T. Wells' contributions to explorations at Kangaroo Well. Global Positioning System data for the three sites are on file at the Museums and Art Galleries of the Northern Territory, Darwin. The location where Wells and Plane collected in *ca* 1978 remains unresolved.

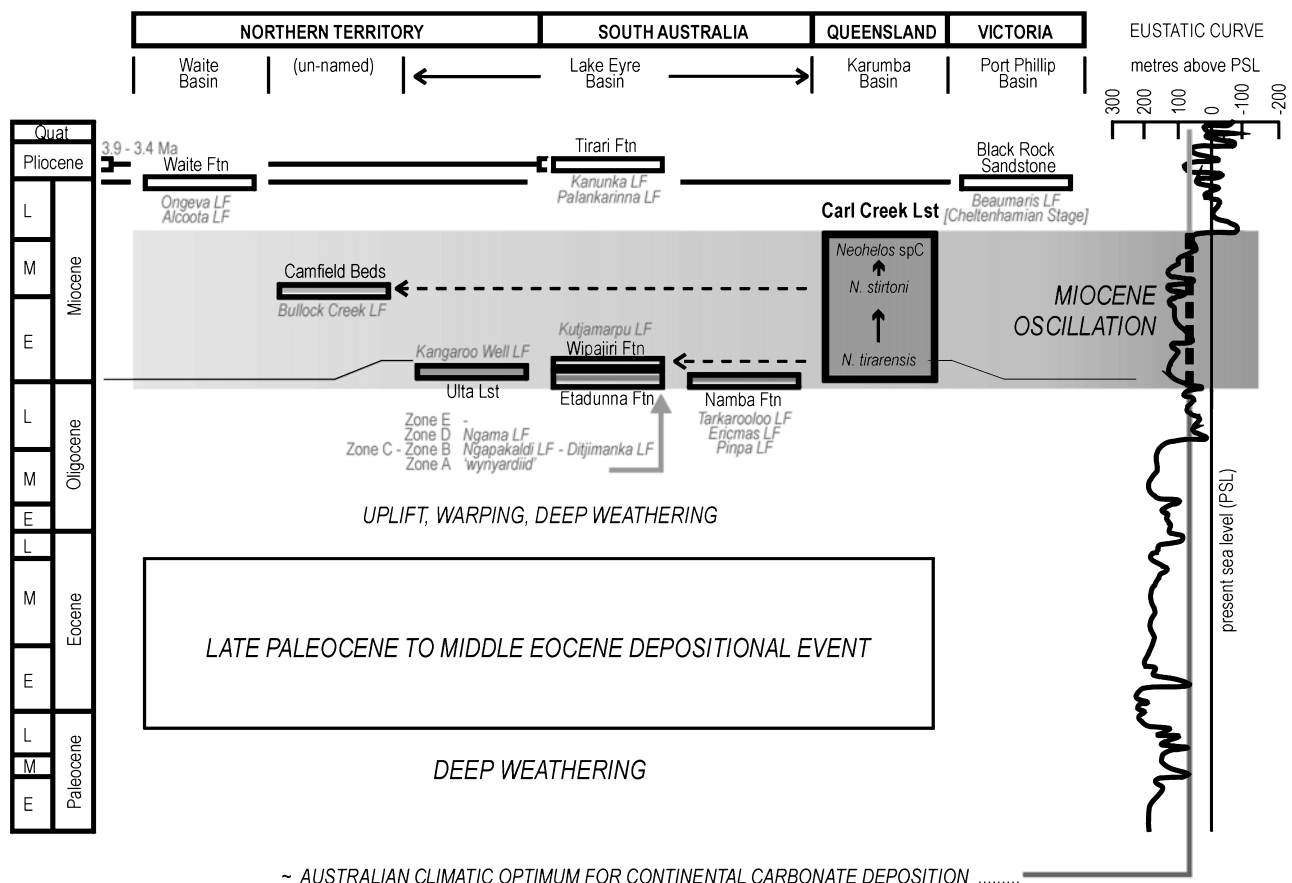
Subdivisions of Lyellian Epochs are deliberately left uncapitalised when applied to formations having ages that can at present be inferred only by the relative stage of evolution of their vertebrate assemblages (Local Faunas),

so as not to imply a level of precision in age determination that does not exist.

## ULTA LIMESTONE

### Definition

The Ulta Limestone, which takes its name from Ulta Creek, occurs as a sinuous line of discontinuous outcrop extending ~50 km across the western part of the Ooraminna Anticline and the eastern part of Orange Creek Syncline, following structure in the Amadeus Basin (Figure 1b). It is mapped on the 1:250 000 Rodinga Geological Sheet SG/53-02 as 'Tb, silcrete (grey billy)' and 'Tl, chalcidonic limestone, siltstone and calcareous sandstone containing freshwater gastropods' (Ranford *et al.* 1968; Cook 1969). These generic map units are widespread across this and adjacent first edition map



**Figure 2** Abbreviated correlation chart. Key reference section for the Australian marsupial biogeochronological scheme (based on land-mammal Local Faunas) is the Etadunna Formation to Tirari Formation succession of the Lake Eyre Basin (Woodburne *et al.* 1985, 1993; Rich 1991); zonal biostratigraphy of the Etadunna Formation follows Woodburne *et al.* (1993); geochronology of the Tirari Formation from Tedford *et al.* (1992); biocorrelation of the Ongeva Local Fauna (Waite Formation) to the Beaumaris Local Fauna (Black Rock Sandstone, marine Cheltenhamian Stage) from Murray *et al.* (1993) and Megirian *et al.* (1996). Previous calibrations of the Etadunna Formation are discussed in the text. Other formations are tied in by simple marsupial biocorrelation or stage-of-evolution comparisons providing relative ages (e.g. *Neohelos* biochronology after Murray *et al.* 2000a). Formations with dark infill are carbonate deposits, those partially infilled are formations with carbonate members. See Lloyd (1968a, b), van de Graaff *et al.* (1977) and Megirian (1992) for overviews of the Miocene continental-carbonate depositional event, which McGowan and Li (1994) correlated to the global Miocene oscillation climatic event. Perspectives on the continental pattern of cyclic deposition and deep weathering since Late Cretaceous times may be found in Smart *et al.* (1980), Callen *et al.* (1995) and Senior *et al.* (1995).

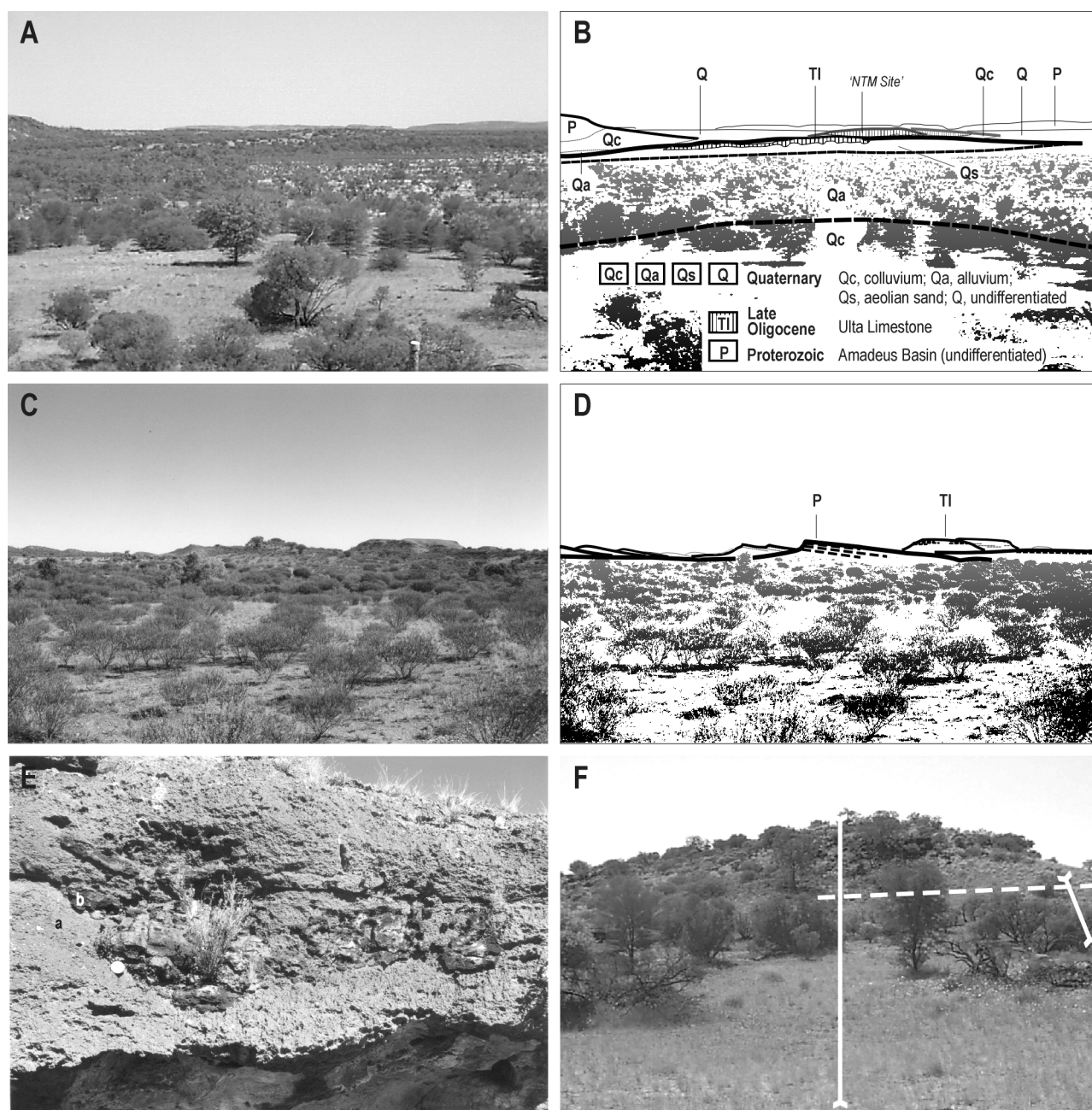


sheets, encompassing strata deposited in a variety of structural settings and of possibly varying age. The concept of the Ulta Limestone is limited to outcrops depicted in Figure 1b.

The formation lies in an area of first-order streams in the Hugh River drainage of the Finke River system (Figure 1b). It is expressed geomorphologically as low mesas with local relief of up to 30 m, but more typically

10–20 m, or as rubbly outcrops exposed by deflation of Quaternary dunes (Figure 3a–d).

Lithologies include white to dark yellowish-orange limestone facies (calcimudstone, calcwacke, calcareous packstone and conglomeratic limestone) deposited in palaeochannels. Diagenetic end-members include varieties of caliche, chalcedonic limestone and chalcedony ('grey billy'). Terrestrial and freshwater gastropods are charac-



**Figures 3** (a, b) Southern aspect and photogeological interpretation viewed from the Ulta Limestone stratotype at 24°13'S, 134°13'E. (c, d) Southwestern aspect and photogeological interpretation from position 24°17'S, 134°12'E showing the angular unconformity between Amadeus Basin strata (Mereenie Sandstone, centre foreground to middle distance, and Shannon Formation, left-hand side, middle to far distance), and the southernmost outcrops of Ulta Limestone on the right-hand side. Although up to ~40 m of Ulta Limestone is exposed in this area, neomorphism and silicification has almost totally obliterated primary features. (e) Outcrop at approximately position 'TI' in (d) composed of a, highly silicified carbonate (chalcedonic limestone), with nodules of b, dense chalcedony ('grey billy'). (f) BMR Site (24°13' S, 134°13' E), type locality of the Kangaroo Well Local Fauna and stratotype of the Ulta Limestone, showing positions of measured sections shown Figure 9.

teristic macrofossils, and gastropods, ostracods and charophyte oögonia are characteristic microfossils. Vertebrate remains are rare and localised in their distribution. Structure includes essentially flat-lying, lenticular bedforms up to ~2 m thick, and palaeokarstic features. Slightly dipping beds might either reflect primary depositional attitudes or could be evidence of mild tilting.

Colluvium, alluvium and aeolian sand typically mask the base of unit, which rests with angular unconformity on strata of the Amadeus Basin. The inferred maximum thickness of the Ulta Limestone is ~40 m. There are no superposed strata other than Quaternary aeolian sand locally draping the formation.

The stratotype at 24°13'S, 134°13'E (Figure 3f) is also the type locality (BMR Site) of the Kangaroo Well Local Fauna. Marsupial biocorrelation and stage-of-evolution comparisons presented below correlate the Ulta Limestone to the Etadunna and Wipajiri Formations of the Lake Eyre Basin (Figure 2). Previous estimates of the geological age of the Etadunna and Wipajiri Formation and their correlatives vary considerably (Woodburne *et al.* 1985, 1993; Wells & Callen 1986; Rich 1991; Megirian 1992; Callen *et al.* 1995; Alley *et al.* 1999). Following the work of Woodburne *et al.* (1993) on the Etadunna Formation, a Late Oligocene age is postulated for the Ulta Limestone.

## Petrography

The Ulta Limestone is composed of poorly sorted, bioclastic, finely to coarsely textured detrital carbonate facies, caliche and chert replacements. The dominant feature of the detrital facies is the presence of reworked carbonate grains that exhibit fabric-specific diagenetic characters indicative of more advanced diagenetic stages

than those exhibited overall by the sediment in which they occur. It thus serves the purposes of description to begin by tracing the sequence of diagenetic stages in order to demonstrate the origin of these grains. A general model of the Ulta Limestone rock cycle, encapsulating the observations presented below, is shown in Figure 4.

Early diagenetic features include micrite envelopes on detrital grains, recrystallisation of carbonate skeletal grains (e.g. gastropods and ostracods), and the occlusion of intragranular and intergranular primary porosity by calcite cements (Figure 5a–c). Subsequent changes basically proceeded along two trajectories. One is characterised by the progressive obliteration of primary and early diagenetic fabrics and textures by neomorphic recrystallisation of carbonate to pseudospar grade (16–50 µm), especially of micritic fabrics (Figure 6c). Features discernible as palimpsests in early stages are progressively obliterated, resulting in homogeneous sparstone (pseudosparite) (e.g. carbonate pebble, right-hand side, Figure 7a). Associated with this neomorphism was the mobilisation and redeposition of silica. Detrital quartz grains commonly show corrosive etching and replacement by pseudospar (Figure 6a), and phosphatic bone fabrics are also commonly affected in the same way (Figure 6b). Pseudosparite zones were loci for the formation of authigenic silica (chert), which progressively replaced pseudosparite (Figures 6i, 7b), resulting in a rock referred to colloquially as 'chalcedonic limestone' (Figure 8e). Further silicification ultimately resulted in the formation of chert nodules (Figure 3e); and grey billy residuals (i.e. chert after dissolution of the more labile carbonate in which it formed) are all that remain of the Ulta Limestone in some places.

The second diagenetic trajectory is characterised by the formation of caliche glaebules (undifferentiated to concentric carbonate fabrics that form in calcareous soil profiles), and laminar and rhizoconcretionary fabrics. Aggregates resulting from brecciation of carbonate-cemented deposits (Figure 6d) were the most likely source of the peloids (sand-sized grains, generally rounded or subrounded, spherical or ellipsoidal to irregular in shape, internally structureless, and composed of microcrystalline carbonate) and coated grains (particles coated with one or more layers of micrite or coarser grades of calcite) that occur in the depositional facies of the Ulta Limestone. If preserved *in situ*, such particles represent palaeosols (Figure 8f), but if worked hydraulically into alluvial or colluvial deposits, they represent transported caliche lithoclasts. Although it is not always certain on purely petrographic grounds whether a particular sample rich in peloids and coated grains represents a palaeosol or a clastic deposit, aggregates, peloids and coated grains are the main constituents of detrital facies of the Ulta Limestone (Figures 6c, e, g, h, j, 7a, c, d–l, 8a–c). Carbonate with vermicular texture probably of rhizoconcretionary origin, and dense laminar micrite occur in association with palaeokarstic features (Figures 6h, 8a, c). Carbonate grains with these textures are also present in the conglomeratic sediments.

A third suite of diagenetic features may be loosely grouped as late-stage changes. Karstic processes, ultimately responsible for the reduction of the Ulta Limestone

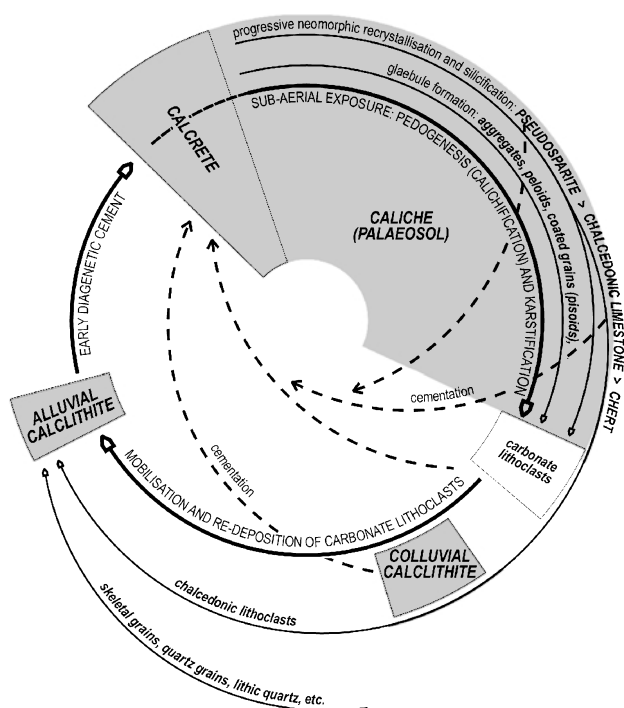


Figure 4 A model of the Ulta Limestone rock cycle.

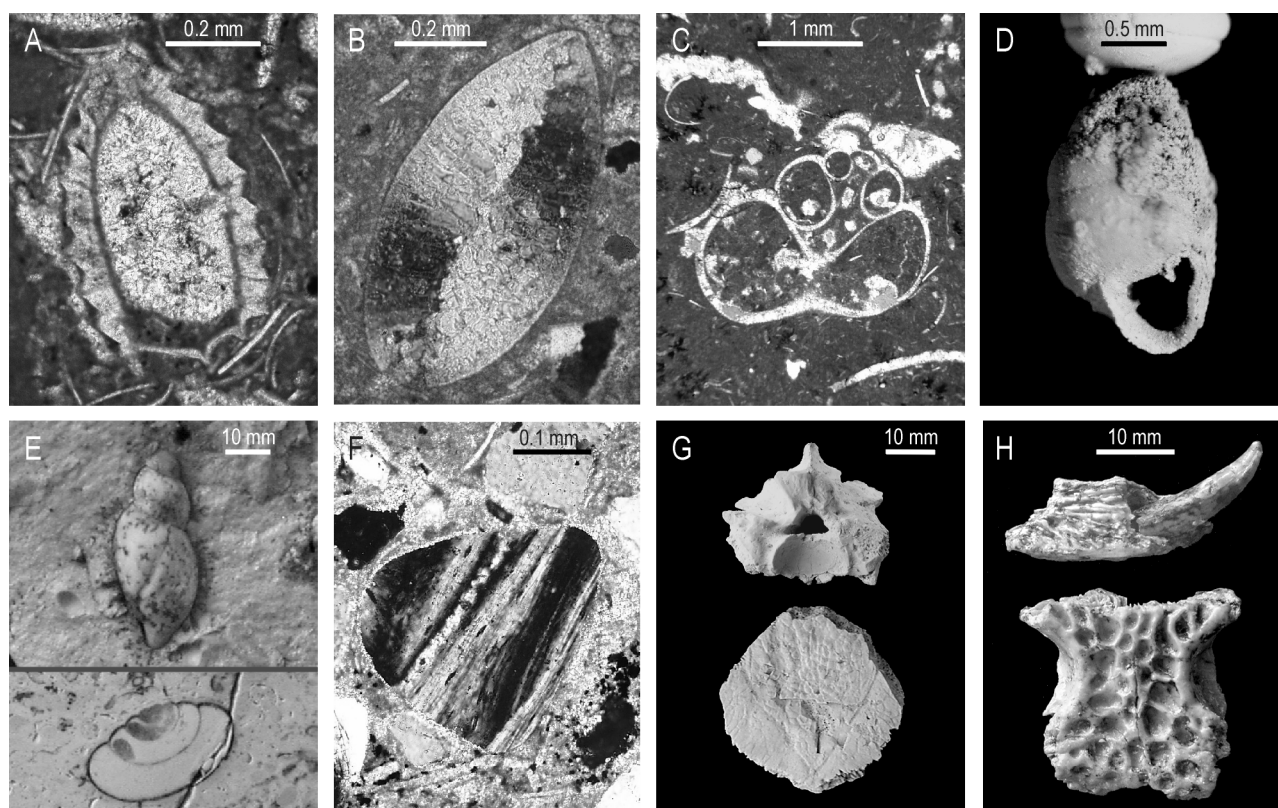
to its present remnant outcrops, resulted in the formation of vugs (secondary porosity), some fabric selective and

**Table 2** Estimated wt% calcium carbonate of selected rock samples.

Sample	wt % CaCO <sub>3</sub>	facies
P2606-	86	Calcwacke
P2692-	94	Calcwacke
P2685-	93	Calcwacke
P2698-	94	Calcwacke
P2690-	83	Conglomerate
P2603-	92	Conglomerate
P2689-	94	Conglomerate
P2597-	89	Conglomerate
P2000-	86	Conglomerate
P2697-	89	Conglomerate
P2684-	80	Conglomerate

Estimated by digesting 50–250 g of whole rock in 10% acetic acid, weighing the insoluble residues, and calculating wt% of the dissolved solids. The only mineral species susceptible to 10% acetic acid identified in thin-sections was CaCO<sub>3</sub>.

some not. Figure 6e, f is an example of non-fabric-selective secondary porosity containing at least two generations of calcite cement, of which the later one is partly replaced by chert. However, whether this particular example formed significantly later than the diagenetic changes described in preceding paragraphs, or was broadly contemporaneous with them, is not certain, but the relative timing of some other changes is clear. Fabric-selective dissolution of skeletal grains, most notably gastropods, was followed by emplacement of ferruginous clay and pyrolusite to produce natural casts (Figure 5d, e). Some rocks preserve evidence of cycles of dissolution, mobilisation of iron, and recementation by calcite (Figure 6j). Pyrolusite dendrites are common throughout the formation (Figures 5e, 6a, b, j, 7a–c), but ferruginisation is more localised and, although these compounds are often concentrated at grain boundaries, no examples of reworked ferruginised or pyrolusitic grains were discovered. The indications therefore are that ferruginisation and pyrolusite emplacement post-dated depositional phases of the Ulta Limestone, as must all carbonate cements and silicifications that occupy later

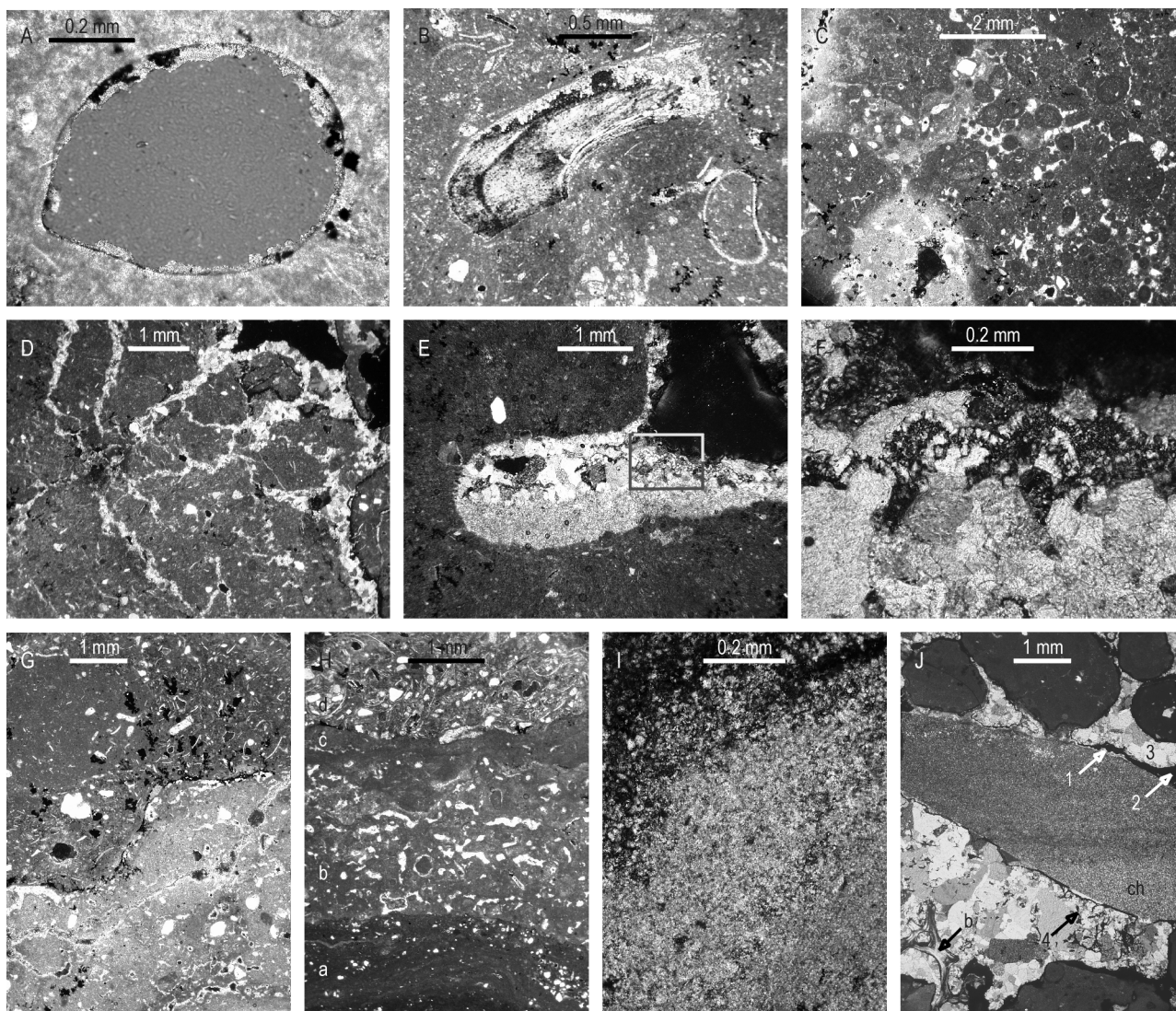


**Figure 5** Examples of Ulta Limestone skeletal grains. (a) Recrystallised oögonium of cf. *Chara*, with internal and external micrite envelopes, internal geopetal calcimudstone and sparry calcite cement (P2690-, TS 0674, crossed nicols). (b) Recrystallised, articulated ostracod valves, with internal, fibrous-calcite cement exhibiting pseudoradial extinction (P2600-, TS 0656, crossed nicols). (c) One of several undescribed small species of gastropod, here preserved as recrystallised calcite (P2687-, TS 0671, crossed nicols). (d) Pupillid land snail cf. *Cyliandrovertilla* in apertural view, preserved as a natural cast in pyrolusite (P2688-2, coated with NH<sub>4</sub>Cl). (e) Above, aquatic planorbid gastropod, *Glyptophysa rodingae* (McMichael 1968), new combination (P2602-2); below, terrestrial camaenid gastropod *Cupedora meracomelon* (McMichael 1968), new combination (P2779-1). These are the most common of the large snails in the Ulta Limestone. Pyrolusite dendrites surround the *G. rodingae* specimen. The outer shell of the *C. meracomelon* has been replaced by pyrolusite, but the septa between whorls remain as recrystallised calcite. (f) Well-rounded, sand-sized, fragment of bone (apatite) (P2600-, TS 0656, crossed nicols). (g) Above, madtsoiid snake, *Yurlungurr* sp. cf. *Y. camfieldensis*, vertebra in anterior view (P2602-3, coated with NH<sub>4</sub>Cl); below, entoplastron of a long-necked chelid turtle, *Chelodina* sp., in ventral (external) view, anterior towards the top (P2602-6, coated with NH<sub>4</sub>Cl). (h) Above, crocodile left dentary fragment with first dentary tooth in symphyseal aspect (P2780-1); below, crocodile parietal in dorsal view, anterior towards the top (P2603-3).

stratigraphic positions, as well as neomorphic overprinting on earlier fabrics.

Pink varieties of caliche (terra rosa) deposited in vugs and along partings, joints and fractures stand out against

the white (Munsell N9), very pale orange (10YR 8/2), greyish-orange (10YR 7/4) and dark yellowish-orange (10YR 6/6) hues typical of fresh surfaces of the Ulta Limestone. These deposits are stratigraphically young, and are

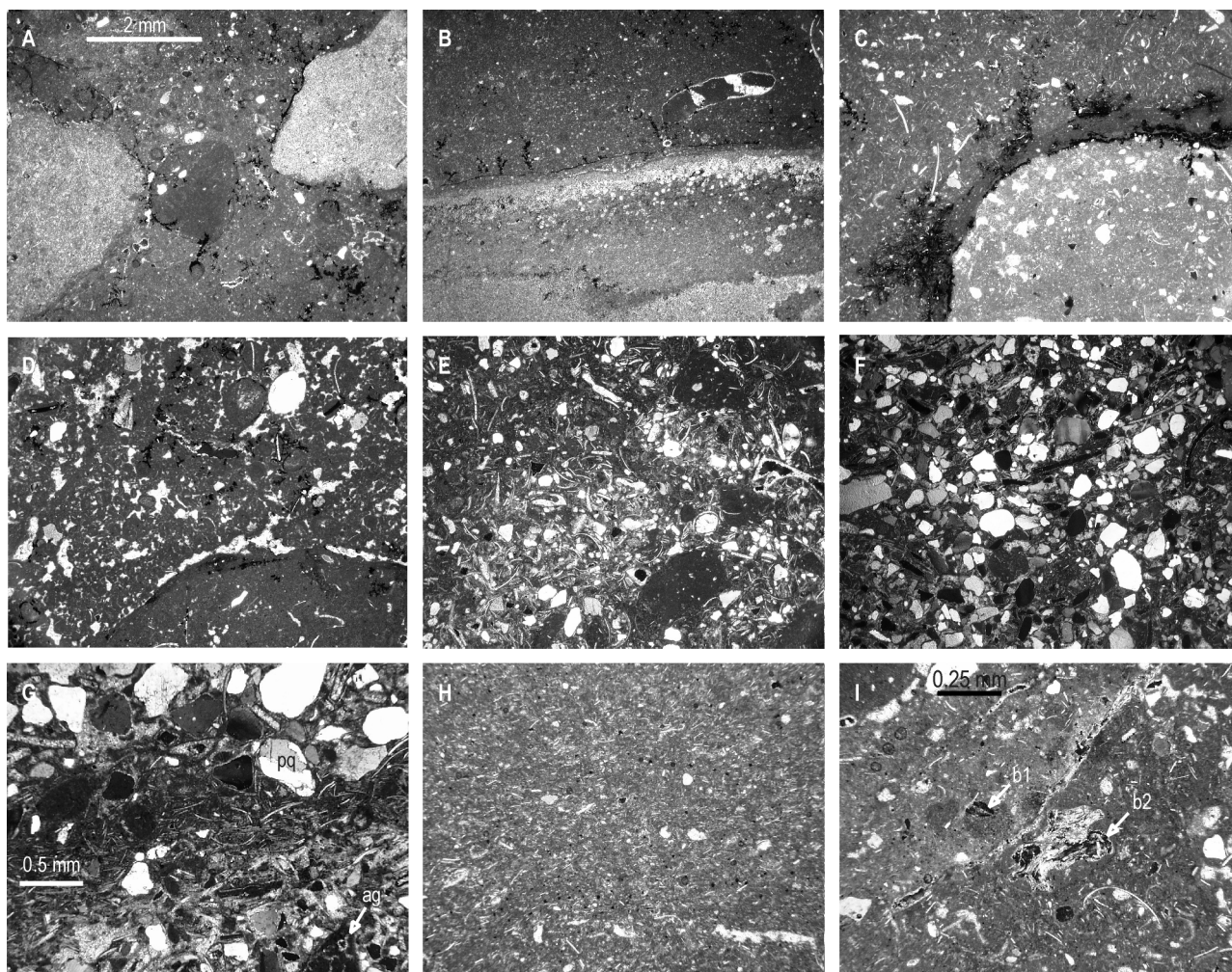


**Figure 6** Examples of diagenetic fabrics and structures resulting from subaerial exposure (karstification, calichification and silicification). (a) Etched quartz grain. A palimpsest of the original, well-rounded shape is preserved by a micrite rim, with calcite of pseudospar grade (16–50  $\mu\text{m}$ ) filling embayments etched into the quartz. Localised dark patches around the original grain boundary are pyrolusite (P2685-, TS 0668, crossed nicols). (b) Etched bone fragment, with bone apatite replaced by pseudospar (P2607-, TS 0663, crossed nicols). (c) Grainstone composed predominantly of peloids and pisolites with patches of obliterative, aggrading neomorphic pseudospar. Palimpsests of the original texture are here still evident in the pseudospar zones (P2697-, TS 0681, crossed nicols). (d) Pedogenic brecciation, with particles recemented by calcite spar (calcrete) (P2683-, TS 0666, crossed nicols). (e, f) Vug in calcwacke, lined with fine calcite spar, partially infilled by geopetal crystal silt, succeeded by coarse, equant cement spar, which is partially replaced by chert, or (detail, f) has been removed by dissolution (secondary porosity, dark area, top right-hand quadrant of e) (P2694-, TS 0676, crossed nicols). (g) Detail of P2694- (Figure 8a), showing the erosional unconformity (palaeokarst surface) between conglomerate beds, with the lower bed showing a more advanced diagenetic stage in the form of partial replacement by neomorphic pseudospar (TS 0684, crossed nicols). (h) Detail of P2600- (Figure 8c). From the base: a, caliche of presumed Quaternary age; b, rhizoconcretionary caliche of the Ulta Limestone with pore spaces filled with calcite spar; c, dense laminar caliche which may represent a lichenised palaeokarst surface; d, calcwacke (TS 0700, crossed nicols). (i) Detail of a pebble of chalcedonic limestone from conglomerate P2689-, showing gradational replacement of pseudospar (bottom right corner) by chert (top left corner) (TS 0673, crossed nicols). (j) Conglomerate in which the intergranular spaces are filled with alternating deposits of blocky calcite cements and ferruginous deposits. An early generation of cement (1) was partially redissolved, followed by an episode of ferruginisation which resulted in the coating of lithoclasts (ch, chert pebble), lining of voids, and geopetal accumulations (2). The rock was then recemented (3), followed by further deposition of iron oxides along cement crystal boundaries (4). Iron oxides are also disseminated unevenly through the carbonate lithoclasts and the bone fragment (b) (P2777-, TS 0686, crossed nicols).



attributed to relatively recent weathering (Figures 6h, 8e). They are not considered part of the Ulta Limestone. The causes of colour variation in the Ulta Limestone were not investigated in detail, but are possibly related to clay mineralogy and proportion, and degree of secondary ferruginisation. Eleven representative samples of conglomeratic limestone and calcwacke ranged from 80 to 94 wt% carbonate (Table 2).

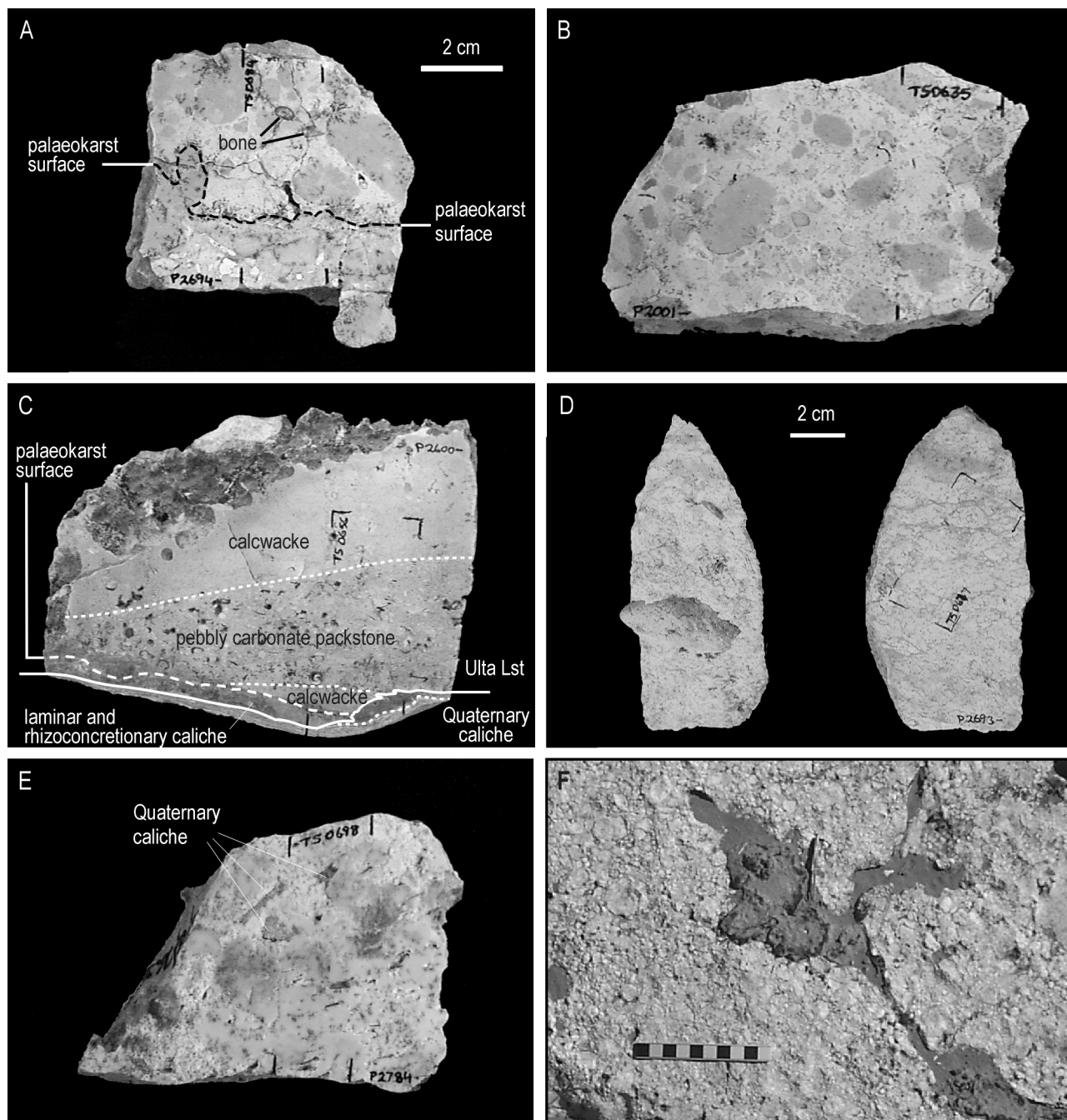
Admixed with the variety of carbonate and chalcidonic lithoclasts already described above are detrital quartz grains (Figure 7), polycrystalline quartz (Figure 7g), chert (Figure 6j) and a variety of bioclasts (Figure 5) that collectively comprise the Kangaroo Well Local Fauna (Table 1). The vertebrate remains range from intact individual bones to indeterminate angular to well-rounded fragments. No articulated series are



**Figure 7** Textural and compositional characteristics of depositional facies of the Ulta Limestone. The petromictic origin of these rocks is clearly evident from the coarser lithotypes. (a, b) Conglomeratic limestone P2689- (TS 0673, crossed nicols). The dark pebble at the centre of (a) is a piece of relatively unaltered carbonate with a bedding surface between calcimudstone and calcwacke facies. To the left is a pebble of neomorphic pseudosparite in which a palimpsest of an original microdetrital peloidal texture is still discernible. Present, although not so obvious at this magnification, are fragments of ostracod valves. The pebble on the right is also composed of pseudosparite, but recrystallisation has obliterated primary features, and some replacement by chert has occurred. The pebble in (b) (bottom half of image) is composed of chalcidonic limestone in which pseudospar (darker, duller zones) has been partially (finely textured, brighter zone at the bottom of the right-hand quadrant), or completely (bright zones, especially towards the margin of the pebble) replaced by chert. (c) Conglomeratic limestone P2598- (TS 0654, crossed nicols). The pebble of calcwacke is more coarsely textured than the surrounding matrix, is partially recrystallised to pseudospar, and has a dense micrite coating of pedogenic origin. The black material, in this view concentrated at, or disseminating from, the micrite cortex is pyrolusite and represents a later diagenetic overprint on the whole rock. (d) Conglomeratic grainstone composed mostly of peloids and pisolites, cemented by spar (P2599-, TS 0661, crossed nicols). (e) Bioclast-rich conglomeratic limestone, with an abundance of fragmentary ostracods and gastropods (P2690-, TS 0674, crossed nicols). (f) Quartz-rich packstone and (g) thin interbed of more finely textured sediment in which peloids and broken ostracod valves are concentrated. Note the poor sorting and variable rounding of the quartz grains. pq, polycrystalline quartz; ag, carbonate-cemented peloid aggregate (P2600-, TS 0656, crossed nicols: see Figure 8c). (h) Bioclastic microdetrital carbonate (P2694-, TS 0678, crossed nicols). (i) Conglomeratic limestone P2694- (TS 0684, crossed nicols: see Figure 8a). Skeletal grains of all types have been reworked into the coarser sediments, as demonstrated here by two bone fragments: b1 is in the conglomerate matrix, whereas b2 is the nucleus of a pisoid that is itself part of an aggregate worked into the rock as a pebble. Scale bar in (a) applies also to (b-f, h).

present. The invertebrates are represented by intact and fragmented gastropod shells, and articulated, disarticulated and fragmented ostracod valves. Apart

from rhizoconcretionary structures, the only plant remains are oogonia of charophyte algae (Figure 5a). The faunal remains and oogonia occur as both primary

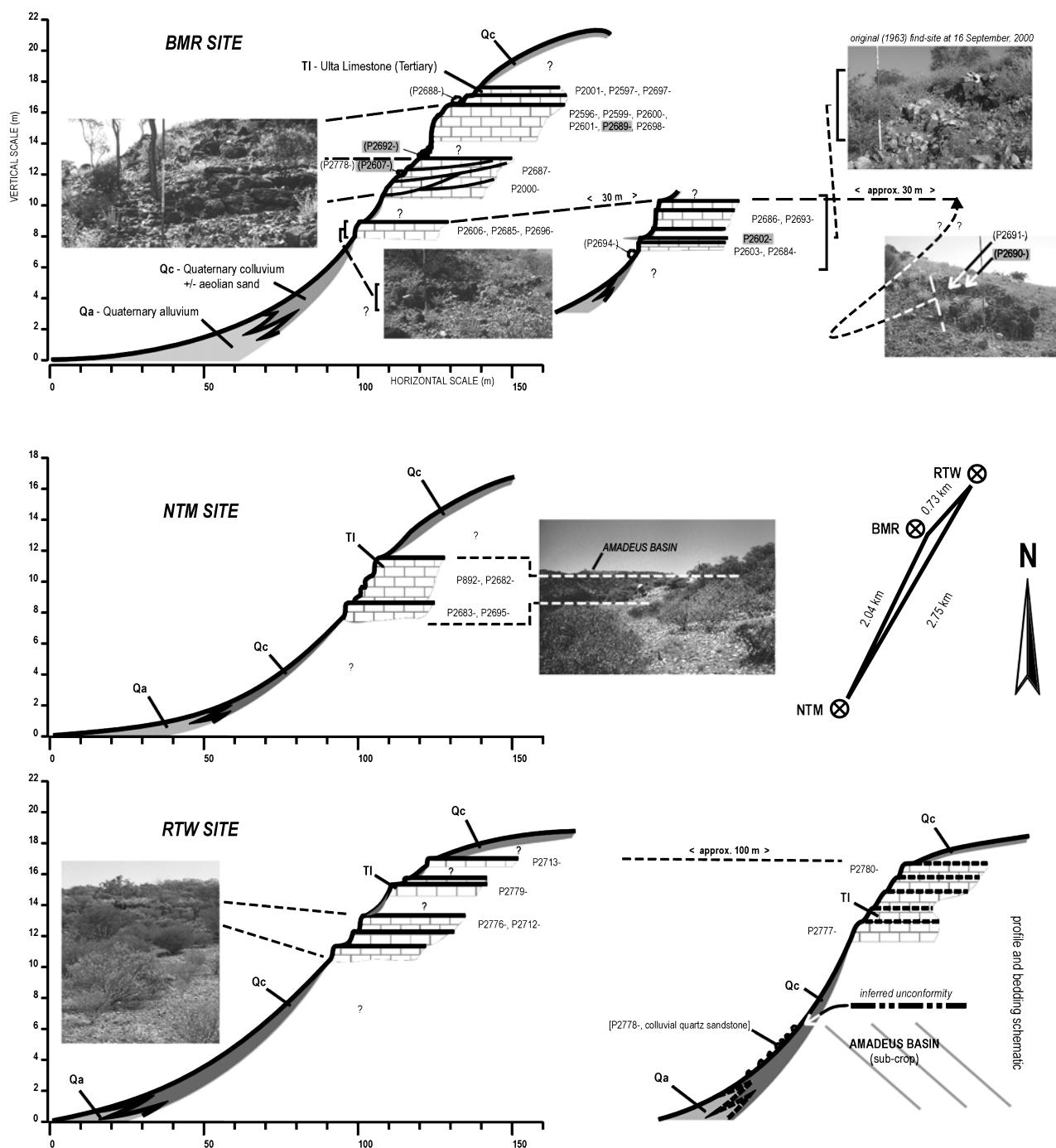


**Figures 8** (a, b) Fossiliferous conglomeratic limestone (a, P2694; b, P2000-). The sub- to well-rounded carbonate pebbles are composed of a variety of calcareous lithotypes, including a variety of pedogenic lithoclasts, making these petromictic orthoconglomerates. (c) Bedded calcwacke and coarse packstone deposited on an intraformational karst surface. The karstified lithotype at the base has pedogenic (caliche) fabrics. Caliche of post-Ulta Limestone weathering (presumably Quaternary) is commonly present, with two generations preserved on this specimen. Quaternary caliche characteristically has reddish hues, in this case pale reddish brown, 10R 5/4 (darker first generation), and moderate orange pink, 5YR 8/4 (lighter second generation), contrasting with the yellowish (10YR) hues of Ulta Limestone facies (P2600-). (d) The planar (horizontal) fabric in this rock (P2693-) is a pedogenic overprint. Diagenetic recrystallisation (aggrading neomorphism) has largely obliterated the depositional texture, but the well-rounded siliceous pebble points to an original, conglomeratic texture. (e) Chalcedonic limestone (P2784-), with mottling reflecting variation in the extent and degree of recrystallisation of carbonate and replacement by chert. Recrystallised zones are loci for replacement authigenic silica (chert) and the formation of grey billy nodules. (f) This rock-type represents either regolith, the product of *in situ* pedogenesis, or possibly colluvium, and a genetic source of carbonate lithoclasts hydrodynamically worked into the alluvial facies of the Ulta Limestone. Natural surface exposed by deflation; dark zones are red Quaternary aeolian sand.

grains and as components of reworked lithoclasts (Figure 7i).

Petromictic, cobble- and pebble-grade conglomeratic limestones are the dominant detrital facies (Figures 7a–c, 8a, b). Wackestones (calcwackes) and packstones (Figures 7e–g, 8c) are less common, and microdetrital carbonates (Figure 7h) and grainstones (Figure 6j)

minor. They are characteristically immature in both texture and composition *sensu* Smosna (1987), although there is variation in degree of sorting, relative proportions of carbonate to non-carbonate grains, and in the representation of non-skeletal, carbonate grain-type (cf. Figures 7a–d, e–f). Although individual carbonate grains are generally not distinguishable in micro-



**Figure 9** Stratigraphic profiles at BMR (Ulta Limestone stratotype), NTM and RTW Sites, showing sample locations. The datum at each site approximates the break in slope between alluvium and colluvium, which is at a similar topographic height at each locality. There is no stratigraphic continuity between sites, bedding is lenticular, and no marker horizons are present. The Ulta Limestone (TI) beds consist predominantly of conglomeratic calcilithite, with minor wackestone. Samples in brackets are colluvial boulders with uncertain stratigraphic origin: they may derive from higher positions than from where they were collected. Shaded samples are the source of biochronologically informative specimens, i.e. specimens of *Ektopodon*, *Marlu*, *Pildra* and *Neohelos*.

detrital facies due to recrystallisation of matrix and cements, incorporated quartz grains are as poorly graded and as variably rounded as both quartz and carbonate grains are in the more coarsely textured sediments.

### Structure and stratigraphy

Although larger scale bedforms are distinct where outcrop expression is reasonable (Figure 9), meso- and micro-scale features in these units include erosional unconformities and irregularly bedded conformable successions of detrital carbonate facies (Figures 7g, 8a, c). Such features are unfortunately hard to observe on karstified and lichenised natural surfaces, making it difficult to trace vertical and lateral facies changes and smaller scale bedding geometries. The dominant macroscale structural features are lenticular bedforms up to ~2 m thick. Their lateral extent is highly variable: the more extensive examples may appear plane-bedded, but thin out when traced laterally, sometimes over distances of several hundreds of metres. No marker horizons are present. The strata typically dip at very slight angles to the west, which may be attributable to slight tilting at a regional scale, but no other tectonic features are apparent. More steeply dipping beds exhibiting cross-cutting relationships (Figure 9) are interpreted as channel cut-and-fill structures.

### Discussion

Sedimentary textures of the Ulta Limestone are characteristic of fluvial channel environments (Miall 1978, 1985, 1992; Reineck & Singh 1986; Collinson 1996) and the predominance of coarse, poorly sorted, texturally and compositionally immature (*sensu* Smosna 1987), bed-load deposits with lenticular cross-sectional geometries is consistent with the proximal (basin-margin) depositional setting of the Ulta Limestone.

As a deposit lithified by carbonate cements, the Ulta Limestone may be classified as a calcrete in accordance with the Lamplugh (1902) original generic definition of the term. The presence of palaeokarstic features and cement stratigraphies recording cycles of dissolution and recementation, together with the presence of finely textured neomorphic spar, geopetal crystal silts, authigenic silica, corroded non-carbonate grains, vermicular texture (rhizocretionary structures), skeletal moulds, brecciation, and laminar crusts are evidence for subaerial exposure and pedogenesis (Esteban & Klappa 1983; Tucker & Wright 1990).

The non-skeletal carbonate grains, which are the main constituents of the detrital facies, were demonstrated above by reference to a set of examples forming hypothetical genetic sequences (Figure 4) to have formed under subaerial exposure and thus to be of terrigenous origin. These facies are therefore calcilithites. No fabrics of phytohermal origin (i.e. intraclasts resulting from either direct or indirect, subaqueous, macrophytal or microphytal mediation) were recognised, and the rocks are therefore not tufas (Pedley 1990) with which they could be confused.

Calcilithites are a relatively uncommon, terrigenous rock clan usually associated with tectonically active areas

where the rate of physical weathering of pre-existing carbonates is such that lithoclasts accumulate faster than the rate at which chemical weathering can remove carbonate from the system by dissolution (Folk 1959; Pettijohn 1975). Such deposits are of autoclastic origin, whereby lithoclast production was in response to tectonic and/or gravitational stresses. However, pedogenesis, a complex interaction of physical and biogeochemical processes, also produces lithoclasts (i.e. caliche fabrics), especially at stable landsurfaces. These caliche fabrics may be worked by downslope gravitational movements into colluvial calcilithite, or by hydraulic traction into alluvial calcilithite (Figure 4).

The association of transported lithoclasts at different, fabric-specific, diagenetic stages of recrystallisation and silicification (Figures 6j, 7a, b), micrite coatings on recrystallised aggregates worked into clastic deposits (Figure 7c) and contrasting diagenetic stages across erosional unconformities (Figures 6g, h, 8a, c) are clear evidence that caliche formation occurred over the timespan of carbonate accumulation. However, the effects of diagenesis are secondary, penetrative and also cumulative, and although the Ulta Limestone could be regarded as a caliche deposit by virtue of its diagenetic attributes, the question arises as to what palaeoclimatic conditions prevailed at times of deposition, which was when the faunal elements of the formation accumulated.

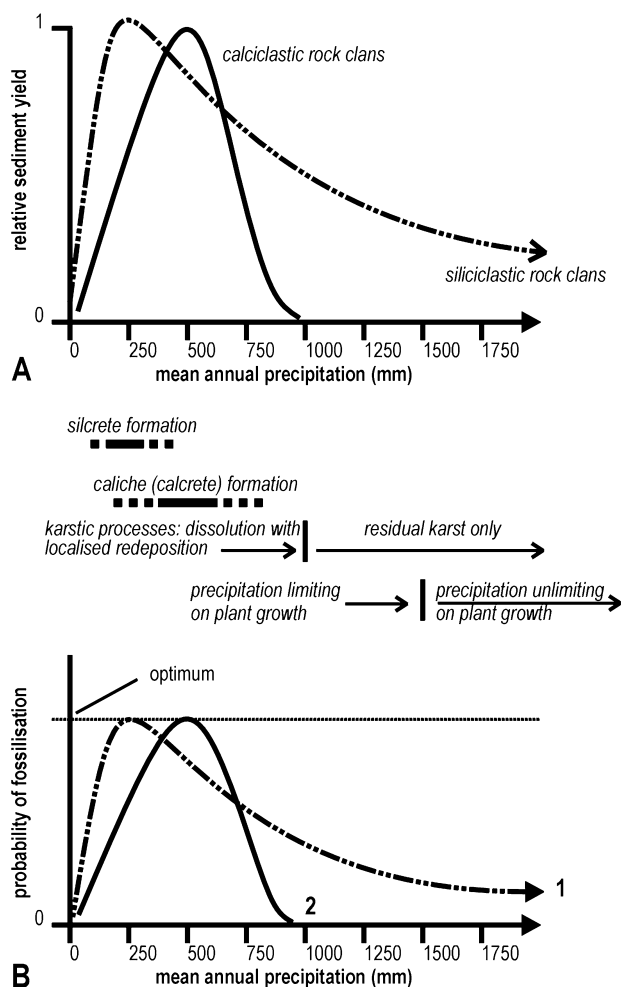
Prospects for the long-term preservation of any type of carbonate deposit, whatever its origin, under subaerial exposure are poor under humid conditions that favour karstic (dissolutional) processes. Figure 10 indicates the precipitation limits under which calcilithites of pedogenic origin are likely, in the first instance, to form, and second (along with carbonates of any origin) to be preserved in near-surface environments. Formation of caliche is optimal around 400–600 mm average annual rainfall, and although mobilisation of lithoclasts may be in response to significant pluvial events, the cementation of detrital deposits by carbonate cements under subaerial conditions requires an overall moisture deficit. The coarseness and textural and compositional immaturity of the Ulta Limestone detrital facies reflect high sediment yields, which in a mature landscape points to incomplete vegetation cover in the catchment, as discussed further below, after corroborating palaeobiological evidence for relatively low annual precipitation during Kangaroo Well Local Fauna times has been presented.

Senior *et al.* (1995) modelled Cenozoic crustal evolution for central Australia based primarily on the Hale, Ti-Tree, Waite, Bunday and Arempra Basins (Figure 1a). Their model of the depositional, weathering and tectonic history of the region, as presented in an abbreviated form in the following paragraphs, provides a basic framework within which to further discuss the Ulta Limestone.

Tertiary rocks of the Alice Springs region occupy elongate intermontane basins (some fault controlled) and flanking palaeodrainages and piedmonts. Some basins appear to have been initiated as early as the Late Cretaceous, and some have more than 200 m of sediment thickness, but outcrops are few and most are deeply weathered. A veneer of unconsolidated Quaternary sediments mantles much of the Tertiary.



In the Late Cretaceous and possibly into the earliest Paleocene there was broad uplift over much of the con-



**Figure 10** (a) Hypothetical clastic sediment yields as a function of mean annual precipitation (after Schumm 1968 figure 1). As volumetrically insignificant contributors to the lithosphere, calclithites were not specifically considered by Schumm (1968). Caliche formation is optimal between ~400 and 600 mm, and yield of pedogenic calcareous lithoclasts would therefore peak under somewhat higher rainfall regimes than the siliciclastic sediment yield maximum at ~250 mm (curve 2). Drier conditions tend to promote the formation of resistant silcrete and calcrete duricrusts on stable surfaces. Sediment yield drops under higher rainfall regimes as higher effective precipitation promotes plant growth, increasing interception, retarding runoff, and reducing sediment mobilisation. In the case of carbonates, clastic sediment yield will effectively drop to 0 when dissolution overtakes the capacity of the system to form, mobilise, deposit and preserve carbonate clasts. Thus there exists a climatic optimum for calclastic deposition, and a point beyond which calclithite accumulation and its long-term preservation is improbable in open systems. (b) McGowran and Li (1994) argued that wetter times were optimum times for vertebrate fossilisation. However, the relative probability of fossil preservation as a function of sedimentation (curve 1, siliciclastic system; curve 2, calclastic system) does not increase monotonically with increasing precipitation, but reaches maxima dependent on lithology under relatively low rainfall, well below the threshold of ~1500 mm under which rainfall is limiting on plant growth when mean annual temperature is ~18°C.

tinent, with concomitant widespread subaerial erosion. In central Australia, however, this interval is marked by a deep weathering event. During the Paleocene and Early Eocene, narrow intermontane basins formed within the Arunta Block as a result of rapid, localised subsidence, and the main present-day drainage systems became established.

The first of two major episodes of sedimentation in the region occurred in the Middle and Late Eocene, resulting in the partial infilling of the intermontane basins in the crystalline Proterozoic Arunta Block, and in the formation of coalescing piedmont fans along its southern flanks and extending on to adjacent parts of the Neoproterozoic to Carboniferous Amadeus Basin. In the present landscape, these piedmont fans crop out as mesas of dissected Tertiary sedimentary rock. Renewed localised subsidence, tilting and updoming occurred during this interval, causing shifts in depositional and erosional areas. Another major, deep-weathering event followed, which ceased by the end of the Eocene.

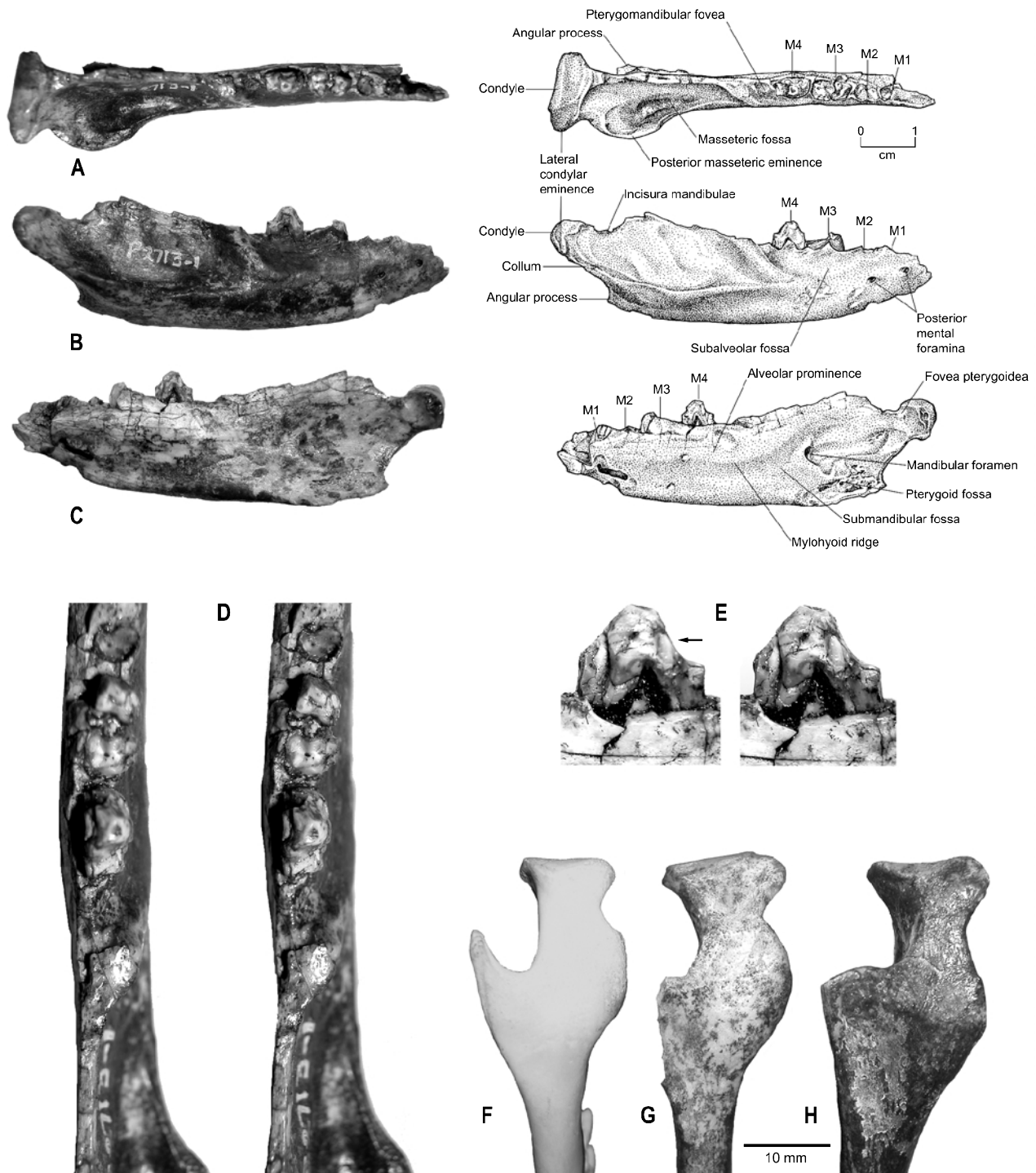
Senior *et al.* (1995) characterised the Oligocene and Early Miocene in central Australia as being a period of uplift and non-deposition, followed by the second major episode of sedimentation, beginning, according to them, in the Late Miocene or Early Pliocene, and associated with localised updoming. These mild tectonic movements resulted in stream rejuvenation and reversals of some drainages, with localised alluviation of restricted drainages, including the formation of salt lakes. Sedimentation continued into the Quaternary with fluvial deposition during pluvial intervals, and the formation of aeolian sand sheets during arid phases.

The Late Oligocene to Middle Miocene interval is of particular interest here, because the Ulta Limestone is shown below to be of probable Late Oligocene age, a correlative of upper parts of the Etadunna Formation, and, from a broader perspective, a representative of a widespread depositional event characterised by carbonate (limestone, dolomitic limestone and dolomite) deposition across western Queensland, South Australia, Western Australia and the Northern Territory (Lloyd 1968a; Wopfner 1974; van de Graaff *et al.* 1977; Wells & Callen 1986; Megirian 1992; Paine 1992; Alley *et al.* 1999). McGowran and Li (1994) linked this event to the Miocene oscillation, the major global climatic reversal between *ca* 26 and 16 Ma within the general trend of Cenozoic cooling (Figure 2). This event may not be distinct from the 'second' major depositional event of Senior *et al.* (1995) (Alley *et al.* 1999), but simply reflects the utilisation of different information for the calibration of the regional geological record to the global time-scale.

Senior *et al.* (1995 figure 1) depicted a small, unnamed Tertiary sedimentary basin where the Ulta Limestone occurs, adjacent to but separate from the Santa Teresa Basin. However, as described above, the Ulta Limestone was deposited in a structurally controlled palaeo-drainage channel, rather than in a localised basin (Figure 1b), and has fluvial depositional attributes. The area abuts the Simpson Desert proper, but Quaternary aeolian sand has partly infilled structural depressions in the Amadeus Basin, partially burying the Ulta Limestone.

The Ula Limestone lies in an area of first-order streams, just within the present Hugh River drainage. It is not clear from relict drainage features whether the Ula Limestone palaeochannel coursed westward along the Deep Well Range before turning south through the gap between the James and Deep Well Ranges to join the Hugh River and then on to the Finke, or whether it consisted of

northern and western tributaries that coalesced, then flowed east of the Deep Well Range to join a more easterly drainage (Figure 1b). The Finke River formerly flowed into Lake Eyre and is now isolated from it by aeolian sand. The northern Simpson Desert between the Finke drainage to the east and the Georgina River drainage to the west is today an area of no surface drainage, and it is no longer



**Figure 11** Kangaroo Well *Nimbacinus* sp. cf. *N. dicksoni* P2713-1. Dentary in (a) occlusal, (b) lateral and (c) medial views with interpretive diagrams. (d) Stereopair of cheek teeth row in occlusal view. (e) Stereopair of  $M_4$  in lateral view: arrow indicates remnant of the premetacristid and metaconid. (f-h) Comparative ventral views of the condylar region of: (f) *Dasyurus maculatus*; (g) *Nimbacinus* sp. cf. *N. dicksoni*; and (h) *N. richi*.

clear from surface features exactly what the course of these rivers was. Today, the major rivers coming off the central Australian mountain ranges east of Alice Springs (including the Todd River drainage: Figure 1b) dissipate into the desert sands, but in the mid-Tertiary, surface flow probably extended to the depocentres of the Lake Eyre Basin.

Wells and Callen (1986 figure 4) aligned the northern margin of the Lake Eyre Basin to present-day exposures of pre-Mesozoic basement, their generalised boundary passing to the south of the Ulta Limestone. Structural geology, palaeodrainage and faunal correlations, however, suggest that the Ulta Limestone represents a basin-margin, palaeochannel-filling formation of the Lake Eyre Basin rather than an intermontane basin. Alley *et al.* (1999 figures 1, 2) depicted the Lake Eyre Basin as encompassing the entire study area of Senior *et al.* (1995) and extending northwards to the margin of the Karumba Basin. This concept of the Lake Eyre Basin encompasses other correlatives of the Ulta Limestone as demonstrated below, such as, for example, the Brunette, Austral Downs and Horse Creek Limestones, as well as several unnamed formations.

## SYSTEMATIC PALAEONTOLOGY

The composition of the Kangaroo Well Local Fauna as currently determined is summarised in Table 1. The faunal list incorporates some provisional determinations of specimens that are the subject of studies that will be published elsewhere. The focus of this section is on particular diprotodontian and phalangeridan marsupials that are geochronologically informative, and on formally revising the taxonomy of two gastropod species founded by McMichael (1968) on material from the Ulta Limestone. Both these species were widespread during the Miocene, and the terrestrial species is of palaeoclimatic signifi-

cance. Bringing their taxonomy into line with modern nomenclature facilitates analogy with extant members of their genera.

Systematics of molluscs follows Smith (1992), reptiles and amphibians follows Cogger (2000), and marsupials follows Aplin and Archer (1987). Marsupial dental terminology has been standardised to the Flower (1869)/Lockett (1993) system: additional dental terminology pertaining to specific groups is provided with the descriptions.

**Mollusca**  
**Gastropoda**  
**Subclass Pulmonata**  
**Order Basommatophora**  
**Family Planorbidae**  
***Glyptophysa* Crosse 1872**

Restricted synonymy following Smith (1992)

*Glyptophysa* Crosse 1872

*Physastra* Tapparone-Canefri 1883

***Glyptophysa rodingae* (McMichael 1968) new combination**

*Isidora* near *pectorosa*, Cameron 1901 p. 14; McMichael (1968).

*Bullinus* sp. nov., Chapman 1937 pp. 50, 63; McMichael (1968)

*Physastra rodingae* McMichael 1968.

**Remarks** The type locality of *Glyptophysa rodingae* (McMichael 1968) is '7 miles north-east of Deep Well homestead, Northern Territory' (McMichael 1968 p. 147), which is in the Ulta Limestone at or very close to its type section. The species (Figure 5e) is the most common large aquatic gastropod in the formation, and is present also in numerous Miocene formations across central and northern Australia, as recorded by McMichael (1968) and Lloyd (1968a). The species is also present in the Camfield beds of the Northern Territory (undescribed material at NTM).

**Table 3** Comparison of dimensions of Kangaroo Well thylacinid NTM P2713-1 with specimens of Camfield beds *Nimbacinus richi* and extant *Dasyurus maculatus*.

	<i>Nimbacinus</i> sp. cf. <i>N. dicksoni</i>	<i>Nimbacinus richi</i>			<i>Dasyurus maculatus</i>	
	P2713-1	P9612-4	P8895-92	P904-7	FN984	FN320
M <sub>1</sub> length of alveoli or external root spans	–	6.8	5.6	–	5.0	5.4
M <sub>2</sub> length of alveoli or external root spans	6.1	7.6	6.4	7.1	5.6	5.7
M <sub>3</sub> length of alveoli or external root spans	6.9	7.9	7.0	7.5	6.0	6.0
M <sub>4</sub> length of alveoli or external root spans	6.6	7.5	6.5	7.5	6.7	6.7
M <sub>4</sub> width of talonid	3.0 <sup>a</sup>	2.5	2.7	2.8	2.5	2.6
M <sub>4</sub> width of trigonid	3.3 <sup>a</sup>	4.1	–	4.0	3.6	3.9
Depth of ramus at M <sub>4</sub>	14.7	17.0	19.4	19.0	13.7	13.9
Width (thickness) of inferior border at M <sub>4</sub>	6.2	7.7	8.4	7.1	5.7	5.4
Dorsoventral thickness of condyle	6.6	7.0	–	–	6.0	5.5
Mediolateral length of condyle	14.2	14.0	–	–	11.5	10.0
Distance from back of condyle to anterior margin of mandibular condyle	21.1	19.0	–	–	20.2	18.5
Minimum width of condylar neck	7.4	6.2	–	–	7.0	7.3
Transverse width of mandibular fossa	10.5	10.5	–	–	10.5	10.7
Distance from back of condyle to back of M <sub>4</sub> root	39.0	37.5	–	–	35.5	34.4

<sup>a</sup>Approximation.

**Order Stylomatophora**  
**Family Camaenidae**  
**Genus *Cupedora* Iredale 1933**

Restricted synonymy following Smith (1992)

*Thersites* Pfeiffer 1855

*Cupedora* Iredale 1933

*Meracomelon* Iredale 1933 (*nomen nudum*); McMichael (1968); Solem (1992a p. 23)

*Meracomelon* Iredale 1937

***Cupedora lloydi* (McMichael 1968) new combination**

'*Therrites*' (error = *Thersites*) *forsteriana* in Cameron (1901); McMichael (1968)

*Thersites* and '*Chlorites*' (error = *Chloritis*) in Whitehouse (1940); McMichael (1968).

*Meracomelon lloydi* McMichael (1968).

**Remarks** The type locality of *Cupedora lloydi* (McMichael 1968) is in the Ulta Limestone, '11 miles north-east of Deep Well homestead, Northern Territory' (McMichael 1968 p. 152). Remains of *Cupedora lloydi* (Figure 5e) are locally common in the Ulta Limestone. McMichael (1968) and Lloyd (1968a) also recorded the species in the Carl Creek Limestone of Queensland and the Etadunna Formation of South Australia, to which may be added the Camfield beds of the Northern Territory (undescribed material at NTM).

**Marsupialia**  
**Australidelphia**  
**Order Dasyuromorphia**  
**Family Thylacinidae**  
***Nimbacinus* Muirhead & Archer 1990**

**Genotypic species** *Nimbacinus dicksoni* Muirhead & Archer 1990 by original designation

**Other species** *Nimbacinus richi* Murray & Megirian 2000

***Nimbacinus dicksoni* Muirhead & Archer 1990**  
***Nimbacinus* sp. cf. *N. dicksoni***  
 (Figure 11, Table 3)

**Material** (from RTW Site, Ulta Limestone, ~0.75 km northeast of its type section at 24°13'S, 134°13'E) P2713-1, fragment of right dentary with worn crown of M<sub>4</sub>, roots of M<sub>3-2</sub>; missing coronoid process and anterior quarter of horizontal ramus; fragment of left squamosal preserving part of glenoid fossa; isolated left petrosal.

**Description** Right dentary within the size range of the Tasmanian spotted quoll, *Dasyurus maculatus*, and closely resembling that species in the prominence of the posterior masseteric eminence, deep posteroventral pocket of the masseteric fossa and transversely broad, deeply notched condylar neck. P2713-1 differs from *Dasyurus maculatus* in having a transversely much wider condyle, less sharply defined, open or grooved anterior margin of the masseteric fossa, flat to concave internal surface of the horizontal ramus, well-developed fovea for the pterygopalatine ligament and subalveolar (m. buccinator) fossa (Figure 11). The length of M<sub>4</sub> alveolus is less than that of M<sub>3</sub> in contrast with *Dasyurus maculatus* in which the M<sub>4</sub> alveolus is longer than M<sub>3</sub> (Table 3). These distinctions from *Dasyurus* are in agreement with those of *Nimbacinus richi*, a similar species from the Bullock Creek Local Fauna,

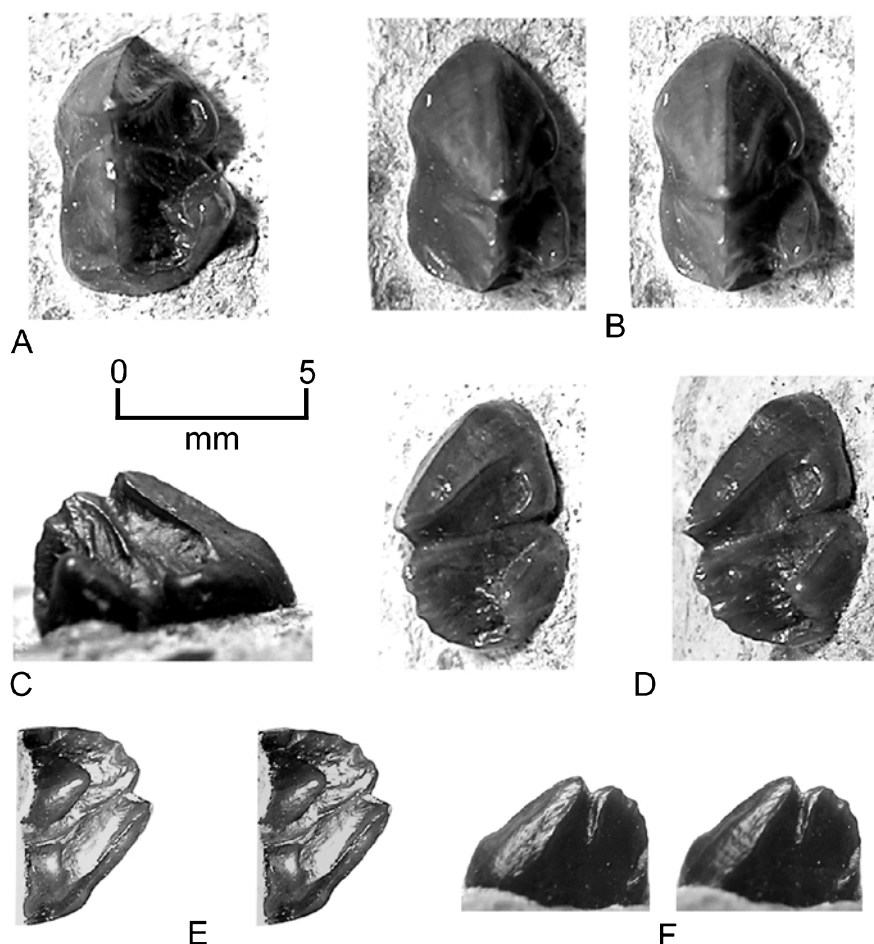
indicating thylacinid affinity in lieu of its poorly preserved molar and absent antemolar dentition. The M<sub>4</sub> crown is heavily worn down to the dentine with only patchy remnants of enamel. The talonid is broad relative to the trigonid, in contrast to *Nimbacinus richi* in which it is narrow. Remnants of the premetacristid and metaconid can be seen in Figure 11e. The posterior root of M<sub>3</sub> is significantly larger than the corresponding root of M<sub>4</sub>, a feature not evident on *Nimbacinus richi* despite its transversely narrower M<sub>4</sub> talonid. The anterior part of the jaw is sheared off anterior to the M<sub>1</sub> alveolus.

**Determination** Dentary much smaller than *Thylacinus cynocephalus* (Harris 1808), *T. potens* Woodburne 1967 and *T. megiriani* Murray 1997; significantly smaller than *T. macknessi* Muirhead 1992 and *Wabulacinus ridei* Muirhead 1997; much larger than *Muribacinus gadiyuli* Wroe 1996 and *Mutpuracinus archibaldi* Murray & Megirian 2000; slightly smaller than *Nimbacinus richi* Murray & Megirian 2000. Differs from all species of *Thylacinus* in having distinct metaconids; from *Wabulacinus* in having stronger metaconids; differs from *Ngamalacinus timmulvaneyi* Muirhead 1997 and *Badjcinus turnbulli* Muirhead & Wroe 1998 in lacking a carnassial notch in the hypocristid. The size and gradient of molar alveoli and basic form of the dentary is most similar to that of *Nimbacinus richi*, in part previously referred to *Nimbacinus dicksoni* (Murray & Megirian 2000). P2713-1 differs from *N. richi* in slightly smaller size of dentary and molar alveoli, broader more acutely notched condylar neck, more rounded, fuller profile of the posterior masseteric eminence, sharper more slender ventral border of the horizontal ramus and transversely wider condyle relative to the overall size and proportions of the dentary.

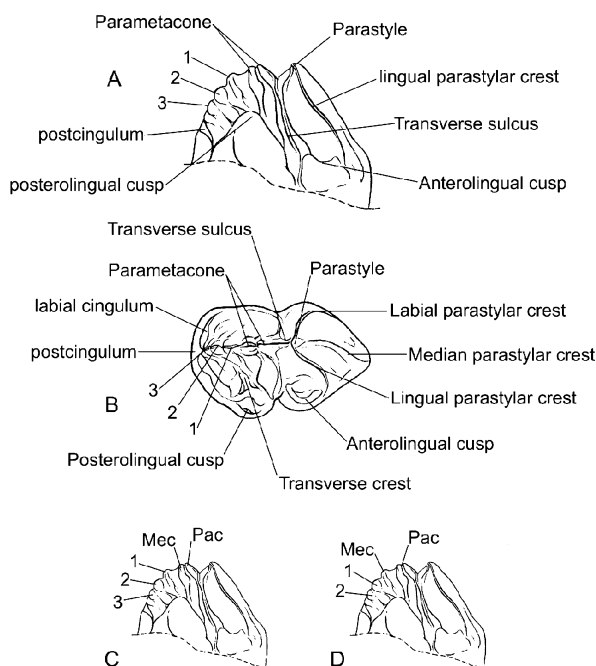
The lower dentition of *Nimbacinus dicksoni* was based on an M<sub>1</sub> (QMF16802, Riversleigh, Henks Hollow Locality), a fragment of M<sub>2</sub> (QMF16809 Riversleigh, Site D Locality) and P<sub>1</sub>-M<sub>1</sub> (P85553-3) from the Bullock Creek Local Fauna, Camfield beds, Northern Territory. Muirhead and Archer (1990 p. 208) noted some of the differences between the heavily worn Bullock Creek specimen (now assigned to *N. richi*) and *N. dicksoni* (broader more angular postero-lingual corner, more rounded anterolingual surface and greater anterior thickness) that were assumed to be within the range of variation for *N. dicksoni*. Consequently there is no *N. dicksoni* dentary available for determination of the Kangaroo Well thylacine. However, its close similarities with *N. richi* but smaller size, and contrasting features with other thylacinid taxa indicate that P2713-1 is close to *N. dicksoni*.

**Order Diprotodontia**  
**Family Wynyardiidae Osgood 1921**  
**Family ?Wynyardiidae**

**Remarks** Wynyardiidae Osgood is monotypic, based on *Wynyardia bassiana* Spencer 1901; the only known specimen of which consists of most of a skeleton, although the dentition is missing. Consequently, other species can be referred to the family only on the basis of post-cranial and non-dental cranial characters. Similar material from the Lake Eyre Basin, referred to *Muramura williamsi* Pledge 1987a, includes dental remains. *Muramura*



**Figure 12** *Ayekaye jaredi* gen. et sp. nov. holotype right P<sup>3</sup> (P2312). (a) Occlusal view with slight posterior aspect. (b) Stereopair in direct occlusal aspect. (c) Lingual aspect showing strong ridges on parastyle and parametacone. (d) Stereopair in oblique, lingual aspect. (e) Stereopair in lingual aspect. (f) Stereopair in labial aspect.



**Figure 13** Diagrammatic drawing of right P<sup>3</sup> of *Ayekaye jaredi* gen. et sp. nov. (a) Lingual aspect. (b) Occlusal aspect. (c, d) Alternative interpretations of cusps and cuspules of parametacrista.

*williamsi* and a dentally similar species, *Namilamadeta snideri* Rich & Archer 1979, have given rise to a concept of a 'wynyardiid' dentition, but it remains to be demonstrated that *W. bassiani* plus ?wynyardiids represent a natural group. The affinities of *W. bassiana* and supposedly closely related forms (i.e. ?wynyardiids) within Marsupialia are controversial (Rich 1991).

***Ayekaye jaredi* gen. et sp. nov.**  
(Figures 12, 13).

**Holotype** P2815-2, unworn right P<sup>3</sup> crown with the base embedded in limestone matrix (Figure 12).

**Type locality and age** RTW Site, Ulta Limestone, ~0.75 km northeast of its type section at 24°13'S, 134°13'E, Late Oligocene on the basis of the relative stage of evolution of associated members of the Kangaroo Well Local Fauna.

**Diagnosis** The diagnosis serves for both the genus and the species until such time as other species are known. Bilobate tuberculosectorial upper third premolar with three major cusps: a large posteriorly slanted parastyle, a weakly divided parametacone with serrated parametacrista and a large, triangular posterolingual cusp in the topographical position of the hypocone; generally resembling *Namilamadeta snideri* Rich & Archer 1979, more closely resembling *Muramura williamsi* Pledge (1987a), but significantly smaller and more delicate than either of

these species. Differs from *N. snideri* in possessing a well-defined anterolingual cusp, and from *M. williamsi* in which both anterolingual and posterolingual cusps are present though rudimentary. Differs from both *N. snideri* and *M. williamsi* in possessing a serrated, bladelike parametacrista. Crown is much narrower and higher relative to length than in any genus and species of Ilariidae, including *Kuterintja* Pledge 1987b, and Phascolarctidae. Among the phascolarctids, the labial crest is more coarsely ridged or fluted and sometimes bears a posterolabial cus-  
pule (e.g. *Madakoala* Woodburne, Tedford, Archer & Pledge 1987), and in which an elevated lingual crest (*Phascolarctos*) or a large cus-  
pule (*Nimiokoala* Black & Archer 1997) enclose a longitudinal cleft.

**Description** The upper third premolar has a relatively narrow, bilobate crown of length 6.7 mm; width of the anterior moiety 4.0 mm; and width of the posterior moiety 4.4 mm. The anterior-half of the crown is dominated by a large, posteriorly directed parastyle, separated from the more blade-like parametacone of the posterior-half by broad shallow grooves buccally and lingually, and a V-shaped notch behind the apex of the parastyle. The parastyle is distinctly rhomboidal in section with strong anteromedial, buccal and lingual ridges. The lingual parastylar ridge connects with the anterior margin of a small basal cusp. The anteromedian crest terminates in a tiny basal swelling. A shallow groove lies between the anteromedian and lingual crests.

The median crest (parametacrista) of the parametacone is finely serrated, commencing behind the transverse groove of the parastyle with the larger of four cus-  
pules slightly lower than the parastyle. Posteriorly, three smaller cus-  
pules with three faint ridges separated by four shallow grooves progressively decreasing in size and strength along the parametacrista, blend into the elevated median salient of the postcingulum (Figure 12a, b). The postcingulum extends a short distance around the posterolabial and posterolingual sides of the posterior moiety, rapidly fading labially; while lingually it emarginates a shallow posterolingual basin then ascends the posterior side of a large triangular posterolingual cusp. The base of the posterolingual cusp extends over much of the length of the posterior moiety and its apex is approximately half the

height of the parametacone. A transverse crest connects the labial side of the cusp to the lingual flank of the parametacone, fully enclosing the tiny posterolingual basin.

**Discussion** The small size, delicate structure and serrated parametacrista readily distinguish P2312 from *Muramura williamsi* and *Namilamadeta snideri*, in which the paracone and metacone are approximately equal sized, distinctly divided, and occupy most of the median crest of the posterior moiety. The median cus-  
pules on P2312 can also be interpreted as a larger paracone and a smaller, closely approximated metacone; or the paracone, which bears a shallow groove, might be interpreted as an incipiently divided parametacone with a serrated post-  
metacrista (Figure 13c, d). Because other ?wynyardiid P<sup>3</sup> specimens are worn, it is not known whether a serrated postmetacrista might not have been present, although it is unlikely due to the large, posteriorly situated metacone in both genera. Regardless of the homology, the parametacrista in P2312 functioned primarily as a shearing crest in contrast to those of *N. snideri* and *M. williamsi*, in which it is more stoutly constructed and distinctly cus-  
pate.

In the context of current opinion on the phylogenetic position of ?wynyardiids (Rich & Archer 1979; Aplin 1987; Pledge 1987a), the phalangeroid-like appearance of the crown would probably be discounted as autapomorphic homoplasy. However, because no compelling analysis of the character polarities of ?wynyardiid premolar morphology has been produced, it seems prudent to at least entertain the implications. If our interpretation of an incipient division of the parametacone is the correct one, then on the basis of trends in other diprotodontians, *Ayekaye jaredi* is the most plesiomorphic ?wynyardiid yet described. Moreover, the general structural correspondence to some phalangeridans such as *Pseudochairus* seems to obviate the phascolarctomorphian basis of vombatomorphian evolution, because virtually any vombatiform P<sup>3</sup> can be derived from this morphology.

**Etymology** *Ayekaye*, Arrente exclamation, approximately equivalent to 'wow!' Species name *jaredi* in gratitude to our sharp-eyed technical officer, Jared Archibald, who found the specimen.

#### Order Diprotodontia Owen

#### Family Diprotodontidae Gill

#### Zygomaturinae Stirton, Woodburn & Plane 1967

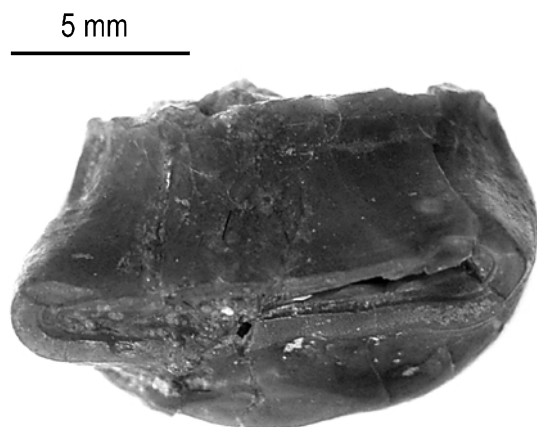
#### *Neohelos* Stirton 1967

#### *Neohelos tirarensis* Stirton 1967

(Figure 14)

**Material** from BMR Site, Ulta Limestone, at its type section at 24°13'S, 134°13'E) P2690-1, right M<sub>3</sub> metalophid.

**Description** The dental and comparative morphology of *Neohelos* species has recently been documented by Murray *et al.* (2000a). Although merely half a tooth (Figure 14), P2690-1 can readily be diagnosed as an *N. tirarensis* M<sub>3</sub> hypolophid on the basis of dental measurements and morphological attributes. The presence of a distinct interproximal wear facet below the postcingulum precludes its identification as an M<sub>4</sub>, which is otherwise morphologically similar. The more buccal position of posterior cingulum, lower crown height, and weaker expression of the postmetacristid relative to how these



**Figure 14** Kangaroo Well Local Fauna *Neohelos tirarensis* right M<sub>3</sub> metalophid (P2690-1) in occlusal view, anterior towards the top of the page.

characters are expressed in  $M_2$  and  $M_1$  further support the identification of the tooth as an  $M_3$ . The width of P2690-1 (= posterior width) is 14.6 mm, which falls in the range of *N. tirarensis* (12.2–15.8 mm,  $n = 10$ ; Murray *et al.* 2000a table 2) and outside the range of *N. stirtoni* [15.9–27.0 mm,

$n = 45$ : the measurement of 12.8 mm given by Murray *et al.* (2000a table 9; 2000b table 3) for NMV P194549 is an error, and should be 17.3 mm (T. H. Rich pers. comm. 2002)].

### Superfamily Phalangoidea

#### Family Ektopodontidae Stirton, Tedford & Woodburne 1967

##### *Ektopodon* Stirton, Tedford & Woodburne 1967

**Genotypic species** *Ektopodon serratus* Stirton, Tedford & Woodburne 1967

**Additional genera and species** *Ektopodon stirtoni* Pledge 1986; *E. sp. cf. E. stirtoni* Pledge 1986; *E. litolophus* Pledge, Archer, Hand & Godthelp 1999; *Ektopodon sp. cf. E. serratus* Pledge, Archer, Hand & Godthelp 1999; *Chunia illuminata* Woodburne & Clemens 1986a; *Chunia sp. cf. C. illuminata* Woodburne & Clemens 1986a; *Chunia omega* Woodburne & Clemens 1986a; *Darcus duggani* Rich 1986.

##### *Ektopodon ulta* sp. nov.

(Figure 15a, b; Tables 4, 5)

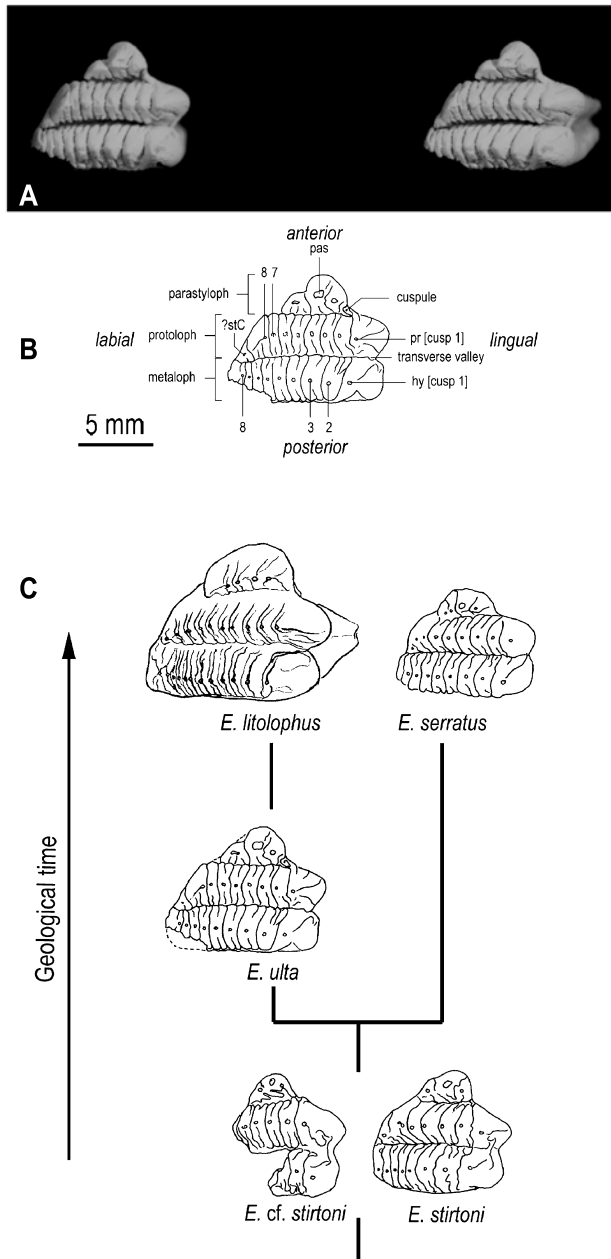
**Holotype** NTM P2607-1, right  $M^1$ .

**Type locality and age** BMR Site, Ula Limestone, at its type-section at 24°13'S, 134°13'E, Late Oligocene on the basis of stage of evolution relative to other species in the genus.

**Diagnosis** A species of *Ektopodon* with a first upper molar ( $M^1$ ) bearing three cusps on the parastyloph, eight on the protoloph and nine on the metaloph. Differs from *E. serratus* in having one less parastyloph cusp and one more metaloph cusp. Differs from *E. stirtoni* in having two more protoloph cusps and one more metaloph cusp. Differs from *E. litolophus* in having one less parastyloph cusp, two less protoloph cusps and two less metaloph cusps.

**Dental terminology** The Ektopodontidae is characterised by very peculiar, highly specialised dentitions. The family, established on isolated teeth of *Ektopodon serratus* Stirton, Tedford & Woodburne 1967, was originally placed, with reservations, in the Monotremata. The phalangeroid affinities of the family were recognised only when additional specimens of *E. serratus* and new genera and species represented by more complete material were discovered (Woodburne & Clemens 1986b). The homology of dental cusps and related structures, however, remains uncertain, but for the purposes of description, terminology pertaining to tribosphenic dentitions has been applied to them, as discussed in Woodburne and Clemens (1986c).

Terminology set out by Woodburne and Clemens (1986c), who also briefly reviewed terms used by Pledge (1986) and Rich (1986), is applied with some minor modification following Tedford and Woodburne (1987) to the Kangaroo Well  $M^1$ , P2607-1, in Figure 15a. The anterior transverse loph of  $M^1$  (and the only molar with this structure) is referred to as the parastyloph, followed posteriorly by the protoloph and metaloph. The anteriormost cusp of the parastyloph is designated a parastyle, the lingualmost cusp of the protoloph is designated a protocone, and the lingualmost cusp of the metaloph is designated a hypocone. The protocone and hypocone count as cusp 1 of their respective lophs, which are numbered sequentially towards the labial side. Pledge (1986) went so far as to suggest that the labialmost cusp of the parastyloph is stylar cusp A, the labialmost cusp of the protoloph is the



**Figure 15** *Ektopodon ulta* sp. nov. NTM P2607-1. (a) Occlusal view stereopair, specimen coated with  $NH_4Cl$ . (b) Interpretive diagram showing structure. (c) Comparison of  $M^1$ s of *Ektopodon* species, drawn approximately to scale and arranged to reflect inferred phyletic relationships within the group, as discussed in the text. Interpretive diagrams of *E. serratus*, (SAM P13847) after Woodburne and Clemens (1986a plate 3.1C), *E. stirtoni* (SAM P22504) after Woodburne and Clemens (1986a plate 3.1B); *E. sp. cf. E. stirtoni* (NMV P48750-1) after Woodburne and Clemens (1986a plate 3.2A), and *E. litolophus* (SAM P30176) after Pledge *et al.* (1999 figure 3); *E. serratus* and *E. sp. cf. E. stirtoni* reversed to aid comparison. hy, hypocone; pas, parastyle; pr, protocone; stC, stylar cusp C.

**Table 4** Comparison of measurements of the upper first molar [ $M^1$ : equivalent to  $M^2$  in Pledge (1986) and Woodburne and Clemens (1986a)] of *Ektopodon* species.

Taxon	Specimen no.	Side	Length L	Width paraloph $W_{pa}$	Width protoloph $W_{pr}$	Width hypoloph $W_{hy}$	L:W <sub>pr</sub>	Source
<i>E. stirtoni</i>	SAM P22504	R	8.75	—	8.90	9.25	0.98	Pledge (1986 table 3.1))
	SAM P35309	L	8.8	—	8.3	9.0	1.06	Pledge <i>et al.</i> (1999 table 1)
<i>E. sp. cf. E. stirtoni</i>	NMV P48750-1	L	8.55	—	8.00	—	1.07	Pledge (1986 table 3.2)
	SAM P19962	R	8.50	—	—	—	—	—
<i>E. serratus</i>	SAM P13847	L	7.2	3.5	7.8	8.4	0.92	Woodburne and Clemens (1986a table 2.2)
<i>E. litolophus</i>	SAM P30176	R	10.6	—	11.7	12.1	0.91	Pledge <i>et al.</i> (1999 table 1)
<i>E. ulta</i>	NTM P2607-1	R	8.00	4.0	9.50	9.60	0.90	Present paper

paracone or stylar cusp B, the cusp closing the labial end of the transverse valley between the protoloph and metaloph represents stylar cusp C, and the labialmost cusp of the metaloph is the metacone or stylar cusp D. Crests extending anteriorly and posteriorly from the apex of most of the cusps are designated pre- and post-cristae: Pledge (1986) referring to them as ‘ribs’ or ‘ridges’. P2607-1 is an almost complete crown, lacking only the posterobuccal margin of the metaloph, and exhibiting slight damage to the anterolabial margin of the parastyloph. The specimen is therefore comparable with the holotype of *E. serratus*, SAM P13847, a complete left  $M^1$  (Stirton *et al.* 1967a figure 6; Woodburne & Clemens 1986a plate 3.1C); the *E. stirtoni* paratype SAM P22504, a complete right  $M^1$  (Pledge 1986 figure 3.5; Woodburne & Clemens 1986a plate 3.1B); *Ektopodon* sp. cf. *E. stirtoni* NMV P48750-1, a partial left  $M^1$  (Woodburne & Clemens 1986a plate 3.2A), and the *E. litolophus* holotype, a complete right  $M^1$  (Pledge *et al.* 1999 figure 3). The generic characters of *Ektopodon* species are evident in Figure 15.

**Description** P2607-1 is short in proportion to its length, and the outline profile more angular than in other species, especially along the labial edges of the protoloph and metaloph, and the lingual edge of the metaloph (Figure 15a). The parastyloph is composed of three cusps of approximately equal height separated from each other by anteroposteriorly aligned commissures, although a tiny cuspule is also present at the posterolingual extremity of the loph, restricting the transverse valley between the parastyloph and the protoloph. The intermediate of the three major cusps, the nominal parastyle, is the largest, and is slightly anterior to the adjacent cusps. In occlusal outline the labial cusp appears to be well separated from both the parastyle and the adjacent protoloph by marginal embayments. These embayments, however, are attributable to slight damage to the crown associated with the breaking off of the underlying root, and the anterolabial profile of the tooth was probably fairly smooth as in other *Ektopodon* species (Figure 15b), and the parastyloph was at least 4.0 mm wide posteriorly at the transverse valley. The apex of the labial cusp is elongated transversely. Three grooves, the middle one the longest, extend from the transverse valley up the posterior face of the cusp. The parastyle has only one such groove, and the labial cusp none.

The protoloph and metaloph are typical of *Ektopodon*, in which the lingual cusps, nominally the protocone and hypocone, are the largest of their respective series. The

**Table 5** Comparison of  $M^1$  cusp patterns in *Ektopodon* species.

Taxon	No. cusps on parastyloph	No. cusps on protoloph	No. cusps on metaloph
<i>E. litolophus</i>	4	10	10
<i>E. ulta</i>	3	8	9
<i>E. serratus</i>	4	9	8
<i>E. stirtoni</i>	3	6	8
<i>E. sp. cf. E. stirtoni</i>	3	?	?

Data for *E. serratus* from Stirton *et al.* (1967b), for *E. stirtoni* and *E. sp. cf. E. stirtoni* from Pledge (1986), and *E. litolophus* from Pledge *et al.* (1999 table 2).



cusps on each loph become progressively narrower towards the lingual side, and the pre- and post-cristae of the intermediate cusps are mostly bifurcated at their bases by linear grooves such as those already described from the parastyloph. The protoloph bears eight cusps, with an additional smaller cusp, possibly representing stylar cusp C, restricting the transverse valley at its labial end. The posterior face of cusp 8 bears two grooves arising from the transverse valley, the lingual one of which nearly reaches the apex. Cusp 8 has a smooth anterolateral face, and its straight marginal profile continues across the nominal stylar cusp C and onto the metaloph to the level of its crest. The form and arrangement of cusps on the metaloph are very similar to those of the protoloph, except that there are nine rather than eight in the series. The parastyloph is, however, more rectilinear in its occlusal outline, as already noted above. A postcingulum arising from the hypocone (= cusp 1) forms the posterior margin of the tooth.

**Comparative remarks** The  $M^1$  of *Ektopodon ulta* is proportionally similar to that of *Ektopodon serratus* and *E. litolophus*, and transversely wider than that of *E. stirtoni* and *E. sp. cf. E. stirtoni* (Table 4). However, the cusp pattern of *E. ulta* does not correspond to any of the

previously described taxa (Table 5). The occlusal profiles of *E. ulta* and *E. litolophus* are more angular than those of the other species (Figure 15c).

Like *E. stirtoni* and *E. sp. cf. E. stirtoni*, *E. ulta* has three cusps on the parastyloph, whereas *E. serratus* and *E. litolophus* have four. The additional one of *E. serratus* and *E. litolophus* is on the labial side of the parastyloph. As described above, the labial cusp on *E. ulta* is transversely elongate, and the presence of a groove approaching the apex up the posterior face of the cusp suggests that a second labial cusp may have arisen by division. Structures similar to the small cusps in *E. ulta* that partially restricts the transverse valley separating the parastyloph from the protoloph on the lingual side appear to be present in *E. stirtoni* (Woodburne & Clemens 1986a plate 3.1B) and *E. sp. cf. E. stirtoni* (Woodburne & Clemens 1986a plate 3.2A), but apparently not in *E. serratus* (Woodburne & Clemens 1986a plate 3.1C) and *E. litolophus* (Pledge *et al.* 1999 figure 3). *Ektopodon ulta* has two more cusps on the protoloph than *E. stirtoni*, one less than *E. serratus*, and two less than *E. litolophus*. *Ektopodon ulta* has one more cusp on the metaloph than *E. serratus*, and one less than *E. litolophus*. Differences in  $M^1$  cusp pattern (Table 5) are therefore sufficient to diagnose each of the known *Ektopodon* species.

**Etymology** The specific epithet refers to the Ulta Limestone.

#### Superfamily Petauroidea (Gill)

#### Family Pseudocheiridae (Winge)

#### *Pildra* Woodburne, Tedford & Archer 1987

**Type species** *Pildra antiquus* Woodburne, Tedford & Archer 1987

**Additional species** *Pildra secundus* Woodburne, Tedford & Archer 1987; *Pildra tertius* Woodburne, Tedford & Archer 1987; *Pildra magnus* Pledge 1987c; *Pildra sp. cf. P. magnus* present work.

#### *Pildra magnus* Pledge 1987c

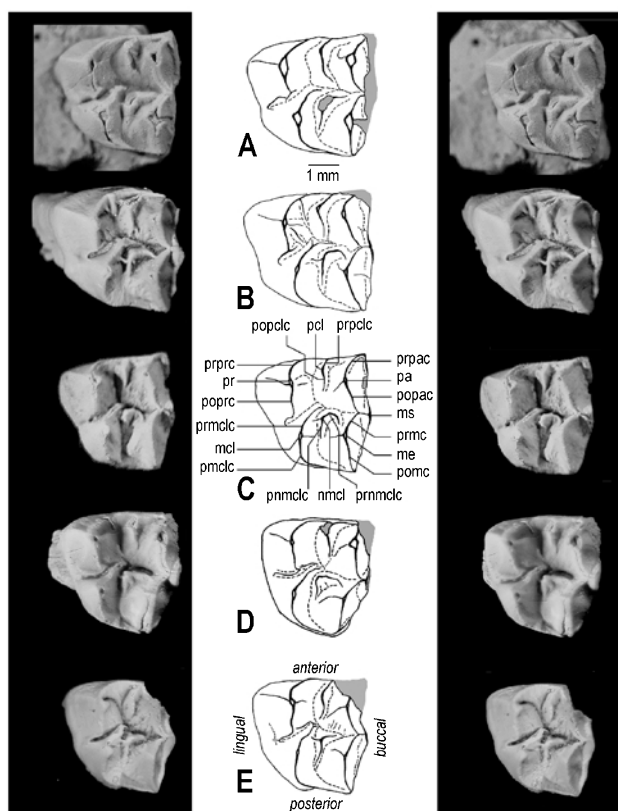
#### *Pildra sp. cf. P. magnus*

(Figure 16; Table 6)

**Material** (all from BMR Site, Ulta Limestone, at its type section at 24°13'S, 134°13'E) P2692-4, left  $M^3$ , complete apart from the loss of a small chip of enamel from the buccal margin of the protocone; P2692-2, left  $M^2$ , lacking enamel from the buccal margin, neometaconule chipped; P2692-7, left  $M^2$ , lacking the anterobuccal (parastylar) corner; P2692-3, left  $M^3$  lacking the anterobuccal corner; P2692-6, left  $M^3$  lacking anterobuccal corner, protoconule chipped; P2607-5, heavily worn right upper molar, probably  $M^2$  or  $M^3$ , missing ectoloph; P2607-6, mid-crown fragment of a left upper molar, probably  $M^2$  or  $M^3$ ; P2602-11, fragment of left upper molar comprising the paracone and paraconule.

**Dental terminology** Pseudocheirid dental terminology follows Woodburne *et al.* (1987), as shown in Figure 16. Woodburne *et al.* (1987) recognised the posterolingual cusp of diprotodontian upper molars as a metaconule, rather than a hypocone, and the accessory cusp between the metaconule and the metacone as a neomorph structure, a neometaconule rather than a hypoconule.

**Description** The assembled isolated Kangaroo Well Local Fauna teeth represent a species of *Pildra* slightly



**Figure 16** Stereopairs of Kangaroo Well Local Fauna *Pildra sp. cf. P. magnus*. (a) P2692-2, left  $M^2$ . (b) P2692-7, left  $M^2$ . (c) P2692-4, left  $M^3$ . (d) P2692-3, left  $M^3$ . (e) P2692-6, left  $M^3$ . nmcl, neometaconulecrista; mcl, metaconule; me, metacone; ms, mesostyle; pcl, protoconule; pmc, pmcl, postmetaconulecrista; pnmcl, postneometaconulecrista; pomc, postmetacrista; popcl, postprotoconulecrista; poprc, postprotocrista; pr, protocone; prmc, premetacrista; prnmcl, premetaconulecrista; prpac, preparametacrista; prpcl, preprotoconulecrista. Specimens coated with  $NH_4Cl$ .

**Table 6** Comparative dental measurements of *Pildra* species.

Taxon/specimen (source)	Side		M <sup>2</sup>			M <sup>3</sup>			M <sub>2</sub>			M <sub>3</sub>		
	L		AW	PW		L	AW	PW	L	AW	PW	L	AW	PW
<i>Pildra</i> sp. cf. <i>P. magnus</i> (present paper)														
NTM P2692-7	3.74	L	3.82	3.32		—	—	—	—	—	—	—	—	—
NTM P2692-2	3.74	L	3.78	3.38		—	—	—	—	—	—	—	—	—
NTM P2692-3	—	L	—	—	3.60	3.34	2.68	—	—	—	—	—	—	—
NTM P2692-4	—	L	—	—	3.60	3.48	2.74	—	—	—	—	—	—	—
NTM P2692-6	—		—	—	3.52	3.26	2.60	—	—	—	—	—	—	—
<i>Pildra magnus</i> (Pledge 1987c table 1)														
SAM P24722	3.4	L	3.5	3.0		—	—	—	—	—	—	—	—	—
SAM P23029	—	R	—	—	3.35	3.3	2.7	—	—	—	—	—	—	—
SAM P23032	—	R	—	—	3.2	—	—	—	—	—	—	—	—	—
SAM P24721	—	L	—	—	3.4	3.2	2.6	—	—	—	—	—	—	—
SAM P24575	—	L	—	—	—	—	—	3.8	2.3	2.3	—	—	—	—
SAM P24543	—	L	—	—	—	—	—	—	—	—	4.1	2.1	2.2	—
SAM P24574	—	L	—	—	—	—	—	—	—	—	—	—	2.1	—
SAM P24724	—	R	—	—	—	—	—	—	—	—	—	—	2.1	—
<i>Pildra antiquus</i> (Woodburne <i>et al.</i> 1987 tables 1, 2)														
	2.6–2.7		2.6–2.8	2.45–2.5	2.25–2.65	2.5–2.7	1.8–2.1	2.65–3.05	1.7–2.0	1.65–1.9	2.4–3.1	1.65–2.0	1.6–1.85	
	<i>n</i> = 4		<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 3	<i>n</i> = 3	<i>n</i> = 3	<i>n</i> = 15	<i>n</i> = 15	<i>n</i> = 15	<i>n</i> = 19	<i>n</i> = 19	<i>n</i> = 19	
<i>Pildra secundus</i> (Woodburne <i>et al.</i> 1987 tables 3, 4)														
	2.35–3.0		2.35–3.0	2.5–2.75	2.65–2.9	2.6–2.8	2.1–2.2	3.0	1.9–2.0	1.85–1.95	2.9	1.9–2.0	1.85–1.9	
	<i>n</i> = 4		<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 3	<i>n</i> = 3	<i>n</i> = 4	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 3	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	
<i>Pildra tertius</i> (Woodburne <i>et al.</i> 1987 table 5)														
	—		—	—	—	—	—	—	—	—	1.4	1.35	1.4	

Measurements in mm, numbers in italics are estimates.

M, molar; L, length; AW, anterior width; PW, posterior width.

larger than *P. magnus*, and markedly larger than *P. antiquus*, *P. secundus* and *P. tertius* (Table 6). Specimens P2692-2 and P2692-7 are interpreted as M<sup>2</sup>s on the basis of their slightly larger overall size, proportionally greater width, slightly more massive metaconule, longer postparaconulecrista, and inconsistent expression of lingual ribs from the paracone and metacone when compared to P2692-3, P2692-4 and P2692-6, which are interpreted to be M<sup>3</sup>s (Figure 16).

**Upper molars, M<sup>2</sup> and M<sup>3</sup>** Apart from the features listed above as distinguishing M<sup>2</sup>s from M<sup>3</sup>s, these molars are very similar (Figure 16). For each specimen, the occlusal outline is subquadratic, with sharp angles at the anterolabial and posterolabial corners, and broadly rounded ones at the anterolingual and posterolingual corners. The anterior and posterior margins converge medially, being just subperpendicular by similar amounts to the buccal margin, to which a prominent mesostyle imparts a slightly sinuous profile. The lingual margin converges posterolabially towards the labial margin.

The occlusal traces of the ectoloph are parallel to and near the buccal margin, a reflection of the steepness of the buccal faces of the paracone and metacone. On all specimens the postparacrista and premetacrista unite at the level of the mid-valley, continuing buccally as a single crest to contact the mesostyle, which (where preserved) is expressed as single cusp with a well-defined anterior and posterior crest (the *kappa* rather than *lambda* expression

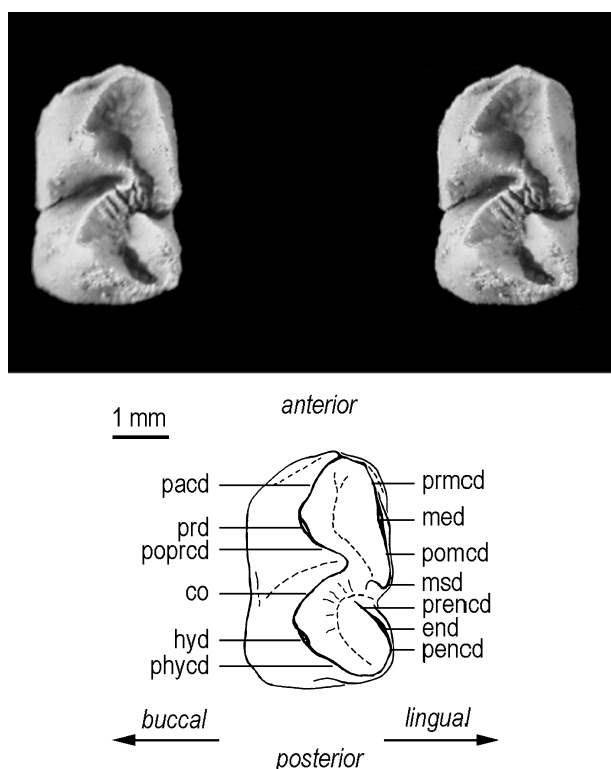
of the mesostyle: Pledge 1987c). In the only specimen with an intact anterobuccal corner of the tooth (P2692-4), the preparacrista merges into the precingulum lingual to the parastyle. The lingual sides of the paracone and metacone are rounded, in contrast to the planar buccal faces. As already mentioned above, a single lingual rib from the paracone and metacone may be weakly expressed or absent on the M<sup>2</sup>s, but are consistently expressed on the M<sup>3</sup>s.

The paraconule presents in occlusal view more as an open chevron than a crescent, with its cusp at the point of flexure anterior to the level of the paracone and protocone, and is marginally closer to the paracone than to the protocone. The preparaconulecrista is confluent with the precingulum, itself a continuation of the protocrista. The greater relative length of the postparaconulecrista in the M<sup>2</sup>s compared to the M<sup>3</sup>s has already been noted. The postmetaconulecrista of P2692-2 swings posterobuccally at its extremity, in contrast to the lingually concave orientation in the other four molars, a difference that is attributed to individual variation.

The neometaconule is more arcuate than the paraconule, the curvature exaggerated in some specimens (P2692-3, P2692-4 and P2692-7) by a strong, posterior recurvature of the preneometaconulecrista onto the anterolingual slope of the metacone. P2692-4, P2692-6 and P2692-7 have a lingual rib connecting the cusp of the neometaconule to the buccal slope of the metaconule, whereas no such structure is present in P2692-2 and P2692-3. These differences are also attributed to individual variation. In all specimens, the cusp of the neometaconule lies well anterior to a line connecting the metacone to the metaconule, and the neometaconule is marginally closer to the metaconule than to the metacone.

The protocone is the most massive cusp, with a concave buccal face and swollen lingual face upon which a lingual rib is developed from the apex nearly to the base of the crown. The preprotocrista arcs smoothly towards the precingulum, with which it is continuous. There is no sign of a protostyle on the precingulum between the protocone and paraconule on any specimen. The postprotocrista is nearly straight, coursing directly posteriorly or slightly posterobuccally towards the median valley. Just short of the median valley, the postprotocrista contacts a variably expressed crest (which alternatively could be regarded as a transverse elaboration of the postprotocrista) that parallels the median valley between the protocone and metaconule. The lingual component of this crest is consistently expressed, but the component buccal to the juncture with the postprotocrista is more variable, ranging from absent (P2692-4), short (P2692-2, P2692-7), or long but discontinuous, extending to the centre of the crown (P2692-6, P2692-3). The lingual extremity in all specimens but P2692-6 curves around posteriorly to close the median valley at its lingual end. The variably expressed features relating to these transverse structures are also attributed to individual differences.

Like the protocone, the metaconule also has a concave buccal side and rounded lingual side, but is smaller (more so in M<sup>3</sup>s than in M<sup>2</sup>s) and lacks a lingual rib. The premetaconulecrista arcs anterobuccally towards the median valley, extending into the centre of the crown. P2992-7 and P2692-6 exhibit a variation in having a small,



**Figure 17** Stereopair of Kangaroo Well Local Fauna *Marlu* sp. cf. *M. kutjampensis* M<sub>2</sub> or M<sub>3</sub>. co, cristid obliqua; end, entoconid; hyd, hypoconid; med, metaconid; msd, mesostylid; pacd, paracristid; pencd, postentocristid; phycd, posthypocristid; prd, protoconid; prencd, preentocristid; prmcd, premetacristid; pomcd, postmetacristid; poprd, postprotocristid. Specimen coated with NH<sub>4</sub>Cl.

anteriorly projecting bifurcation near the tip. The post-metacrista courses posteriorly from the cusp before rounding buccally to continue as the postcingulum to the tooth, which extends to the posterobuccal corner, where it contacts the postmetacrista, the point of contact representing the mesostyle.

**Comparative remarks** *Pildra* sp. cf. *P. magnus* from the Kangaroo Well Local Fauna differs from *P. antiquus*, *P. secundus* and *P. tertius* in the same ways as Ngama Local Fauna *P. magnus* does, as detailed by Pledge (1987c). The Kangaroo Well Local Fauna form differs from *P. magnus* in the following ways: the teeth (M<sup>2</sup>s and M<sup>3</sup>s) are slightly larger; their para- and neometacristae are a little more strongly developed and appear fractionally closer to the protocone and metacone (and further away from the paracone and metacone), and the neometacrista on M<sup>3</sup> is better developed. Some additional minor differences, although ones that appear to be subject to some individual variability, include apparently less-crenulated enamel in basal areas of the crown, and lack of any indication of a protostyle in any specimen.

Lower jaws and teeth were selected as holotypes of the Miocene pseudocheirids described in 1987, including *Pildra* spp., because these allowed for the greatest range of comparisons between the known taxa, and hence underpinned differential generic and specific diagnoses. In the absence of comparable lower teeth we classify the Kangaroo Well Local Fauna form as a *Pildra* sp. cf. *P. magnus*.

#### *Marlu* Woodburne, Tedford & Archer 1987

**Type species** *Marlu kutjampensis* Woodburne, Tedford & Archer 1987

**Additional species** *Marlu praecursor* Woodburne, Tedford & Archer 1987; *M.* sp. cf. *M. kutjampensis* Pledge 1987c; *M.* sp. cf. *M. kutjampensis* present work.

#### *Marlu kutjampensis* Woodburne, Tedford & Archer 1987

*Marlu* sp. cf. *M. kutjampensis*  
(Figure 17; Table 7)

**Material** (from BMR Site, Ulta Limestone, at its type section at 24°13'S, 134°13'E) P2689-1, right lower molar, probably M<sub>2</sub> or M<sub>3</sub>.

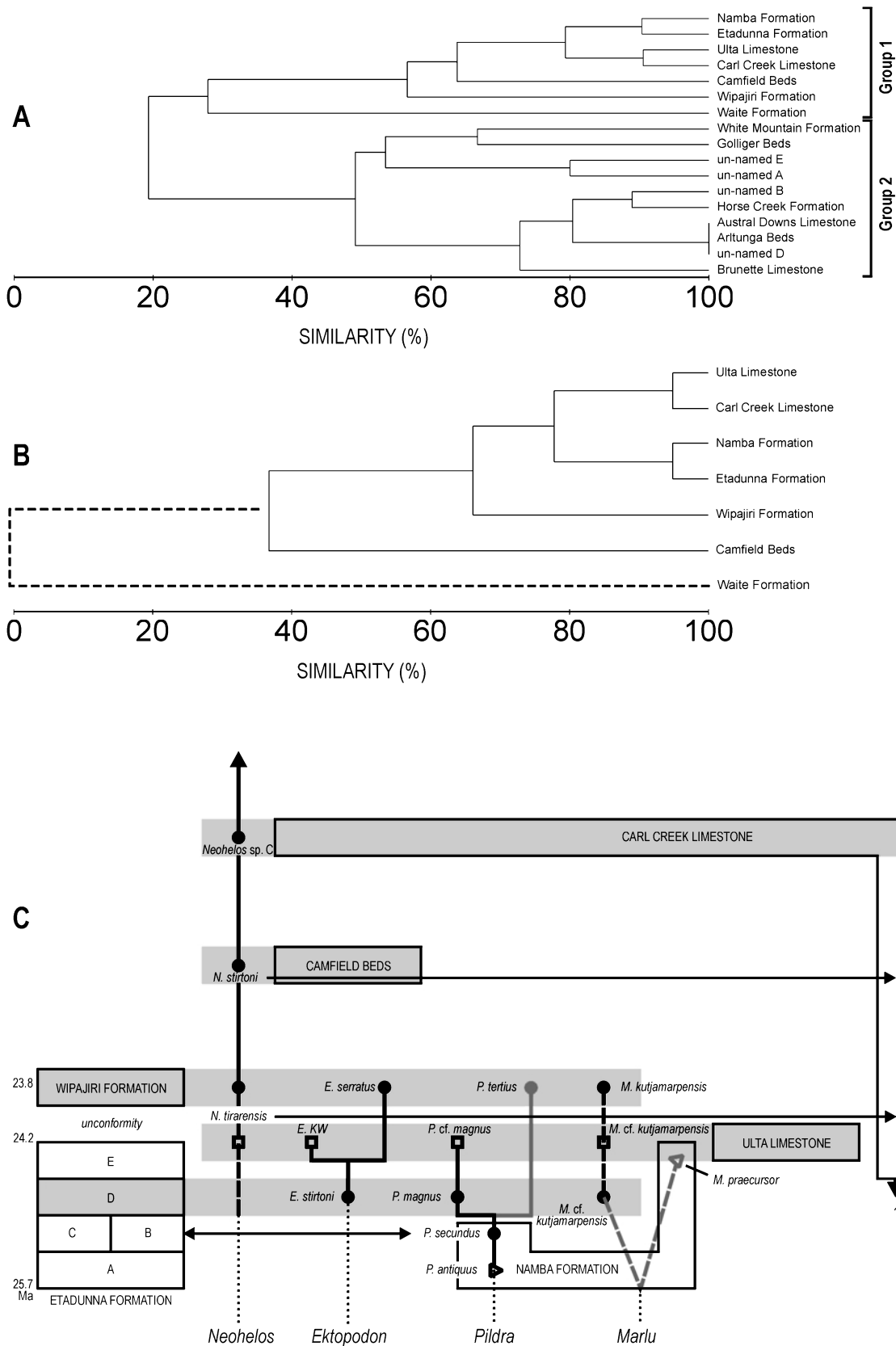
**Description** P2689-1, an unworn M<sup>2</sup> or M<sup>3</sup>, is essentially rectangular in occlusal view, approximately three-quarters as wide as it is long (Figure 17; Table 7). The lingual and buccal sides are parallel, the posterior margin describes a gentle arc, and the anterior margin is very broadly pointed, the apex at the midline of the tooth where a paraconid is found in some pseudocheirid species. However, no distinct paraconid arises from the lingual extremity of the anterobuccal cingulum in P2689-1.

The paracristid courses anterolingually in a gentle arc from the protoconid almost to the anterior apex of the tooth, before arcing lingually to meet the premetacristid at a right angle. The conjunction of the premetacristid and the paracristid is right on the anterior margin of the tooth, separating the anterobuccal cingulum from the anterolingual cingulum. The metaconid is an elongate cusp with a postmetacristid extending posterolingually to converge on the lingual margin, posterior to the midpoint of its length. At its posterior extremity is a well-developed metastylid at the level of, but lingual to, the anterior margin of a short preentocristid, which descends steeply from the entoconid anterobuccally in the direction of the protoconid. The postentocristid is basically collinear with the preentocristid from the apex of the cusp into the posterolingual corner of the tooth, where it joins the posthypocristid. The posthypocristid is a linear, posterolingually directed crest from the hypoconulid to the posterior margin of the tooth, where it turns lingually to parallel the lingual quarter of the posterior margin to join the postentocristid. A very slight inflation at the point of inflection may represent a rudimentary hypoconulid. There is no sign of an entostylid. The hypoconid is the tallest of the four principal cusps, the other three having approximately equal height. Cristid obliqua extends a short anterobuccal distance from the hypoconid before making a right-angled turn into the centre of the crown. A series of parallel crenulations course from cristid obliqua

**Table 7** Comparative dental measurements (mm) of *Marlu* species.

Taxon/specimen (source)	Side	M <sup>3</sup>			M <sub>2</sub>			M <sub>3</sub>		
		L	AW	PW	L	AW	PW	L	AW	PW
<i>Marlu</i> sp cf. <i>M. kutjampensis</i> , Kangaroo Well LF (present paper)										
NTM P2689-1	R	—	—	—	3.90	2.38	2.46	—	—	—
<i>Marlu</i> sp. cf. <i>M. kutjampensis</i> , Ngama LF (Pledge 1987c table 2)										
SAM P24569	R	3.4	3.4	2.9	—	—	—	—	—	—
<i>Marlu kutjampensis</i> Woodburne <i>et al.</i> (1987) tables 6, 7)										
UCMP 119448	L	3.45	3.45	3.05	—	—	—	—	—	—
SAM P19961	L	—	—	—	—	—	—	3.6	1.85	1.95
UCMP 119450	R	—	—	—	3.45	—	—	—	—	—
UCMP 66808	R	—	—	—	3.5	2.0	2.0	—	1.95	—
UCMP 119449	R	—	—	—	3.4	1.9	2.15	—	—	—
UCMP 66810	L	—	—	—	3.4	2.05	2.15	3.25	2.0	2.0
UCR 16685	R	—	—	—	3.5	2.1	—	—	—	—
UCMP 99165	R	—	—	—	3.9	2.1	2.1	—	—	—

Only measurements of *M. kutjampensis* relevant to the interpretation of the Kangaroo Well Local Fauna specimen or comparable to *M.* sp. cf. *kutjampensis* from the Ngama Local Fauna are provided.  
M, molar; L, length; AW, anterior width; PW, posterior width.



**Figure 18** Correlation diagrams. (a) Similarity clustering by all attributes shown in Table 8. (b) Similarity clustering of Group 1 formations using only terrestrial vertebrates. (c) Correlation by relative stage-of-evolution biochronology.

**Table 8** Correlation matrix of mid and late Tertiary formations with an ecological classification of faunal elements.

	Sediment type	Aquatic plant	Aquatic invertebrates				Aquatic vertebrate	Amphibious vertebrates		
				<i>Syrioplanorbis</i>	<i>Glyptophysa</i>	<i>Potamopyrgus</i>				
			Limestone	Charophyta	Ostracoda	<i>hardmani</i>		<i>rodingae</i>	<i>sp.</i>	Teleostei
Ulta Ls	1	1	1	1	1	1	1	1	1	1
Carl Creek Ls	1	1	1	–	1	–	1	1	1	–
Etadunna Fm	1	1	1	1	–	–	1	1	1	1
Namba Fm	1	1	1	–	–	–	1	1	1	1
Wipajiri Fm	–	–	–	–	–	–	1	1	1	–
Camfield beds	1	1	1	–	1	–	1	1	1	–
Waite Fm	–	–	–	–	1	–	–	1	1	–
Arltunga beds	1	1	1	–	–	–	–	–	–	–
Austral Downs Ls	1	1	1	–	–	–	–	–	–	–
Brunette Ls	1	–	1	1	–	–	–	–	–	–
Golliger beds	1	–	–	–	1	–	–	–	–	–
Horse Creek Ls	1	1	1	1	–	1	–	–	–	–
Unnamed A	1	–	–	–	–	1	–	–	–	–
Unnamed B	1	1	1	1	–	–	–	–	–	–
Unnamed D	1	1	1	1	–	–	–	–	–	–
Unnamed E	1	–	–	–	–	–	–	–	–	–
White Mountain Fm	1	–	1	1	1	–	–	–	–	–

Characters are scored as present (1) or absent (–). The listed formations lie within or between the Karumba and Lake Eyre Basins, and the area west of Bullock Creek (= Camfield beds), as shown in Figure 1a: see also Lloyd (1968a figure 1) and Megirian (1992 figure 1a).

Ls, Limestone; Fm, Formation.

into the valley separating the hypoconid from the entoconid. The postprotocristid is a relatively short, anterolingually concave crest that recurves sharply at its lingual extremity to enclose the median valley separating the protoconid from the hypoconid, and thence onto cristid obliqua. This structure may represent a mesostyle. This structure and the crevice lingual to it are therefore interposed between cristid obliqua and the buccal slope of the postmetacristid. A short, straight, lingual cingulum (damaged in P2689-1) encloses the median valley buccally.

**Comparative remarks** P2689-1 represents a large Miocene pseudocheirid species, comparable to *Marlu kutjampensis* (Table 7) from the Kutjamp Local Fauna and *Pildra magnus* (Table 6). The presence of an anterobuccal cingulum, lack of a distinct paraconid, presence of a crevice between the postmetacrista and cristid obliqua, and absence of an entostylid diagnose P2689-1 as a species of *Marlu* rather than a species of *Pildra*.

P2689-1 is comparable in length to the largest recorded *M. kutjampensis* M<sub>2</sub>, UCMP 99165, but is proportionally broader (Table 7). In proportions it resembles UCMP 66180, an M<sub>3</sub>, but is notably larger. The available *M. kutjampensis* M<sub>2</sub>s and M<sub>3</sub>s, however, show considerable variation in size and proportions, but have similar crown morphology. In the holotype, SAM P19961, the only individual in which the two teeth can be compared, M<sub>3</sub> is proportionally narrower than M<sub>2</sub>. *Marlu* sp. cf. *M. kutjampensis* from the Ngama Local Fauna (Pledge 1987c) is unfortunately represented only by an M<sub>3</sub>, precluding any direct comparison with the Kangaroo Well specimen. *Marlu praecursor* from the Wadikali Local Fauna (Woodburne *et al.* 1987) is significantly smaller than any other *Marlu*, but further comparison with P2689-1 is not possible due to a lack of overlap in the representative specimens. A specific determination for the Kangaroo Well

*Marlu* is therefore not possible using only P2689-1. P2689-1 is obviously close to *M. kutjampensis* though, and accordingly we assign it to *M. sp. cf. M. kutjampensis*. In doing so we are not implying that P2689-1 is necessarily any closer to the Ngama Local Fauna *M. sp. cf. M. kutjampensis* described by Pledge (1987c) than it is to *M. kutjampensis* s.s. Clarification of the relationships between these various forms will become resolvable only on recovery of more specimens.

## CORRELATION

### Methodology

The question arises as to whether correlated attributes are indicative of spatial (environmental) factors, or whether they are of chronological significance. No geochronometric techniques have been applied to the Ulta Limestone, and the Australian vertebrate fossil record is so sparse and discontinuous that only a few mammal biochrons have been defined in biostratigraphic terms, and no land-mammal Stages or Ages have yet been formalised. In such circumstances, hypotheses of phyletic succession within natural groups (clades) may be applicable to establishing the relative geological ages of vertebrate assemblages (Local Faunas), and hence the bodies of rock from which they were collected. The method, known as mammal stage-of-evolution biochronology, is based on the premise that identical morphospecies may indicate the same or very similar age, while a species at a more primitive stage of evolution than a very closely related form from a different area is possibly geologically older (Woodburne *et al.* 1985; Rich 1991; Megirian 1994; Murray *et al.* 2000a). Compared to other vertebrates, morphological evolution in mammals appears, in general, to have been rapid. In practice, as many lineages as possible are assessed from an assem-

[illegible]

blage to establish whether or not a consistent pattern is expressed.

The stratigraphic positions from which samples were collected in the Ula Limestone are shown in Figure 9. Palaeontological data are too sparse to quantify a time-span between the top and bottom of the stratigraphic sections examined, or between the three sections sampled. All taxa are regarded as being members of single Local Fauna until such time as it can be demonstrated otherwise (Megirian 1994).

Table 8 is a compilation of mid-Tertiary formations that share one or more attributes with the Ulta Limestone. Similarity analyses of presence/absence data were carried out to determine how the formations correlated, and the attributes responsible for similarity within groups (or taken from the alternative perspective, dissimilarity between groups) at different levels assessed for palaeo-environmental or temporal meaning. The objective of this section is to arrive at the likely geological age of the Ulta Limestone: attributes identified in the course of the analysis as having primarily palaeoenvironmental significance are examined in more detail in the following section. The age of the Kangaroo Well Local Fauna relative to comparable vertebrate assemblages is then determined using stage-of-evolution methods, as outlined in Woodburne *et al.* (1985), Rich (1991), Megirian (1994) and Murray *et al.* (2000a).

Table 8 is based on Table 1 but with a few omissions and a few additions. Taxa represented in the Ulta Limestone are scored as present or absent at whatever taxonomic level permits correlation. Added to attributes drawn from Table 1 are Charophyta, and each formation is scored as either being composed of carbonate facies, or including fossiliferous carbonate facies or members (+ carbonate present), or siliciclastic (= carbonate absent). Omitted from consideration are the frogs *Australobatrachus* sp., *Limnodynastes* sp. and *Litoria* sp., the potoroid cf. *Wakiewakie lawsoni*, birds and saurians. These taxa are not informative at these levels of classification. The pupillid snail cf. *Cylindrovertilla* sp. represents a unique

occurrence and is thus not applicable to correlation. The matrix and subsets of it were analysed in PRIMER version 5 (Clarke & Gorley 2001) using Bray–Curtis similarity on presence/absence data with results presented as standardised dendrograms resulting from hierarchical cluster analysis (Figure 18a, b). Quoted similarity and dissimilarity percentages are rounded to the nearest whole number.

## Results

## CORRELATION BY ALL ATTRIBUTES

The data (Table 8) show that the main shared attributes of the sampled formations are carbonate facies, aquatic invertebrates and aquatic Charophyta. Lloyd (1968a, b) postulated that formations with these attributes were part of a widespread depositional event, citing the similarities in their fossil content and their reported stratigraphic positions in relation to regionally extensive, ancient land-surfaces representing major bounding discontinuities. The Early Miocene to Holocene foraminifer, *Ammonia beccarii*, from the White Mountain Formation, Brunette Limestone and Austral Downs Limestone was the only invertebrate taxon that provided Lloyd (1968a, b) with any direct indication of the possible age range of the correlated formations. The continental pattern of cyclic deposition since the retreat of the Late Cretaceous seas is now more firmly established, as already outlined above, although details remain to be resolved.

The notable absence of aquatic invertebrates and Charophyta in the Wipajiri Formation, and recorded presence of only one aquatic gastropod species in the Waite Formation are attributed to preservational factors. Neither of these siliciclastic formations are noted for their preservation of microfossils, but both have produced larger taxa dependent on aquatic habitat, e.g. amphibious vertebrates in both, and teleost fish in the Wipajiri Formation (Table 8). The Wipajiri Formation also contains bivalve molluscs (Callen *et al.* 1995 p.194). The Etadunna and

Namba Formations also contain abundant, undetermined gastropods (Callen *et al.* 1995 p. 194), and it is likely that among them are some of the widespread taxa listed in Table 8. All formations therefore contain evidence for aquatic habitats, some of the attributes of which will be examined in the next section. Widespread, broadly similar aquatic and amphibious assemblages and limestone facies are manifestations of the Miocene depositional event as characterised above.

The correlated formations fall into two distinct groups (Groups 1 and 2 in Figure 18a) at approximately the 20% similarity level, with the dissimilarity between the two groups attributable largely to the presence of vertebrates and terrestrial gastropods in Group 1 formations. The Ulta Limestone is most similar (~90%) to the Carl Creek Limestone, with most of the similarity attributable to terrestrial vertebrates, as demonstrated below. The terrestrial gastropods are of palaeoclimatic significance, while some vertebrates are of biochronological significance.

#### CORRELATION BY TERRESTRIAL VERTEBRATES

Analysis of Group 1 formations by terrestrial vertebrates only aligns the Ulta Limestone very strongly with the Carl Creek limestone (100% similarity), followed by the Etadunna + Namba Formations (~78% similarity), Wipajiri Formation (~66%), and the Camfield beds (~37%) (Figure 18b). The Waite Formation contains two vertebrate assemblages in stratigraphic superposition: the Ongeva Local Fauna unconformably above the Alcoota Local Fauna; and, although these Local Faunas have direct phyletic links to those of the other formations (Woodburne *et al.* 1985; Murray & Megirian 1992), they share no terrestrial vertebrate taxa at the taxonomic levels being analysed. The Ongeva Local Fauna is correlated to the Beaumaris Local Fauna [Cheltenhamian Stage (marine) of the Black Rock Sandstone, i.e. Late Miocene – Early Pliocene] by the zygomaturines *Kolopsis yperus* (Ongeva Local Fauna) and *Zygomaturus gilli* (Beaumaris Local Fauna), which if not actually synonymous, are at zygomaturine stage-of-evolution equivalence (Murray *et al.* 1993; Megirian *et al.* 1996). This correlation provides an important calibration age for the Australian land-mammal biochronological scheme. Because the faunas of the Etadunna, Namba and Wipajiri Formations, and the Carl Creek Limestone, Camfield beds and Ulta Limestone are much more similar to each other than any one of their faunas is to those of the Waite Formation, it follows that there is probably a significant temporal gap separating them (Figure 2).

#### STAGE-OF-EVOLUTION ANALYSIS

Stage-of-evolution biochronological significance has previously been argued for species of *Balbaroo* (Flannery *et al.* 1983), *Ektopodon* (Woodburne *et al.* 1985, 1993; Woodburne & Clemens 1986a, d), *Pildra* and *Marlu* (Woodburne *et al.* 1987; Pledge 1987c), and *Neohelos* (Stirton *et al.* 1967a; Woodburne *et al.* 1985; Murray *et al.* 2000a). For all these genera except *Balbaroo*, there is some chronostratigraphic evidence from the Lake Eyre Basin, particularly from the

Etadunna Formation and superposed Wipajiri Formation (Figure 18c), for temporal succession in these lineages.

Woodburne *et al.* (1993) defined five informal marsupial faunal zones (A–E) in the Etadunna Formation, as shown in Figure 18c. The vertebrate assemblages from these zones were previously assigned to Local Faunas in accordance with the conventions of land-mammal biochronology. The Namba Formation (Callabonna Sub-basin) and Etadunna Formation (Tirari Sub-basin) of the Lake Eyre Basin are lithologically very similar and correlated by many species, but stratigraphic continuity between them has not yet been demonstrated. Although no zonal scheme has been erected for the Namba Formation, the stratigraphic succession of its vertebrate assemblages is at least partly resolved, and corroborates the zonal scheme erected for the Etadunna Formation (Woodburne *et al.* 1993).

Archer *et al.* (1989) claimed that the ‘Systems’ framework they introduced to express the biochronology of the Carl Creek Limestone was partly based on stratigraphy. However, no empirical evidence to support the claim has been forthcoming. Interpretations of the faunal succession in the Carl Creek Limestone are actually based on correlations to South Australian and Northern Territory Local Faunas rather than on chronostratigraphic evidence from Riversleigh itself (Megirian 1994, 1997). Fossils from the Carl Creek Limestone have been described in the literature as coming from ‘higher’ or ‘lower’ positions than other fossils, but whether these relative positions are actually stratigraphic or merely topographic is ambiguous (Creaser 1997). The Etadunna/Wipajiri/Tirari Formations succession therefore remains the primary reference standard for the continental marsupial biochronological scheme (Woodburne *et al.* 1993).

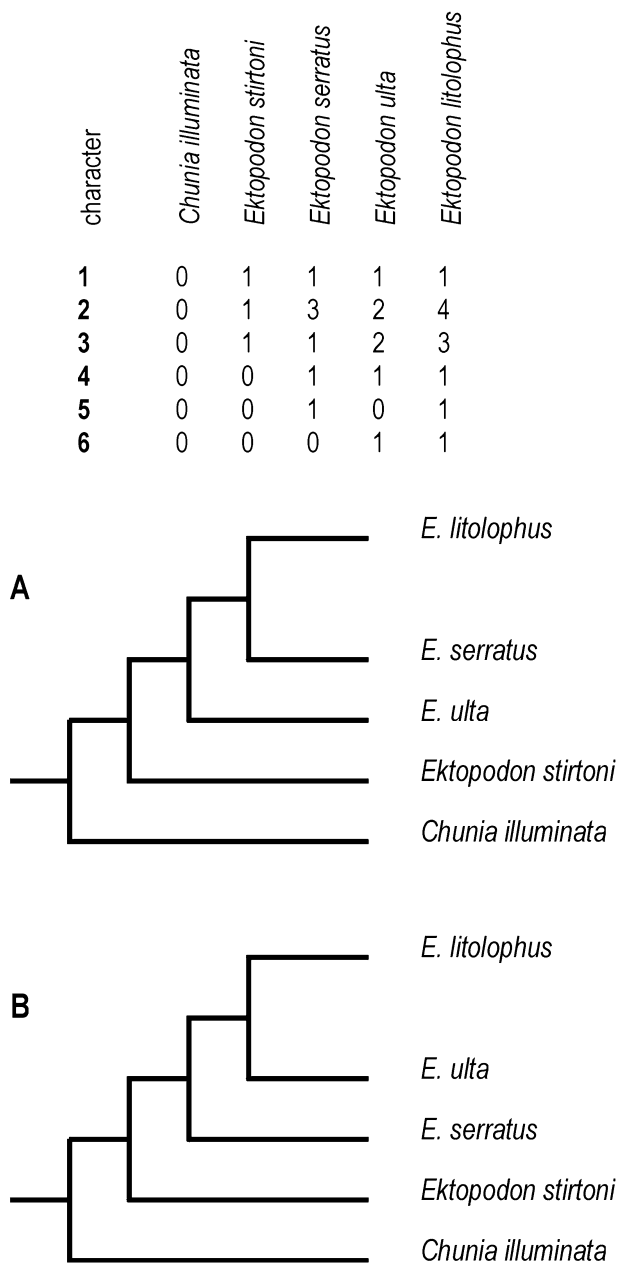
The omitted taxa are briefly commented upon before assessing the biochronological implications of the Kangaroo Well Local Fauna representatives of the taxa singled out above.

Without a specific determination for the Ulta Limestone *Nambaroo* sp., the generic occurrence of *Nambaroo* in every formation except the Waite Formation simply further emphasises the uniqueness of the Waite Formation.

Phyletic relationships within the ‘marsupial wolf’ family, Thylacinidae (represented in Table 8 by *Nimbacinus*) are currently too poorly understood to have stage-of-evolution utility, and the Tertiary biochronology of the group can be expressed at present only in terms of, for example, associated zygomaturine diprotodontids (Murray & Megirian 2000). *Nimbacinus dicksoni* is associated with both *Neohelos tirarensis* and *Neohelos stirtoni* in the Carl Creek Limestone, while *Nimbacinus richi* occurs in association with *Neohelos stirtoni* in the Camfield beds (Murray & Megirian 2000 table 5). Murray and Megirian (2000) interpreted this as an indication that the two species of *Nimbacinus* might represent collateral lineages.

The ?Wynyardiidae, Pilkipildridae and Miralinidae are also presently useful mainly by association with better resolved lineages. Representatives of all three families occur in the Etadunna Formation, but not in the overlying Wipajiri Formation. However, they may have persisted beyond deposition of the Etadunna Formation. In the Carl Creek Limestone and Ulta Limestone, representatives of all





**Figure 19** Phylogenetic analysis of relationships within *Ektopodon* using  $M_1$ , with *Chunia illuminata* as the outgroup. Characters are expressed as plesiomorphic (0), derived (1), or ordered derived states (1, 2, 3 ...), and analysed using HENNIG86 (Farris 1988). Characters analysed are basically a subset of those used by Pledge *et al.* (1999) to analyse the Ektopodontidae, here redefined and expressed where appropriate as ordered derived states to suit the objectives of this analysis. Character definitions: 1, alignment of crests on cusps: radial (0), anterior and posterior (1); 2, number of protoloph cusps: five or fewer (0), six (1), eight (2), nine (3), ten (4); 3, number of metaloph cusps: seven (0), eight (1), nine (2), ten (3); 4, length to width ratio: approximately  $\geq 1.0$  (0), approximately  $= 0.9$  (1); 5, number of parastyloph cusps: three or fewer (0), four (1); 6, comparative occlusal outline: rounded (0), more angular (1). Two equally short trees result (A and B): consistency index = 0.84, retention index = 0.61. Hypothesis A is regarded as less likely than hypothesis B for reasons outlined in the text. A phyletic/biochronological hypothesis of relationships within *Ektopodon* consistent with phylogenetic hypothesis B is presented as Figure 14c.

three families occur in association with *Neohelos tirarensis* (Table 8). At Gag Site in the Carl Creek Limestone, the pilkipildrid *Djilgaringa gillespiei* occurs in association with *N. stirtoni*, but no pilkipildrids are known from the Camfield beds, the type locality of *N. stirtoni*. The phylogenetic relationships of the Kangaroo Well ?wynyardiid *Ayekaye jaredi* to other ?wynyardiids of the genera *Muramura* and *Namilamadeta* and to *Wynyardia bassiana* are unresolved.

Madtsoid snakes of the genus *Yurlungurr* have no biochronological value. Only one species (*Y. camfieldensis* Scanlon 1992; from the Camfield beds) has been described, but additional species occur in the Carl Creek Limestone (Scanlon 1997). The affinities of the Ulta Limestone form, beyond having a general similarity to *Y. camfieldensis*, are not known.

**Neohelos** The Zygomaturinae is one of the best-resolved lineages in Australian marsupial biochronology, spanning the Neogene and Quaternary, and is central to the Australian land-mammal biochronological scheme as it currently stands (Stirton *et al.* 1967b; Woodburne *et al.* 1985; Megirian 1994; Murray *et al.* 2000a). *Neohelos* encompasses the more primitive species, and of particular relevance here is an apparently orthogenetic phyletic succession progressing from *Neohelos tirarensis* at the base, to *Neohelos stirtoni* (= *Neohelos* sp. B of Murray *et al.* 2000a), to *Neohelos* sp. C, after which this lineage underwent a phylogenetic radiation, the members of which are variously assigned to *Kolopsis*, *Zygomaturus*, *Hulitherium* and *Maokopia* (Murray *et al.* 2000a figure 78).

Although a *Neohelos* sp. is present in zones D and E of the Etadunna Formation (Woodburne *et al.* 1993), the available material is not adequate to determine whether it conforms to *N. tirarensis* from its type locality in the Wipajiri Formation, or whether it actually represents a distinctly more primitive structural stage. *Neohelos tirarensis* occurs in the Carl Creek Limestone in assemblages that may be slightly older than the Kutjamarpu Local Fauna of the Wipajiri Formation, as examined in more detail as part of the discussion below.

**Balbaroo** As reviewed in the Introduction, the Kangaroo Well Local Fauna *Balbaroo* sp. was interpreted by Flannery *et al.* (1983) as representing a more primitive stage of evolution than *Balbaroo camfieldensis* from the Camfield beds and *B. gregoriensis* from the Carl Creek Limestone, on the basis of smaller size. *Balbaroo fangaroo* Cook (2000), also from the Carl Creek Limestone, is the only additional *Balbaroo* species described since then, although there are undescribed species from the Carl Creek Limestone (Cook 1997) and from the Wipajiri Formation (Woodburne *et al.* 1993).

Cook (2000) considered *B. fangaroo* to be structurally more primitive than both *B. gregoriensis* and *B. camfieldensis* on the basis of  $M_1$  morphology, but he made no comparisons between *B. fangaroo* and the Kangaroo Well Local Fauna *Balbaroo* sp. The *B. fangaroo*  $M_1$  (AR1017; length 6.7 mm, anterior width 4.9 mm, posterior width 4.4 mm: Cook 2000 table 1) is slightly smaller than that of *Balbaroo* sp. [CPC 7349; length 7.9 mm, anterior width 6.9 mm, posterior width 4.7 mm: Flannery *et al.* 1983 table 1

(mislabelled as a 'M<sub>3</sub>'). Although a number of marsupial lineages show general patterns of increasing body size over longer periods of geological time, size is not a particularly reliable indicator of relative stage of evolution over shorter intervals (e.g. *Pildra* and *Marlu* below), and certainly not when sample sizes are too small to provide any indication of size variability within populations, and thus to establish whether small size differences are of any temporal significance. Whether the proportional differences in the comparable M<sub>4</sub>s are of any significance is also unclear.

Flannery *et al.* (1983) made the first attempt at applying stage-of-evolution methods to interpreting the possible age of the Kangaroo Well Local Fauna. However, evolutionary relationships within *Balbaroo* are still poorly understood, and it remains a taxon for which there are no chronostratigraphic data against which to compare the rather tenuous inferences of evolutionary progression that have been made. *Balbaroo* sp. is therefore not particularly useful in determining the possible age of the Ulta Limestone.

However, *Balbaroo* sp. is associated with *Neohelos tirarensis* in the Ulta Limestone. In the Carl Creek Limestone, *B. gregoriensis* co-occurs with *N. tirarensis* in Camel Sputum, Inabeyance, Nevilles Garden, and Waynes Wok sites (Cook 1997; Murray *et al.* 2000a). Few details are available on the fauna of the two sites (Outasite and Margans Immense Might) that have produced *B. fangaroo* (Cook 2000). Outasite is in the tufa facies association at Godthelps Hill, in the same member as the Camel Sputum and Inabeyance sites (Megirian 1992 figure 7; Megirian 1997 appendix 5, figure 21; Murray *et al.* 2000a figure 77), so there is some association with *N. tirarensis* there too.

**Ektopodon** Biochronological utility was originally ascribed to *Ektopodon* by Woodburne *et al.* (1985), Woodburne and Clemens (1986d) and Pledge (1986). *Ektopodon serratus* (Wipajiri Formation) is stratigraphically higher than *E. stirtoni* (zone D of the Etadunna Formation), leading Pledge (1986) to hypothesise that in *Ektopodon* the evolutionary progression (here only characters of M<sup>1</sup> considered) was an increase in the number of cusps and an increase in the relative width of the tooth. Woodburne and Clemens (1986a) inferred the same progression by deriving an *Ektopodon* dentition from an ancestral phalangeroid state. More recently, Pledge *et al.* (1999) applied these and additional character-state polarities to a phylogenetic analysis of an expanded Ektopodontidae, of which the *Ektopodon* clade is of direct relevance here.

A matrix of shared, derived characters, with *Chunia illuminata* as the outgroup (Figure 19), was analysed with HENNIG86 (Farris 1988), and produced two equally short dendrograms (Figure 19). Phylogenetic hypothesis B is the preferred hypothesis because it encapsulates a possible succession within *Ektopodon* that does not require any hypothetical structural intermediates in order to express possible phyletic ties between the known species. *Ektopodon stirtoni* and *E. sp. cf. E. stirtoni* are structurally primitive forms expressing character states that could give rise to all other *Ektopodon* species. Neither *Ektopodon litolophus* nor *E. serratus* could have given rise to the other except by invoking structural reversals, and their stratigraphic coexistence also points to a common ancestry at some earlier time. *Ektopodon litolophus* would have had

to lose one protoloph and two metaloph cusps in order to achieve a structural stage that could have given rise to *E. serratus*, whereas *E. serratus* would have had to lose a parastyloph cusp in order to achieve a structural stage that could have given rise to *E. litolophus*. *Ektopodon ulta*, on the other hand, expresses states that could give rise directly to *E. litolophus*, but not to *E. serratus* because it would also have had to lose a parastyloph cusp. The possibility that *E. litolophus* is directly descended from *E. ulta* is further supported by their synapomorphous expression of the relatively more angular occlusal outline of their M's (character 6). Figure 15c shows the most parsimonious hypothesis of phyletic relationships in *Ektopodon*, which is consistent with the phylogenetic hypothesis in which *E. serratus* is the plesiomorphic sister taxon to *E. ulta* + *E. litolophus* (i.e. B in Figure 19). The biochronological implication is therefore that *E. ulta* represents a biochron intermediate between the *E. stirtoni* biochron (Etadunna Formation, zone D) and the *E. serratus* + *E. litolophus* biochron (Wipajiri Formation, Kutjamarpu Local Fauna).

An *Ektopodon* sp. cf. *Ektopodon serratus* is described by Pledge *et al.* (1999) from the Waynes Wok site of the Carl Creek Limestone, from which *Neohelos tirarensis* has also been recovered (Murray *et al.* 2000a).

**Pildra** One small species of *Pildra*, *P. secundus*, occurs in zone B of the Etadunna Formation, and a large species, *P. magnus*, occurs in zone D. *Pildra tertius* is a small species from the overlying Wipajiri Formation. *Pildra secundus* is also known from the Namba Formation, where it has been found stratigraphically above *P. antiquus*. As the names of the three small species imply, the stratigraphic succession of the small species is from *P. antiquus* to *P. secundus* to *P. tertius*, and these species also exhibit progressively more advanced structural stages in reduction of crenulation in basinal areas of tooth crowns, stronger expression of paraconules and neometaconules, and small increases in body size (Woodburne *et al.* 1987). *Pildra magnus* must lie on a collateral lineage, because it occurs stratigraphically below *P. tertius*: i.e. *P. magnus* and *P. tertius* at least must share a common ancestor. Neither *P. antiquus* nor *P. secundus* express any derived features that preclude them from the ancestry of either *P. tertius* or *P. magnus*.

Kangaroo Well Local Fauna *Pildra* sp. cf. *P. magnus* is morphologically very close to *P. magnus*, and if the *P. magnus* lineage expresses the same general pattern of evolution as observed in the small members of the genus, then *Pildra* sp. cf. *P. magnus* may be very slightly derived relative to *P. magnus* (see Comparative remarks for *Pildra* sp. cf. *P. magnus* above) and, on that basis, the Ulta Limestone may be of slightly younger age than zone D of the Etadunna Formation.

In the Carl Creek Limestone, a *Pildra* sp. (Archer *et al.* 1991 p. 197) occurs at Gag Site in association with *Neohelos stirtoni* (= *Neohelos* sp. B: Murray *et al.* 2000a), but its relative stage of evolution compared to the Lake Eyre basin forms is undetermined.

**Marlu** *Marlu* is less diverse than *Pildra*, with only two named species, *Marlu praecursor* from the Namba

Formation and *M. kutjampensis* from the Wipajiri Formation. However, a *Marlu* sp. cf. *M. kutjampensis* is also present in Zone D of the Etadunna Formation. Although *M. praecursor* is small, and interpreted as being structurally more primitive than *M. kutjampensis*, Woodburne *et al.* (1987) referred to data suggesting that the Namba Formation beds that produced *M. praecursor* may be younger than zone D of the Etadunna Formation. The implications are that *M. praecursor* is not ancestral to *M. kutjampensis*, but represents a structurally conservative collateral lineage.

The lack of comparable material from the formations producing *M. kutjampensis* s.s. and the two *M.* sp. cf. *M. kutjampensis* forms precludes a phylogenetic analysis of their relationships at this time. *Marlu* sp. cf. *M. kutjampensis* in the Kangaroo Well Local Fauna suggests only that the Ulta Limestone may be approximately as old as Zone D of the Etadunna Formation, or as young as the Wipajiri Formation.

In the Carl Creek Limestone, a *Marlu* sp. occurs at Gag Site (Archer *et al.* 1991 p. 197) in association with *Neohelos stirtoni* (= *Neohelos* sp. B: Murray *et al.* 2000a), but its

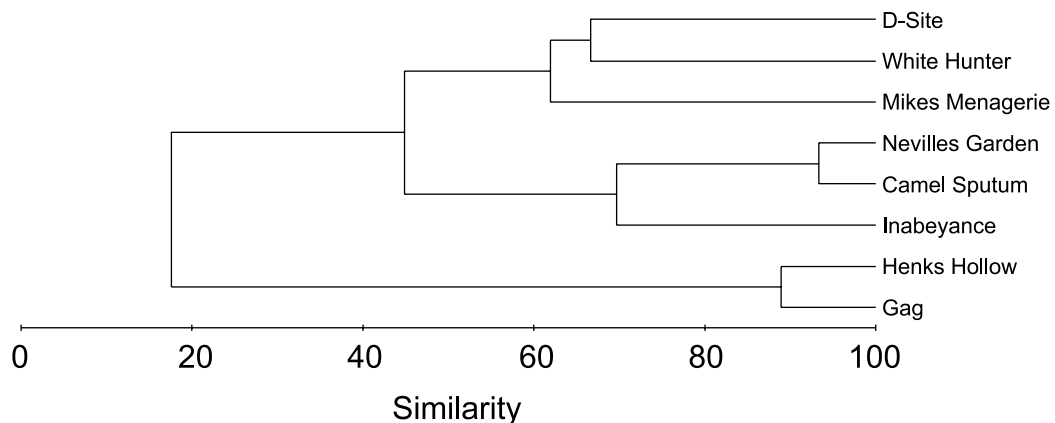
relative stage of evolution compared to the Lake Eyre basin forms is undetermined.

## Discussion

Precision in inter-regional biocorrelation is presently hampered by poor faunal overlap across formations, especially at the species level, with the only data on the biostratigraphic succession of taxa under scrutiny coming from the Lake Eyre Basin. *Neohelos tirarensis* is the only marsupial species present in the Ulta Limestone that is shared with any other formation, and serves to correlate the Ulta Limestone with the Wipajiri Formation and parts of the Carl Creek Limestone. The only other shared species is the frog, *Australobatrachus ilius*, that otherwise occurs in zones B, C and D of the Etadunna Formation, and in the Yanda Local Fauna of the Namba Formation (Tyler 1976, 1982, 1986).

Circumstantial evidence from the Carl Creek Limestone suggests that the temporal range of *Neohelos tirarensis* may extend back into Etadunna Formation time. White Hunter site contains the ilariid *Kuterintja ngama*

	<i>Burramys brutyi</i>	<i>Bulungamaya delicata</i>	<i>Neohelos tirarensis</i>	<i>Wabularoo naughtoni</i>	<i>Balbaroo gregoriensis</i>	<i>Nambaroo sp5</i>	<i>Nowidge matrix</i>	<i>Nimiokoala graystanesi</i>	<i>Bematherium angulum</i>	<i>Neohelos stirtoni</i>	<i>Litokoala kanunkaensis</i>	<i>Ganawamaya sp2</i>	Archer <i>et al.</i> (1989) 'system' classification	Cook (1997: table 1) 'system' classification	Topographic position (m) (Creaser 1997)
Gag	1	1								1	1	1	C	C	188
Henks Hollow	1									1	1	1	C	C	198
Nevilles Garden	1	1	1	1	1	1		1					probable system B equivalent'	?B	175
Inabeyance	1		1		1			1					B	B	ns
Camel Sputum	1	1	1	1	1	1	1	1					B	B	ns
Mikes Menagerie			1	1									B	B	ns
D-Site		1	1	1				1					A	A	175
White Hunter	1		1	1			1	1					D-Site equivalent'	?A/B	162



**Figure 20** Intraformational correlation of the Carl Creek Limestone. (Upper) Site-taxon matrix of Murray and Megirian (2000 table 5B), with 'systems' classifications of Archer *et al.* (1989) and Cook (1997) and relative topographic position from Creaser (1997). (Lower), similarity cluster.

Pledge 1987b (Myers & Archer 1997), otherwise known only from its type locality in zone D of the Etadunna Formation. While no *Neohelos* species has been determined from the White Hunter site itself, the assemblage correlates faunally to other Riversleigh sites containing *N. tirarensis* (Figure 20: after Murray & Megirian 2000 table 5B).

The Kangaroo Well Local Fauna representatives of *Neohelos*, *Marlu*, *Pildra* and *Ektopodon* constrain the relative age of this assemblage more satisfactorily than has previously been possible (Figure 18c). The *Marlu* sp. cf. *M. kutjamparpensis* and *Neohelos tirarensis* bracket the age to within Ngama Local Fauna to Kutjamparu Local Fauna time, but *Ektopodon ulta* provides the best resolution. *Ektopodon ulta* is interpreted above as being at a more advanced stage of evolution and therefore younger than *E. stirtoni*, but more primitive and therefore older than *E. litolophus*, suggesting that the Kangaroo Well Local Fauna represents a biochron younger than the Ngama Local Fauna (zone D of the Etadunna Formation), but older than the Kutjamparu Local Fauna (Wipajiri Formation). The *Pildra* sp. cf. *P. magnus* may also represent a slightly more advanced stage of evolution than *Pildra magnus* s.s. from the Ngama Local Fauna. The evidence from all four lineages is concordant.

The most recent calibrations of the age of the Etadunna and Wipajiri Formations are those of Woodburne *et al.* (1993) using palaeomagnetic data. These data provided an age of 25.7–24.2 Ma for the Etadunna Formation, and a suggested age of ca 24 Ma for the Wipajiri Formation. The Etadunna ages are consistent with several other datasets, but at variance with some palynological data that suggest somewhat younger ages (Woodburne *et al.* 1993; Callen *et al.* 1995; references therein), but the weight of evidence favours an age somewhere close to the Oligocene–Miocene boundary, as argued by Woodburne *et al.* (1993), McGowran and Li (1994) and Alley *et al.* (1999). Accordingly we regard the Ulta Limestone to be at least nominally of Late Oligocene age.

Although currently having no stage-of-evolution utility of their own, the presence of a ?wynyardiid (*Ayekaye jaredi*) and a *Nimbacinus* sp. cf. *N. dicksoni* in the Kangaroo Well Local Fauna, also point towards this interpretation. Although our interpretation of the age of the Kangaroo Well Local Fauna relative to other Local Faunas is consistent, or largely so, with opinions expressed previously by Stirton *et al.* (1968), Godthelp *et al.* (1989) and Flannery *et al.* (1983), the bases for them (*Balbaroo* sp. and cf. *Wakiewakie lawsoni*) are tenuous. Flannery *et al.* (1983) suggested that the Kangaroo Well Local Fauna might be older than the Riversleigh Local Fauna, which is regarded by Archer *et al.* (1989, 1991) to be a basal assemblage of the Carl Creek Limestone. Overall, the Kangaroo Well Local Fauna is taxonomically closer to the fauna from the Carl Creek Limestone than it is to any of the Lake Eyre Basin assemblages (Figure 18a, b). Mention was made above of the presence of *Kuterintja ngama* in the Carl Creek Limestone, a taxon otherwise known from zone D of the Etadunna Formation, which suggests that some Carl Creek Limestone assemblages could be marginally older than the Kangaroo Well Local Fauna.

Apart from *K. ngama* and *N. tirarensis*, the only other Carl Creek Limestone species shared with the Lake Eyre Basin are *Wakiewakie lawsoni* (Kutjamparu Local Fauna, Wipajiri Formation) and *Litokoala kanunkaensis* Springer 1987 (zones D and E of the Etadunna Formation: Woodburne *et al.* 1993).

What is curious is that in the Carl Creek Limestone, *Litokoala kanunkaensis* occurs in so-called 'System C' sites (Black & Archer 1997), two of which (Henks Hollow and Gag) have produced *Neohelos stirtoni* (= *Neohelos* sp. B: Murray *et al.* 2000a) (Figure 19). The Riversleigh 'Systems' are conceptualised by Archer *et al.* (1989, 1991) as representing a chronostratigraphic succession progressing from A to C. Although in the Lake Eyre Basin *L. kanunkaensis* occurs stratigraphically below its more derived congener, *L. kutjamparpensis* Stirton, Tedford & Woodburne 1967 (Kutjamparu Local Fauna of the Wipajiri Formation), at Riversleigh the more primitive form occurs in the *Neohelos stirtoni* biochron (=Bullock Creek Local Fauna, Camfield beds) that is generally accepted as being distinctly younger than the Kutjamparu Local Fauna (Woodburne *et al.* 1985; Archer *et al.* 1989, 1991; Murray & Megirian 1990; Murray 1990; Rich 1991; Murray *et al.* 2000a). This apparently anomalous association drew neither comment nor discussion from Black and Archer (1997), who simply reiterated the Archer *et al.* (1989, 1991) System C classification for sites containing *L. kanunkaensis*, and System C remained '... the same age or slightly younger than, the Kutjamparu Local Fauna' (Black & Archer 1997 p. 227).

Figure 20, based on the sample used by Murray and Megirian (2000) to correlate Riversleigh sites containing thylacinids, is representative of a general pattern found by more extensive analyses (i.e. all useable published site and taxon data: D. Megirian unpubl. data), in that faunal correlation of Riversleigh sites does not discriminate 'System A' sites from 'System B' sites. In contrast, System C sites cluster away from System A + System B sites, but part of the similarity within the System C cluster is due to an association, particularly at the Henks Hollow and Gag sites, of ostensibly younger (e.g. *N. stirtoni*) with ostensibly older taxa (e.g. *L. kanunkaensis*). The presence of a *Pildra* sp. and a *Marlu* sp. at the Gag site mentioned above may be a further example of this phenomenon, because these pseudocheirid genera are found in the Lake Eyre Basin in the *N. tirarensis* and older biochrons.

Such apparently anomalous associations of taxa at some Riversleigh sites merit investigation, because either the temporal range of species regarded as index taxa is greater than previously thought, or else some of the Carl Creek Limestone site assemblages are diachronous, possibly resulting from sampling across unconformities. As Figures 6g and 8a show, an unconformity in a palaeo-channel carbonate formation could be very easily overlooked when quarrying for fossils, and similar examples occur in the Carl Creek Limestone (Megirian 1997). At some Riversleigh sites, fossil material has been extracted from colluvial boulders that may not necessarily have come from the same stratigraphic horizon (e.g. D-Site: Megirian 1997; Murray *et al.* 2000a).

## PALAEOENVIRONMENTAL RECONSTRUCTION

Certain aspects of the Ulta Limestone depositional environment have already been established above, or else alluded to in anticipation of further examination. Briefly, the formation was deposited in a structurally controlled palaeochannel flanking the central Australian massif. The detrital facies have fluvial characteristics and are of extraclastic origin, being composed largely of caliche fabrics. The coarse textures and compositional immaturity imply high sediment yields in the catchment, which points to incomplete vegetation cover on a relatively stable land-surface conducive to the formation of caliche. Phytohermal fabrics are absent in the sediments that yield the Kangaroo Well Local Fauna, suggesting that the assemblage did not accumulate in permanent water bodies. Clearly though there must have been permanent bodies of water in the catchment, because the Kangaroo Well Local Fauna contains a diversity of aquatic and amphibious organisms. The idea that the vertebrate remains were transported for some distance is supported by their fragmented condition, with some bone fragments being well rounded. The invertebrates are present as both fragmented or complete bioclasts, for example ostracods with valves still in articulation. Bioclasts are present as both constituents of extraclasts and as primary particles.

### Aquatic habitats

Four aquatic gastropods have been identified from the Ulta Limestone: *Potamopyrgus* sp., *Glyptophysa rodingae*, *Syrioplanorbis hardmani* and *Gyraulus chapmani* (Tables 1, 8). All extant Australian species of *Gyraulus*, *Glyptophysa* and *Plotiopsis* [as *Thiara* (*Plotiopsis*)] live in lentic (standing) and/or lotic (flowing) freshwater (Smith 1992). *Syrioplanorbis*, however, has no extant Australian representatives.

McMichael (1968) interpreted the mid-Tertiary species (including additional taxa not found in the Ulta Limestone and therefore not listed in Table 8) as indicative of '...virtually pure freshwater' (McMichael 1968 p. 154). However, in one or other of the Horse Creek Limestone, White Mountain Formation and Brunnette Limestone, *Potamopyrgus* sp., *G. rodingae* and *Syrioplanorbis hardmani* are associated with the foraminifer *Ammonia beccarii*, which can tolerate brackishwaters, leading Lloyd (1968b) to postulate a possible extensive Miocene transgression across northern Australia, further evidence for which is lacking (Paine 1992; Senior *et al.* 1995). *Ammonia beccarii* is listed by Anadon (1992) as an indicator taxon for 'thalassic' biotas of lakes in arid and semiarid areas. Thus, in the case of the Australian formations containing *A. beccarii*, the freshwater snails may have been washed into brackish lakes or pans. A similar situation may have occurred in the Lake Eyre Basin, where the foraminifer *Buliminoides* sp. cf. *B. chattonensis* (Finlay) has been recorded from the Etadunna Formation (Lindsay 1987). The monospecific fauna was not taken as indicative of a marine transgression by Lindsay (1987), but as possibly indicative of a marine influence of some kind, such as exoreic drainage from the Lake Eyre Basin from time to time (Alley *et al.* 1999).

The taxonomy of mid-Tertiary charophytes has not been determined. The division Charophyta are rooted plants generally found in fresh- or brackish-water bodies. The only truly halophilous extant species is *Lamprothamnium papulosum*, which can tolerate hypersalinities as high as 80‰ (Burne *et al.* 1981). The fragility of charophytes makes them unsuited to growth in high-energy aquatic environments. They require sandy or muddy substrates, and while generally restricted to shallow waters, may grow in depths of up to 12 m (Chapman & Chapman 1973).

Ostracods may be very useful palaeoenvironmental indicators (Carbonel *et al.* 1988; De Deckker 1988), but the Australian mid-Tertiary fauna is not well known. De Deckker (1976) described a *Trigonocypris* sp. from the Horse (not House) Creek Limestone (a correlative of the Ulta Limestone: Table 8; Figure 18a) and from the Old Cork beds (probably early Tertiary: Lloyd 1968a; Smart *et al.* 1980; p. 7) of central western Queensland. *Trigonocypris* sp. is based on the extant genotypic species *T. timmsi* De Deckker (1976), which was found in freshwater in the same general area as the fossils (De Deckker 1976). The Ulta Limestone forms, and those in other comparable formations are, however, undetermined. Examinations of thin-sections prepared by DM for the present study and also from various correlatives of the Ulta Limestone (including Carl Creek Limestone: Megirian 1997) suggest that there was little species diversity within and between these correlative formations. This may indicate broadly similar conditions across the region, in which blooms occurred when normally dry lakes and pans flooded (De Deckker 1988). Such environments may have been present lateral to active channels in the Ulta Limestone, and other palaeochannel deposits such as the Camfield beds and Carl Creek Limestone. Articulated ostracods and complete aquatic gastropods present as primary particles might therefore represent waning flood accumulations.

Teleost fish remains in the Ulta Limestone are rare, and consist of fragmentary skull elements and vertebral centra, most of which were recovered from the 1 mm screen, and are representative of small animals. They, together with the remains of the frogs and amphibious reptiles, were evidently transported from permanent water bodies upstream. Notably absent in the Kangaroo Well Local Fauna are remains of lungfish, which were widespread across the region during the Miocene (Kemp 1991, 1997a, b).

The amphibious vertebrates indicate that their ecological needs, especially in terms of feeding and reproduction, were met. The frogs and chelid turtles required freshwater habitat or access to such habitat, but until their affinities are better resolved, they can provide little in the way of additional detail. Some habitat requirements of crocodilians are outlined in the following section.

### Palaeoclimate

The two most important climatic variables are precipitation and temperature. In the Kangaroo Well Local Fauna are three taxa that have extant analogs that are especially good as proxies for temperature and rainfall. These are crocodilians and the terrestrial gastropods *Bothriembryon*



season. The shorter the active season, the slower the growth rate, the more vulnerable the individual is to predation, and more limited are the opportunities for successful reproduction.

The geographical distribution of the two extant crocodilians found in Australia, *Crocodylus porosus* and the endemic species *C. johnstoni*, is shown in Figure 21a. Areas experiencing coldest month mean temperatures  $<5.5^{\circ}\text{C}$  are today restricted to the Australian Alps (southeastern Australia) and the highlands of Tasmania, both outside the areas where mean annual temperature is  $>14.2^{\circ}\text{C}$ . The *C. johnstoni* range extends in places a little beyond the calculated  $24^{\circ}\text{C}$  mean annual range of temperature, but has been observed to aestivate (or something similar) in stream-bank caverns during the dry season, especially in places where water temperatures in drying pools may exceed the maximum activity temperature. Occupation of the water body is consequently not an effective strategy for maintaining activity temperature (Walsh 1989).

There are in Australia four additional geographical areas that on the basis of the thermal properties defined above might sustain crocodilians (although not necessarily *Crocodylus* species): three in Western Australia and one in South Australia (Figure 21a). Their absence from the three Western Australian areas is attributable to thermal and/or geographical barriers, especially coastal sand plains and limestone terrain (e.g. Nullarbor Plain), where surface water is virtually absent. The Eyre Peninsula of South Australia is today also isolated thermally, but was almost certainly not isolated during the Pleistocene. Inland occurrences of Pleistocene crocodilians (Figure 21a) indicate that in relatively recent geological times, an interior thermal and habitat corridor extended from northern Australia into the Lake Eyre Basin of South Australia along major drainage axes and into the geographical range of extant *Cupedora* species. *Cupedora* and *Bothriembryon* both occur today on the Eyre Peninsula and on Kangaroo Island within a thermal zone hypothetically still capable of sustaining crocodilians (Figure 21a, b).

The Camaenidae is one of the most diverse family of land snails living on Australia today, and its members are widespread throughout the semiarid regions between the Kimberley, southern Arnhem Land and the tip of the Eyre Peninsula of South Australia. The combined geographical range of the 16 or so extant *Cupedora* species is centred on the Flinders Ranges of South Australia, as shown in Figure 21b. Throughout their range, water is limiting, with precipitation being either seasonally variable or unpredictable in its distribution. *Cupedora* species become active after soaking rains, aestivating between rainfall events. They are associated with rock talus and creviced hillsides that hold moisture longer than more open habitats. The snails seal themselves into their shells to aestivate, free-sealing rather than attaching themselves to rocks or other hard surfaces (Solem 1992a).

*Bothriembryon* (Bulimulidae) species dominate the terrestrial gastropod fauna of southern and western Western Australia, extending along the southern coast into South Australia (Figure 21b), with an additional species confined to several small islands off the east coast of Tasmania and one restricted to a small area in central Australia. The species are found mainly in dry areas, with

several being partially arboreal, and others saxicoline (living under or among rocks) or present in leaf litter (Smith 1992). McMichael (1968) identified *B. barretti* from the Nullarbor Plain of Western and South Australia as being the closest living form to *B. praecursor*, and possibly its direct descendent. *Bothriembryon barretti* is one of the species adapted to the cooler (lower average annual temperature) and drier areas of the geographical range of the genus.

*Bothriembryon* and *Cupedora* thus occur in temperate areas that range from fairly reliable low to moderate winter rainfall, warm to hot summers and cool to mild winters in coastal areas, to adjacent inland areas where rainfall is lower and much less reliable. In these drier inland areas, summers are hot to extreme, and winters cool to mild (Bureau of Meteorology 1989). *Bothriembryon* is basically confined to areas where precipitation is between  $\sim 200$  and  $800$  mm, and average annual temperature is  $\sim 14$ – $21^{\circ}\text{C}$ . *Cupedora* has very similar thermal tolerances ( $\sim 13$ – $20^{\circ}\text{C}$  average annual temperature), but seems to be adapted to slightly drier conditions ( $\sim 150$ – $600$  mm median annual rainfall).

The tip of the Eyre Peninsula and Kangaroo Island (Gulf St Vincent region of South Australia), where *Bothriembryon* and *Cupedora* species coexist (Figure 21b) and temperature characteristics hypothetically also suit crocodilians (Figure 21a), thus have the closest analogous climate for the Kangaroo Well area during the Late Oligocene. The biogeographical area identified has an average annual temperature of  $\sim 14$ – $16^{\circ}\text{C}$ , and median annual rainfall of  $\sim 300$ – $600$  mm. While rainfall of  $<600$  mm is indicated by *Cupedora* distribution, average annual temperature during Kangaroo Well Local Fauna time could have been a bit higher than suggested above, possibly as high as  $20^{\circ}\text{C}$ , which is at or close to the upper limit of both *Cupedora* and *Bothriembryon*. A higher average temperature, all other factors being equal, would certainly have been more optimal for crocodilians.

### Palaeovegetation

Although there are no palaeobotanical data available from the Ulta Limestone (and indeed relatively few for the mid-Tertiary outside of Australia's marginal basins), some general inferences about palaeovegetation are possible on the basis of rainfall and temperature characteristics. Precipitation (rainfall,  $r$ ) and warmth (temperature,  $t$ ) are the two main determinants of plant growth, and of critical importance is what proportion of the rainfall is able to be utilised for plant growth, known as the effective precipitation. Effective precipitation is a function of  $r/t$  and the seasonal variation in  $r$  and  $t$ . There are of course many additional factors that influence plant growth response, such as soil characteristics (especially fertility and water-holding capacity), but temperature and rainfall are the two major determining factors. Plant growth in response to effective precipitation underpins widely used, generic climate classifications (Bureau of Meteorology 1989; Barry & Chorley 1992).

Figure 21c shows the generalised distribution of various vegetational structures across Australia prior to European land-clearing, and also set out are some basic

characteristics of each structural type (grade), and approximate rainfall and temperature bounds within which they occur on Australia today. Each of these structural types occurs somewhere on the continent where winter rain or summer rain dominates, or rainfall distribution is relatively even over the year. The two most restricted structural types are tall forests, which are confined to moist, temperate places (latitudinally and/or altitudinally determined), and closed forests, which occur where effective precipitation is unlimiting on plant growth. Closed forests are classic rainforests, but the term 'rainforest' has also been applied in Australia to restricted but widespread and comparatively depauperate stands of vegetation that occur in drier parts of Australia, where the physiological needs of certain plant taxa usually associated with closed forests are locally satisfied (Beadle 1981; Lange 1982; Webb *et al.* 1984; Adam 1999). These occurrences are therefore controlled by geographical, edaphic and/or hydrogeological factors rather than effective precipitation.

The Eyre Peninsula and Kangaroo Island were predominantly covered by scrub prior to European land-clearing, but the indicated palaeotemperature and palaeo-rainfall for the Ulta Limestone (i.e. <600 mm median annual rainfall and  $>14, \leq 20^{\circ}\text{C}$  average annual temperature) was equally capable of sustaining hummock grasses, tussock grasses, forbs and low forest, but not tall forest and closed forest (Figure 21c). At Kangaroo Well, different vegetational structures may have been present depending on geographical factors. In more exposed areas of higher relief where soils were thin and/or had low water-holding capacity, grasses, forbs and low shrubs might have been present. In lower, more sheltered parts of the landscape where soils were thicker and groundwater more generally accessible, scrub or low forest may have been present. Graminoids may have been present around playas and pans where evaporative concentration of salts might have occurred. Vegetation cover in the catchment therefore probably ranged from ~10 to 70%. Only in riparian settings were higher vegetational grades possible, and although riparian vegetation might have had some rainforest-like characteristics, any such attributes must be ascribed to hydrological factors other than high effective precipitation. The vegetation of the Ulta Limestone depositional environment was therefore probably very much like that modelled by Alley *et al.* (1999) for South Australian Miocene palaeochannels.

### Broader perspectives

A broadly similar palaeoclimate to that under which the Ulta Limestone formed is also postulated for the Etadunna Formation, Carl Creek Limestone and Camfield beds, all of which contain crocodylians + *Cupedora lloydi* +/- *Bothriembryon praecursor* (Table 8). It does not follow, however, that palaeoclimate over such a large geographical area and considerable temporal span (i.e. earliest Etadunna Formation to latest Carl Creek Limestone time: Figure 2) was necessarily homogeneous, or unfluctuating over the Miocene oscillation. The approximate rainfall and temperature maxima and minima postulated above allow for a fair degree of variation between regions and over time, and it is also possible that biogeographical ranges contracted

or migrated when climate exceeded these parameters, and areas were recolonised when it became optimal again for the indicator taxa. What may be surmised from these taxa, however, is that the latitudinal temperature gradient across the continent during Etadunna Formation times (Late Oligocene) at least, must have been considerably lower than it is now, and the climate of the interior generally much more equable. The eustatic curve, an indicator of the overall pattern of global climate change, shows cyclic variation at the less than  $10^7$  years scale of the Miocene oscillation climatic event, which McGowran and Li (1994) identified as the possible causal agent of widespread continental deposition in Australia between the end of the Late Oligocene to the end of the Middle Miocene (Figure 2).

As part of their 'conciliation of induction', McGowran and Li (1994) attempted to reconcile the strongly contrasting palaeoenvironmental reconstructions for the Carl Creek Limestone advanced by Megirian (1992) *vs* that of Archer *et al.* (1986, 1989, 1991). Like the Ulta Limestone, the Carl Creek Limestone (and the Camfield beds) are palaeochannel deposits (Murray & Megirian 1990; Megirian 1992, 1997). Briefly, Archer *et al.* (1986, 1989, 1991) interpreted the Carl Creek Limestone as having been deposited in rainforest (= closed forest), primarily on the basis of vertebrate community structure and composition. They proposed a general model of faunal evolution for the entire continent, the Green Cradle hypothesis of Archer *et al.* (1986), in which hypothetical widespread, closed forests of the Late Oligocene contracted as climate became drier, with progressive aridification being the main selective pressure on the Australian fauna, elements of which either became extinct, became confined to rainforest refugia, or else adapted to expanding mesic and ultimately arid environments. Adam (1999) and Megirian (1992) pointed out that these vegetational inferences and their timing were incongruent with sedimentological, palaeobotanical, palaeobiological and/or geochronological datasets, and also called into question some of the vertebrate biological premises relied upon by Archer *et al.* (1986, 1989, 1991).

McGowran and Li (1994) observed that ocean palaeotemperatures, as determined by stable oxygen isotope ratios of planktonic microfossils, show a high degree of correlation with the eustatic curve. They contended that when sea-levels were high, continents experienced generally warmer and wetter conditions, and that erosion and sedimentation were enhanced. With greater sedimentation went a greater probability of the preservation of (vertebrate) fossils. By this reasoning, they identified the Miocene oscillation as being a time generally more suitable in Australia for fossil preservation than the preceding Oligocene and the subsequent Late Miocene. McGowran and Li (1994) went on to suggest that the discordance of the Megirian and Archer *et al.* models for the Carl Creek Limestone might be attributable to cyclic climate variation at a  $10^6$  years scale within the  $10^7$  year scale of the Miocene oscillation, i.e. Megirian may be right for drier times, and Archer *et al.* may be right for wetter times. Because the geochronology of the Carl Creek Limestone is far from resolved at the  $10^6$  year scale, the idea can be examined at this time only in terms of some of the limiting factors on carbonate deposition in the non-marine realm.



Implicit in the McGowran and Li (1994) model is that in general terms, sediment yield rises as precipitation increases. The empirical evidence, however, suggests otherwise. Modern (silici)clastic sediment yields in vegetated terrains peak in dry areas, and then decreases asymptotically as precipitation increases (Figure 21). The more effective the precipitation, the greater the vegetation cover, resulting in greater rainfall interception and retardation of runoff, and therefore reduction in sediment mobilisation. The corollary of increased rates of erosion following land-clearing are too well known to need any elaboration here.

Megirian (1992) argued that for terrigenous detrital carbonates to aggrade in channel environments, plant cover had to be incomplete and rainfall had to be sufficient to mobilise particles, but if conditions generally became too wet, the carbonate system would cross a threshold from the formation, mobilisation, and re-deposition of clastic particles, to net dissolution. Beyond this threshold, only siliciclastic sedimentation would occur. Thus, there existed a climatic optimum for calciclastic deposition, and a point beyond which significant carbonate accumulations would not aggrade in open systems (Figure 21a). This point lies well short of the minimum median annual rainfall that is typically required to sustain closed forests. Although Figure 21 indicates that precipitation as low as ~1200 mm sustains closed forests in Australia today, this applies to cool areas where mean annual temperatures are as low as ~6°C. The 1500 mm threshold shown in Figure 21 corresponds to a mean annual temperature closer to ~18°C, i.e. within the range modelled above for the Ulta Limestone, Carl Creek Limestone, Camfield beds and Etadunna Formation.

We agree with McGowran and Li (1994) that the Miocene oscillation was more optimal for continental sedimentation than at least the preceding Oligocene, which is widely marked in the continental rock record by non-deposition, deep weathering and siliceous duricrusts. The Miocene oscillation itself, however, appears to have been an optimal time for carbonate deposition (Figure 2; Table 8) and suboptimal for siliciclastic deposition. A return to drier conditions in the Late Miocene and an overall trend of aridification into Holocene times generally favoured siliciclastic sedimentation over calciclastic sedimentation.

Any pluvial intervals >~800 mm annual rainfall during the Miocene oscillation are likely to be recorded in palaeochannel carbonate formations by unconformities rather than vertebrate fossil assemblages indicative of regionally extensive closed forest (Figure 21). Furthermore, plant macrofossils from the Carl Creek Limestone reported by Arena (1997) do not appear to support the rainforest hypothesis of Archer *et al.* but seem to have been largely ignored by vertebrate palaeontologists working at Riversleigh. In any case, reconstructing regional palaeoclimate from plant fossils collected from incised valley deposits is risky for reasons outlined by Demko *et al.* (1998), and these risks extend to relying on animals with ecological needs that might be locally satisfied by, or in, riparian vegetation adjacent to their preservational environment.

The biogeography of extant *Bothriembryon*, *Cupedora* and crocodilians appears to be fundamentally controlled by temperature and/or rainfall, rather than particular vege-

tation structures, making them ideal palaeoclimatic indicators. The widespread association of these three groups in the fossil record points to relatively dry (<600 mm median annual rainfall) and temperate conditions (14–20°C average annual temperature) from the northern to the southern continental margins right across the interior during the Miocene oscillation. Their co-occurrence in the Carl Creek Limestone is at odds with the notions of Archer *et al.* (1986, 1989, 1991) that regionally extensive closed forest environments were centred at Riversleigh during the Miocene oscillation.

## CONCLUSIONS

The Ulta Limestone is a lithoclast carbonate deposited in a structurally controlled palaeochannel on the southern flank of the central Australian massif, at the northern margin of the Lake Eyre Basin. The carbonate extracasts comprising the depositional facies are of pedogenic (caliche) origin.

Biochronologically informative marsupials of the Kangaroo Well Local Fauna of the Ulta Limestone suggest that it is probably older than the Kutjamarpu Local Fauna of the Wipajiri Formation, and younger than the Ngama Local Fauna (zone D) of the Etadunna Formation, both of the central Lake Eyre Basin. This implies a Late Oligocene age for the Ulta Limestone if the palaeomagnetic ages for the Etadunna and Wipajiri Formations of Woodburne *et al.* (1993) are correct.

The Ulta Limestone and its equivalents are part of a Tertiary depositional event correlated by McGowran and Li (1994) to the Miocene oscillation, the global climatic event manifest in the marine record spanning the latest Oligocene to the end of the Middle Miocene. Sedimentological and biological palaeoclimatic indicators from the Ulta Limestone and correlative continental strata point to temperate, relatively dry and equable conditions across what is now the Australian arid region during the Miocene oscillation. Extant crocodilian and terrestrial gastropod analogs for taxa present in the Ulta Limestone, Etadunna Formation, Camfield beds and Carl Creek Limestone indicate that across the region, mean annual temperatures were probably in the range 14–20°C, median annual rainfall was probably <600 mm, and mean annual ranges of temperature were less than ~24°C.

Lithoclastic palaeochannel carbonates such as those present in the Ulta Limestone, similar facies also being present in the Carl Creek Limestone and Camfield beds, were unlikely to have accumulated when median annual rainfall exceeded ~800 mm, a threshold well below what is required to sustain closed forests, as proposed for Riversleigh (Carl Creek Limestone) and extrapolated to the continent by Archer *et al.* (1986, 1989, 1991).

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