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PLEISTOCENE PALAEOECOLOGY AND ENVIRONMENTAL CHANGE ON THE  
DARLING DOWNS, SOUTHEASTERN QUEENSLAND, AUSTRALIA.

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A diverse Pleistocene fossil assemblage was recovered from a site (QML1396) exposed in the southern banks of Kings Creek, Darling Downs, southeastern Queensland. The site includes both high-energy lateral channel deposits and low-energy vertical accretion deposits. The basal fossil-bearing unit is laterally extensive, fines upward and its geometry and sedimentary structures suggest deposition within a main channel. The coarse channel fill passes upward into overbank levee deposits made up of lenticular sandy-shelly strata alternating with muds. Several taphonomic biases relating to preservation of different faunal groups and skeletal elements was discerned. Biases may be related to fluvial sorting of the assemblage, but causes for differences between the preservation and accumulation of mammal versus non-mammal terrestrial vertebrates remain unclear. In general, the vertebrate material was accumulated and transported into the deposit from the surrounding proximal floodplain. The assemblage is composed of 44 species including molluscs, teleosts, anurans, chelids, squamates, and small and large-sized mammals. Palaeoenvironmental analysis suggests that a mosaic of habitats, including vine thickets, scrublands, open sclerophyllous woodlands interspersed with sparse grassy understories, and open grasslands, were present on the floodplain during the late Pleistocene. From sedimentological and ecological data, it is evident that increasing aridity during the late Pleistocene led to woodland and vine thicket habitat contraction, and grassland expansion on the floodplain. At present, there is no evidence to support the suggestion that the retraction of late Pleistocene Darling Downs habitats was due to anthropogenic factors. □ *Pleistocene, Darling Downs, Kings Creek catchment, taphonomy, sedimentology, habitat change, megafauna.*

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The Darling Downs, southeastern Queensland, contains some of the most extensive and significant Pleistocene megafauna deposits in Australia. Molnar & Kurz (1997) recognised more than 50 specific Darling Downs localities where fossil material has been collected. Species lists are dominated by large-sized taxa such as *Diprotodon* spp., *Macropus titan*, and *Protemnodon* spp. (Bartholomai, 1976; Molnar & Kurz, 1997). More recently, Roberts et al. (2001a) suggested that some Darling Downs fossil deposits are among the youngest deposits known to contain megafauna remains. As Pleistocene fossils have been known from the Darling Downs since the 1840's (Owen, 1877a), it is generally assumed that the palaeoenvironmental record is well established. Darling Downs palaeoenvironments have been interpreted as consisting of vast grasslands and woodlands, as indicated by an abundant and

diverse range of grazing and browsing megafauna species preserved in the deposits (Bartholomai, 1973; 1976; Archer, 1978; Molnar & Kurz, 1997). However, Molnar & Kurz (1997) recognised a collecting bias towards large-sized species suggested that smaller-sized taxa have generally been overlooked. Additionally, there have been few attempts to document sedimentologic and stratigraphic aspects of the Pleistocene deposits of the region. Macintosh (1967), Gill (1978), and Sobbe (1990) provided limited stratigraphies for sections along creeks from the southern Darling Downs, introducing the terms 'Toolburra silt', 'Talgai pedoderm' and 'Ellinthorpe clay'. However, those names have not seen subsequent use and are not considered valid stratigraphic units (Molnar & Kurz, 1997). Taphonomic aspects of the deposits are also largely unknown. Molnar et al. (1999) reported a deposit that contained articulated remains of

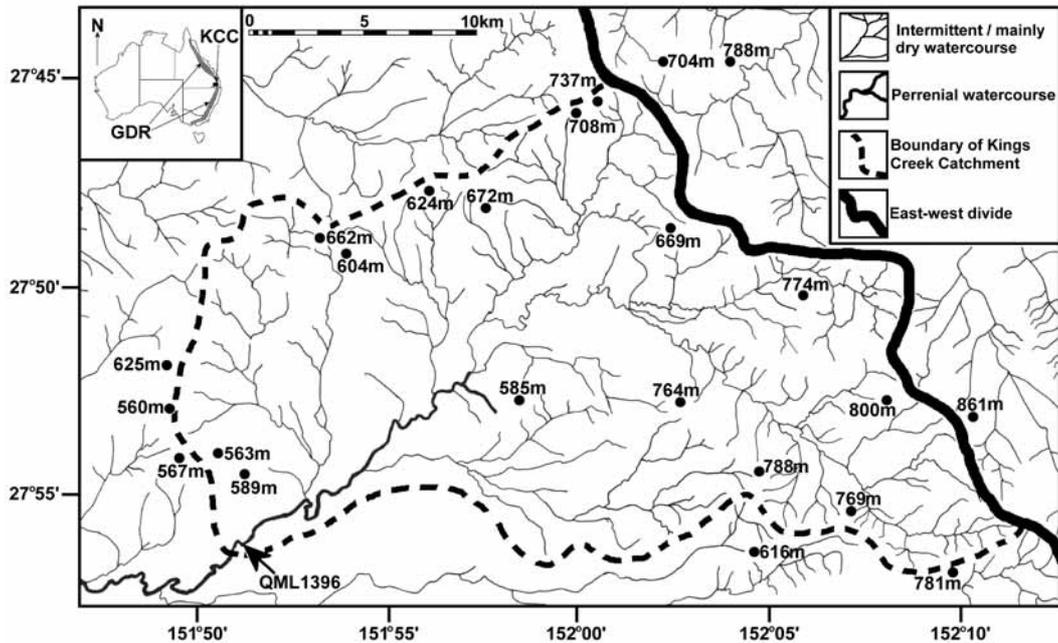


FIG. 1. Modern Kings Creek Catchment with heights (metres) of surrounding peaks, and the current study area, QML1396 (GDR: Great Dividing Range; KCC: Kings Creek Catchment).

megafauna taxa, but noted that articulation of fossil skeletal material was relatively uncommon in the region. Collectively, palaeoenvironmental interpretations of the region are limited owing to the poor understanding of stratigraphic, sedimentologic and taphonomic aspects of the deposits, as well as past collecting biases that have focused on the recovery of large-sized taxa.

Recent systematic collecting of a deposit (site QML1396) from the Darling Downs targeted the recovery of both large and small-sized taxa. Consequently, a comprehensive faunal assemblage has been uncovered. Typical Darling Downs megafauna taxa are represented, as well as an extensive small-sized fauna that includes a diverse range of molluscs, teleosts, anurans, chelids, squamates, and small and large-sized mammals. Such assemblages are beginning to demonstrate that Pleistocene Darling Downs palaeoenvironments were much more complex than previously thought (Price, 2002; Price, 2004; Price et al., in press). The aim of the present paper is to describe a multidisciplinary approach integrating sedimentologic and taphonomic information, as well as ecological information obtained from mammals and non-mammals that occur in the deposit. The combined data sets

allow a better understanding of Pleistocene palaeoenvironments and possible climate change in the region. In light of the ongoing debate over the causes and timing of Australian megafauna Pleistocene extinctions (e.g. Field & Fullager, 2001; Roberts et al. 2001a, b; Brook & Bowman, 2002; 2004; Barnosky et al., 2004; Johnson & Prideaux, 2004; Wroe, 2004), studies of Pleistocene palaeoenvironments may provide important information that could aid in elucidating the causes of faunal change.

#### SETTING

The Darling Downs, southeastern Queensland, encompasses low rolling hills and plains west of the Great Dividing Range. Fluvial sediments of the region consist of clays, silts and sands that are generally derived from the erosion of Mesozoic sandstones (Gill, 1978) and Miocene basalts of the Great Dividing Range (Woods, 1966). Site QML1396 is exposed laterally over 70 metres in the southern bank of Kings Creek, southern Darling Downs (Fig. 1). The modern Kings Creek catchment, bounded to the north, east and south by the Great Dividing Range, is fed by several mainly dry or intermittent watercourses (Fig. 1), resulting in a relatively small geographic

sampling area. Considering relatively low rates of erosion and uplift since the late Pleistocene, it is unlikely that the Pleistocene Kings Creek catchment was markedly larger than present (Price, 2004). Therefore, it is unlikely that material from QML1396 was subjected to long distance fluvial transport from a significantly larger catchment.

### METHODS

**SEDIMENTOLOGY.** A section was measured representing the entire depositional sequence exposed in the creek bank. Stratigraphic horizons were distinguished on the basis of lithological criteria. Sediment samples were collected from each stratigraphic horizon for the purpose of grain size analysis. The sediment samples were disaggregated by applying alternating cycles of bleach and detergent. Disaggregated sediments were dried and sieved according to Wentworth size classes (-2 to +4 phi; Wentworth, 1922). Differentiation and identification of calcrete followed Arakel (1982).

One unit (Horizon D; Fig. 2) contained abundant lenses of the freshwater gastropod, *Thiara (Plotiopsis) balonnensis*. The orientations of 100 gastropods from one such lense were measured to determine whether fluvial transport acted on the gastropods in influencing their final orientations. The angle was measured between north and the spire of the shell (long direction).

**TAPHONOMY.** Cranial and post-cranial elements from horizons B and D formed the basis for the taphonomic study. The units of element representation were NISP (number of identified specimens), MNI (minimum number of individuals- as determined by counting the most abundant element referable to a particular species represented in the sample), and MNE (minimum number of elements) (following Andrews, 1990). For vertebrates, calculation of MNI was based on maxillary and dentary remains, except in the case of fish, frogs, turtles and some squamates where vertebrae, pelvi, shell fragments and osteoderms were used respectively.

Several indices were used to characterise and describe the taphonomic features of the assemblage based on the skeletal remains of large and small mammals, as well as squamates.

**Relative abundance.** Relative abundance of each skeletal element was calculated following the equation:

$$R_i = N_i \times 100 / (MNI)E_i \quad (1)$$

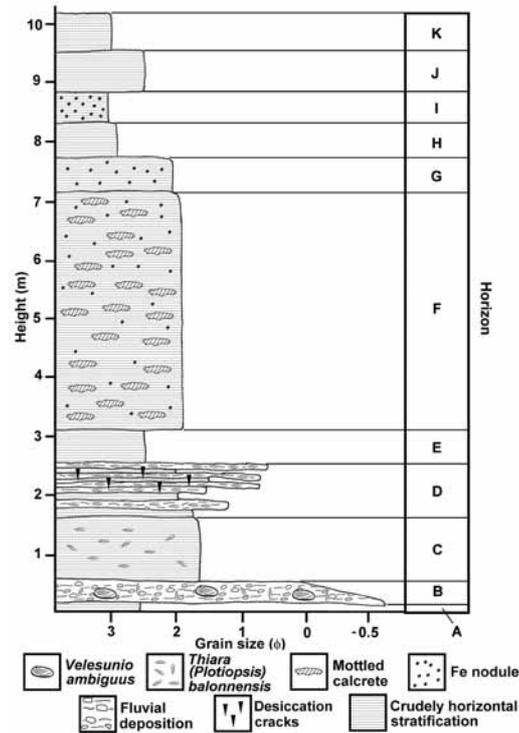


FIG. 2. Measured section of QML1396.

following Andrews (1990), where  $R$  = relative abundance of element  $i$ ,  $n$  = minimum number of element  $i$ ,  $MNI$  = minimum number of individuals, and  $E$  = expected number of element  $i$  in the skeleton. The relative abundance equation allows the comparison of different skeletal elements that occur in varied proportions in mammal or squamate skeletons. Determination of  $E$  was based on modern comparative skeletons for mammals and follows Greer (1989) for squamates.

**% Post-crania to crania.** The percentage of post-crania to crania follows Andrews (1990). The number of post cranial elements (femur, tibia, humerus, radius and ulna [ $n=10$ ]) are compared to cranial elements (dentary, maxilla and molars [ $n=16$  for murids, 20 for marsupials, 4 for squamates]). As the ratio of post crania to crania is not 1:1, the post crania and crania are corrected by 10/16 for murids, 10/20 for marsupials, and 10/4 for squamates, to match numbers of skeletal elements.

*% Distal element loss.* Distal element loss was measured by comparing the number of distal limbs (tibia and radii) to proximal limbs (femura and humeri). The ratio measures preferential loss of distal limbs.

*% Fore limb element loss.* Limb element loss was measured by comparing the number of fore limb bones (humeri and radii) to hind limb bones (femora and tibiae). The ratio measures any preferential loss of fore limbs.

*% Molar tooth loss.* Molar tooth loss was measured by comparing the number of isolated molars in the sample to the number of available alveoli spaces in the dentaries or maxillae. Values >100% indicates the loss or destruction of dentaries or maxillae (Andrews, 1990).

*% Relative loss of molar tooth sites.* Relative loss of molar tooth sites was calculated by comparing the actual number of tooth sites in the sample (regardless of whether they contain teeth or not) to the theoretical number of molar tooth sites assuming that there was no breakage. Relative loss of molar tooth sites was used as an independent check for cranial breakage (Kos, 2003).

*Cranial modifications.* The cranial breakage patterns of squamates and mammals were identified within the deposit following Andrews (1990; Figs 3 & 4). The percentage of representation of each pattern was calculated to attempt to distinguish any differences between large and small-sized mammals, as well as between agamid and scincid lizards.

*Breakage of post-crania.* Identification of breakage patterns of major post-cranial limb bones (humeri, femora, ulnae and tibiae) follows Andrews (1990). Broken limb bones were scored as to whether the represented proximal, shaft, or distal portions.

*Comparison to "Voorhies Groups".* The experimental work of Voorhies (1969) and Dodson (1973), on hydraulic dispersive mechanisms for mammal bones, forms a comparative framework for explaining the dispersal of skeletal elements in the fossil record. Their studies documented transportability of different skeletal elements at constant rates of

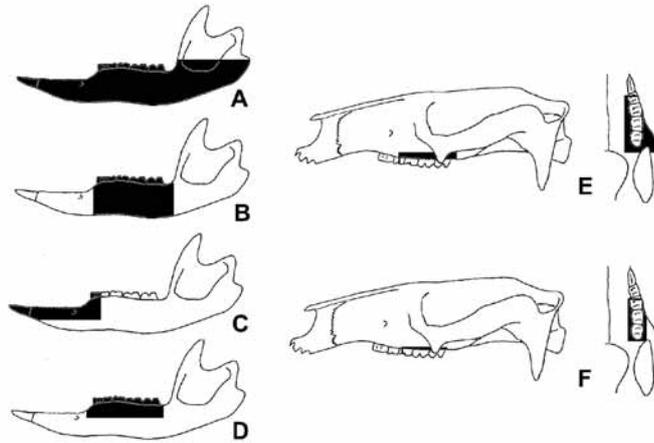


FIG. 3. Mammal cranial breakage categories from the QML1396 assemblage (shaded areas indicates the preserved portions). Refer to table 5 for definition of the breakage categories.

water flow, and concluded that different skeletal elements disperse at different rates in relation to stream flow velocity. Differences in the dispersal potential of skeletal elements reflect the density and shape of the elements. Relative abundance of elements from the QML1396 assemblage were compared to the published results for skeletal element transportability in hydraulic systems.

**FAUNA.** Fossils were recovered by in situ collecting and sieving of sediment specifically to target smaller specimens. Fossil material was generally restricted to Horizons B and D (Fig. 2). All fossil material collected was labeled according to the stratigraphic horizon where it was collected. Sediments were washed using graded sieves of 10mm to 1mm. Approximately 700kgs of sediment were processed from Horizon D, and 200kgs of sediment were processed from Horizon B. The disparity in collecting efforts between Horizons D and B reflects the position of Horizon B below the present water table. Collecting of Horizon B was generally possible only during drought conditions. Most material was collected from Horizon B in November and December 2002.

Descriptions of the fossil fauna have been limited to diagnostic features in most cases. Molluscan shell terminology follows Smith and Kershaw (1979). Squamate cranial morphology terminology follows Withers and O'Shea (1993). Marsupial dental nomenclature follows Luckett (1993), where the adult unreduced cheek tooth

TABLE 1. Description of stratigraphic horizons at QML1396.

Horizon (height)	Fill type	Mean $\phi$	Characteristics	Notes
A (0-0.2m)	Fine montmorillonite clay	2.65	crudely horizontal bedding; poorly sorted, strongly fine skewed grains	pebbles to 20mm rare; shelly marterial rare; vertebrate material rare
B(0.2-0.6m)	coarse grain fill bed	-0.78-0.19	fining upwards sequence; poorly sorted; finely skewed grains	Freshwater molluscs abundant; vertebrate material abundant; rounded basalt, calcrete and sandstone pebbles and cobbles abundant
C(0.6-1.7m)	brown-grey clay	1.7	crudely horizontal bedding, poorly to very poorly sorted; strongly finely skewed grains	Mollusc shell rare; vertebrate material rare
D (1.7-2.6m)	coarse to fine-sized quartz sand beds	0.6-2.0	Sand beds 3cm to 10cm thick overlain by laterally discontinuous horizontal and sloping shelly lenses 2-10cm thick; shell beds with desiccation cracks, in filled by fine clays; very poorly sorted, fine skewed grains	Freshwater gastropods and small bivalves common, large-sized bivalves rare; polymodal orientation of <i>Thiara (Plotiopsis) balonnensis</i> gastropods (Fig. 5); vertebrate material abundant; shell and vertebrate fossil material commonly cemented by calcrete
E (2.6-3.1m)	brown clay	2.53	Crudely horizontal bedding; poorly sorted, strongly fine skewed grains	Mollusc shell rare; vertebrate material rare
F (3.1-7.2m)	brown clay	1.88	Crudely horizontal bedding; in-situ, mottled, grey-white calcrete; iron nodules to 5mm diameter present; poorly sorted, strongly fine skewed grains	Mollusc shell rare; vertebrate material rare
G (7.2-7.7m)	black clay	2.0	Crudely horizontal bedding; iron oxides to 5mm diameter present; poorly sorted, strongly fine skewed grains	Organic rich clay; mollusc shell rare; vertebrate material rare
H (7.7-8.3m)	grey-white clay	2.8	Crudely horizontal bedding; poorly sorted, strongly fine skewed grains	Mollusc shell rare; vertebrate material rare
I (8.3-8.8mm)	grey-white clay	3.0	Crudely horizontal bedding; iron oxides to 5mm diameter present; poorly sorted, strongly fine skewed grains	Mollusc shell rare; vertebrate material rare
J (8.8-9.5m)	grey clay	2.4	Crudely horizontal bedding; poorly sorted, strongly fine skewed grains	Mollusc shell rare; vertebrate material rare
K (9.5-10.2m)	black clay	2.98	Moderately sorted, strongly fine skewed grains	Organic rich, likely altered by modern agriculture

formula is P1-3 and M1-4 in both upper and lower dentitions. Marsupial dental morphology follows Archer (1976). Higher systematics follows Beesley et al. (1998) for molluscs, Glasby et al. (1993) for amphibians and reptiles, and Aplin and Archer (1987) for mammals. All material is deposited at the Queensland Museum (QMF: Queensland Museum Fossil; QML: Queensland Museum Locality).

**DATING.** Samples of charcoal and freshwater bivalves (*Velesunio ambiguus*) were submitted to ANSTO (Australia Nuclear Science and Technology Organisation; Lawson et al., 2000) for the purpose of AMS<sup>14</sup>C dating. Only complete, conjoined bivalves were submitted for dating. Con-joined, apparently well-preserved bivalves are unlikely to have been reworked in comparison to disarticulated or fragmentary shell remains.

## RESULTS

**SEDIMENTOLOGY.** The entire deposit is characterised by a fining-upwards sequence (Fig. 2). The section is comprised of: 1) grey-white to black clays; 2) in-situ mottled calcretes; 3) iron nodules; 4) quartz sand in channel fills; 5) basalt, calcrete and sandstone pebbles and cobbles (predominantly in coarser fills); and 6) invertebrate and vertebrate fossils (Table 1). Freshwater bivalves (*Velesunio ambiguus* and *Corbicula (Corbiculina) australis*) and thiarid gastropods (*Thiaria (Plotiopsis) balonnensis*) are more abundant in coarser-grained horizons such as Horizon B and D, than fine-grained horizons. Vertebrate fossil material is generally restricted to Horizons B and D.

Horizon B exhibits the largest grain sizes (Fig. 2, Table 1). The horizon is laterally extensive, being recorded over approximately 70 metres. The majority of the lower portion of Horizon B is

TABLE 2. Species NISP and MNI for Horizons D and B at QML1396 (\* Extinct on Darling Downs; \*\* Totally extinct).

Species	Horizon D		Horizon B	
	NISP	MNI	NISP	MNI
<i>Velesunio ambiguus</i>	10+	5+	20+	10+
<i>Corbicula (Cobiculina) australis</i>	100+	100+	50+	50+
<i>Thiara (Plotiopsis) balonnensis</i>	1000+	1000+	50+	50+
<i>Gyraulus gilberti</i> *	249	249	0	0
<i>Coencharopa</i> sp.*	9	9	0	0
<i>Gyrocochlea</i> sp. 1*	35	35	0	0
<i>Gyrocochlea</i> sp. 2*	5	5	0	0
<i>Austroccinea</i> sp.*	1	1	0	0
<i>Xanthomelon pachystylum</i> *	1	1	0	0
<i>Strangesta</i> sp.*	1	1	0	0
<i>Saladelos</i> sp.*	1	1	0	0
Teleost	89	1	0	0
<i>Limnodynastes tasmaniensis</i>	8	8	0	0
<i>L. sp. cf. L. dumerili</i>	3	3	0	0
? <i>Limnodynastes</i>	1	1	0	0
<i>Neobatrachus sudelli</i>	2	2	0	0
<i>Kyarranus</i> sp.*	1	1	0	0
chelid	4	1	0	0
<i>Tympanocryptis "lineata"</i> **	15	4	0	0
" <i>Sphenomorphus</i> group" sp. 1	19	13	0	0
" <i>Sphenomorphus</i> group" sp. 2	6	2	0	0
<i>Tiliqua rugosa</i> *	6	1	0	0
<i>Cyclodomorphus</i> sp.*	1	1	0	0
<i>Varanus</i> sp.	1	1	0	0
<i>Megalania prisca</i> **	4	1	0	0
elapid	14	1	0	0
<i>Sminthopsis</i> sp.	1	1	0	0
<i>Dasyurus</i> sp.	1	1	0	0
<i>Sarcophilus</i> sp.*	0	0	1	1
<i>Thylacinus cynocephalus</i> **	0	0	1	1
<i>Perameles bougainville</i> *	1	1	0	0
<i>Pe. nasuta</i>	1	1	0	0
<i>Diprotodon</i> sp.**	0	0	1	1
<i>Thylacoleo carnifex</i> **	0	0	1	1
<i>Aepyprymus</i> sp.	1	1	0	0
<i>Troposodon minor</i> **	0	0	2	2
<i>Macropus agilis siva</i> **	5	2	1	1
<i>M. titan</i> **	1	1	5	2
<i>Protomnodon anak</i> **	2	1	3	1
<i>Pr. brehus</i> **	2	1	1	1
<i>Pseudomys</i> sp.*	4	2	0	0
<i>Rattus</i> sp.	2	1	0	0
unidentified murid	182	26	0	0

TABLE 3. MNE and expected relative abundance of skeletal elements recovered from Horizons D &amp; B at QML1396.

skeletal element	Horizon D						Horizon B	
	<5kg mammals		<5kg squamates		>5kg mammals		>5kg mammals	
	n	%	n	%	n	%	n	%
dentary	7	10.6	29	72.5	1	8.3	6	30
maxilla	7	10.6	17	42.5	4	33.3	0	0
incisor	101	76.5	na	na	2	8.3	4	20
molar	97	19	na	na	23	24	19	11.9
femur	11	16.7	0	0	0	0	0	0
tibia	18	27.3	0	0	0	0	0	0
pelvis	2	3	0	0	1	8.3	0	0
calcaneum	10	15.2	0	0	1	8.3	0	0
humerus	4	6.1	2	5	0	0	0	0
radius	2	3	0	0	0	0	0	0
ulna	8	12.1	0	0	0	0	0	0
ribs	6	0.9	0	0	0	0	0	0
vertebra	57	3.9	196	12.6	20	7.6	0	0
phalange	53	3.5	2	0.2	1	0.4	2	0.4

below the modern watertable. Large-sized bivalves (*Velesunio ambiguus*) are more abundant in Horizon B than in Horizon D.

Horizon D is represented by a series of coarse to fine quartz sand beds that are overlain by laterally discontinuous horizontal and sloping shelly lenses (Fig. 2, Table 1). Desiccation cracks within the shelly lenses are filled with fine clay. A rose diagram plot of the orientations of freshwater gastropods (*Thiaria (Plotiopsis) balonnensis*) indicates a polymodal distribution (Fig. 5).

In-situ, non-reworked mottled calcretes occur in Horizon F. Iron oxide nodules were also present within that horizon, as well as Horizons G and I. Few sedimentary structures other than crudely horizontal bedding were observed within other stratigraphic horizons (Fig. 2, Table 1).

TAPHONOMY. Vertebrate fossil material was generally restricted to Horizons B and D. Fossil material from other horizons is poorly preserved. Hence, the following taphonomic observations are based on fossil material from Horizons B and D. Additionally, a large number of unidentifiable bone fragments were collected from the main fossiliferous horizons. Few meaningful data could be obtained from those fragments, hence, the taphonomic component was based solely on identifiable elements.

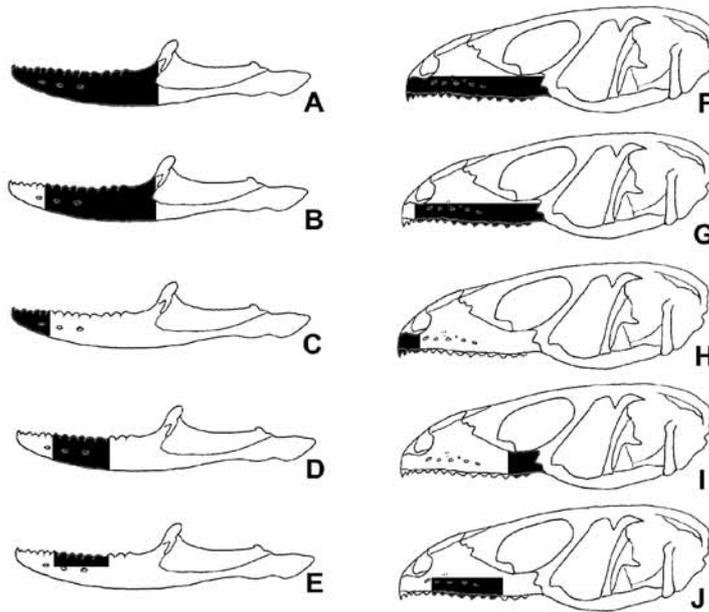


FIG. 4. Squamate cranial breakage categories from the QML1396 assemblage (shaded areas indicates the preserved portions). Refer to table 6 for definition of the breakage categories.

*Species representation.* In terms of diversity, land snails, frogs, squamates and small mammals dominated the terrestrial faunal component represented in the Horizon D assemblage (Fig. 6, Table 2). Large mammals were the least represented size group in Horizon D, and the only represented terrestrial group in Horizon B (Fig. 6).

*Skeletal relative abundance.* Skeletal relative abundance was calculated for large and small mammals, as well as squamates (Table 3). In terms of relative abundance, cranial elements of squamates are the most well represented element for the three major groups of terrestrial animals in Horizon D. However, overall, the relative abundance of all skeletal elements suggests that they are underrepresented. Incisors are the most abundant cranial element recovered for small mammals in Horizon D, but that may reflect a processing bias as incisors are among the most easily identifiable small mammal remains (Andrews, 1990). The dentary is a relatively robust element and that may account for the higher proportion of skeletal elements for squamates and mammals in both horizons. There is a greater loss of squamate post-cranial remains in comparison to mammals in Horizon D.

Small-sized terrestrial vertebrates were not recovered from Horizon B.

*Skeletal modifications.* Indices of skeletal modifications (Table 4) indicate that there is significant loss of post-cranial elements in each horizon. Horizon B is completely devoid of large-sized mammal limb bone elements. For Horizon D mammals there was a slight loss of proximal limbs (femora and humeri) in comparison to distal limbs (tibiae and radii). Additionally, there was a significant loss of forelimb elements in comparison to hind limbs. Reasons for the loss of different limb elements remain unclear, but may simply be the result of using statistically small numbers for comparison. Indices for the loss of molar teeth and molar tooth sites indicate the loss or destruction

of dentaries or maxillae for mammals within each main fossiliferous horizons (Table 4).

*Breakage of crania.* There were no complete mammal skulls or dentaries recovered from the deposit (Table 5). Mammal dentary breakage appears slightly greater for Horizon D than Horizon B. A high proportion of broken maxillae retained only a small portion of the zygomatic arch in Horizon D.

TABLE 4. Skeletal modifications for arbitrary faunal groups from QML1396

skeletal modification	Horizon D			Horizon B
	<5kg mammals	< 5kg squamates	>5kg mammals	>5kg mammals
% post-crania to crania	24.2	17	0	0
% distal element loss	133.3	0	0	0
% fore limb loss	41.4	0	0	0
% molar tooth loss	741	na	no available tooth spaces	150
% relative loss of molar tooth sites	275	na	160	109

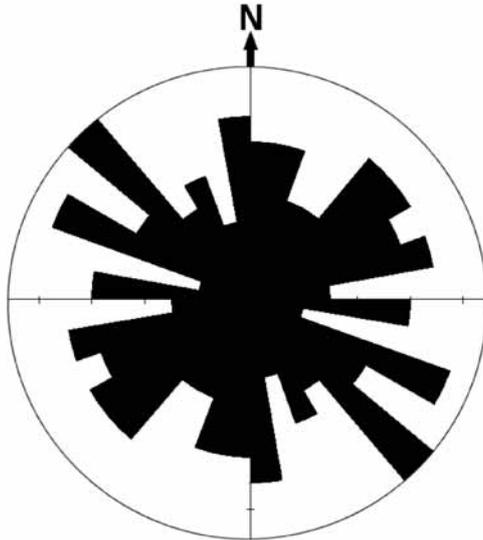


FIG. 5. Orientations of *Thiara (Plotiopsis) balonnensis* gastropods (n: 100) from a single shelly lense within Horizon D at QML1396.

There also were no complete squamate skulls or dentaries preserved (Table 6). Reasonably complete dentaries are equally abundant in both agamids and scincids. However, particular breakage patterns appear to be exclusive to each squamate family (Table 6). For agamids, the central portion of the dentary and central to anterior portions of the maxilla are preserved; for skinks, the majority of the dentary and central to posterior portions of the maxilla are preserved. Overall, scincid dentaries are more completely preserved than those of agamids. However, a reverse trend exists for the maxillae, where a greater portion are preserved in agamids than scincids (Table 6).

*Breakage of post crania.* There were no complete major limb bones (i.e. humeri, ulnae, femora, tibiae) preserved in the deposit (Table 7). Additionally, major limb bones were mostly restricted to small-sized mammals from Horizon D. Most broken limb bones have transverse fractures perpendicular to the bone surface and indicate post-mortem fracturing of dry or fossilised bone (Johnston, 1985). Additionally, the broken ends of the limb bones do not appear to be significantly

TABLE 5. Mammal cranial modifications from QML1396 (following breakage patterns Fig. 3)

Breakage pattern	Horizon D		Horizon B
	<5kg mammals	> 5kg mammals	<5kg mammals
% dentary with ascending ramus mostly absent (Fig. 3A)	0	-	17
% dentary with ascending and anterior ramus mostly absent (Fig. 3B)	33	-	50
% dentary with anterior ramus only, lacking inferior border (Fig. 3C)	67	-	0
% dentary with horizontal ramus only lacking inferior border (Fig. 3D)	0	-	33
% maxilla with most of zygomatic missing (Fig. 3E)	100	75	-
% maxilla alveoli or tooth row only (Fig. 3F)	0	25	-

rounded or abraded, suggesting minimal reworking or transport of fossil material. Squamates were represented by only two proximal humeri from Horizon D. However, high numbers of unidentifiable limb element shafts from small-sized animals (n~120) could equally be referable to either squamates or mammal post-cranial limb bones.

*Comparison to "Voorhies Groups".* For Horizon D small-sized mammals, the majority of the skeletal elements comprise those that would disperse in the middle to late categories of dispersal (Table 8). Additionally, the high number of limb bone shafts (see earlier discussion) would presumably fit within that category of stream transportability. There was no clear trend for small-sized squamates from

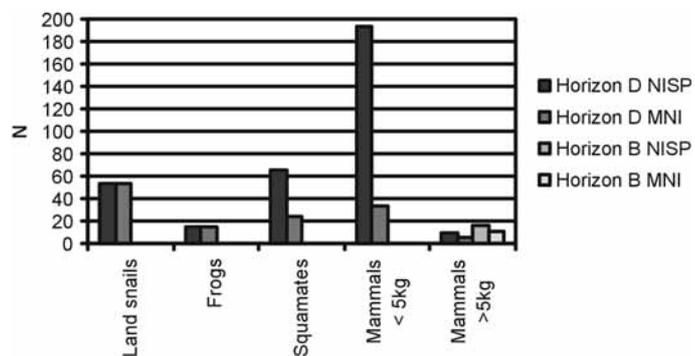


FIG. 6. Comparison of MNI and NISP of terrestrial taxa from Horizons B and D at QML1396.

TABLE 6. Squamate cranial modifications from Horizon D, QML1396

Breakage pattern	agamids	skinkids
% dentary mostly complete (Fig. 4A)	38	43
% posterior portion of dentary only (Fig. 4B)	0	33
% anterior portion of dentary only (Fig. 4C)	0	24
% central portion of dentary only (Fig. 4D)	38	0
% central portion of dentary only, lacking inferior border (Fig. 4E)	25	0
% premaxilla and maxilla mostly complete (Fig. 4F)	22	0
% maxilla mostly complete, lacking premaxilla (Fig. 4G)	67	0
% premaxilla only (Fig. 4H)	11	0
% posterior portion of maxilla only (Fig. 4I)	0	25
% central portion of maxilla only (Fig. 4J)	0	75

Horizon D. For large-sized mammals from Horizon D, the majority of elements comprised those that are progressively the last to be transported in flowing water. Horizon B is dominated by middle-late transported elements (i.e. dentaries; Table 8).

#### SYSTEMATIC PALAEOONTOLOGY

A much abbreviated treatment of the systematic palaeontology is given in order to document the specific material for which taxa are assigned. The fundamental purpose of the taxonomic work was to facilitate ecologic and assemblage information. Thus, only the diagnostic features of the material are provided, as all faunal elements are well known fossil or extant taxa. At the end of each description the primary authority used for identification is given in closed brackets. Two other publications deal with the amphibians (Price et al., in press) and the bandicoots (Price, 2004).

Phylum MOLLUSCA Linnaeus, 1758  
Class BIVALVIA Linnaeus, 1758  
Family HYRIIDAE Ortmann, 1910

**Velesunio** Iredale 1934

**Velesunio ambiguus** (Philippi, 1847) (Fig. 7A)

REFERRED MATERIAL. QMF44633; QMF44651; QMF44653.

DESCRIPTION. Equivalved, length to 110mm, moderately to well inflated; shell thin to very thick; weak ridge runs posteriorly from umbone; pallial line well developed; pallial sinus absent; anterior and posterior adductor muscle scars well

TABLE 7. Breakage patterns of major post cranial limb bones from Horizon D, QML1396.

Limb bone	<5kg mammals		<5kg squamates	
	n	%	n	%
<i>humerus</i>				
complete	0	0	0	0
proximal	1	17	2	100
shaft	4	66	0	0
distal	1	17	0	0
<i>femur</i>				
complete	0	0	0	0
proximal	7	39	0	0
shaft	0	0	0	0
distal	11	61	0	0
<i>ulna</i>				
complete	0	0	0	0
proximal	8	73	0	0
shaft	2	18	0	0
distal	1	9	0	0
<i>tibia</i>				
complete	0	0	0	0
proximal	0	0	0	0
shaft	3	15	0	0
distal	18	85	0	0

developed; teeth lamellar, cardinal teeth absent; hinge moderately developed; beak cavity moderately developed. [Lamprell & Healy, 1998]

Family CORBICULIDAE Gray, 1847

**Corbicula** Mühfeld, 1811

**Corbicula (Corbiculina)** Dall, 1903

**Corbicula (Corbiculina) australis** (Deshayes, 1830)  
(Fig. 7B)

REFERRED MATERIAL. QMF44628-30.

DESCRIPTION. Equivalved, length to 20mm, slightly inflated; pallial line entire but weak; anterior and posterior adductor muscle scars weakly defined; anterior and posterior pedal retractor muscle scars hidden by overhang of anterior and posterior teeth respectively; three cardinal teeth, and anterior and posterior lateral teeth well developed; beak cavity very deep; hinge line narrow. [Lamprell & Healy, 1998]

TABLE 8. Skeletal element transportability for small mammals (Dodson, 1973) and large mammals (Voorhies, 1969) compared to the relative abundance of skeletal elements from Horizons B and D at QML1396 (listed in decreasing abundance). Elements higher in the Dodson (1973) and Voorhies (1969) columns were the last to be transported by moving water in flume experiments.

Relative movement	Dodson (1973) small mammals	Voorhies (1969) large mammals	Horizon D			Horizon B
			<5kg mammals	< 5kg squamates	>5kg mammals	>5kg mammals
late	mandible	skull, maxilla	tibia femur, calcania, ulna, dentary maxilla humerus, vertebrae radius	dentary, maxilla, vertebrae humerus	maxilla dentary pelvi vertebrae	dentary
middle-late	calcania, radius, ulna	mandible				
middle	skull tibia-fibula, femur, humerus	femur, tibia humerus pelvis radius				
early-middle	pelvis, cervical and caudal vert.	ulna				
early	thoracic vert maxilla	vertebra				

Class GASTROPODA Cuvier, 1797  
Order SORBEOCONCHA Fischer, 1884  
Family THIARIDAE Troschel, 1857

**Thiara (Plotiopsis) Brot** 1874  
**Thiara (Plotiopsis) balonnensis**  
(Conrad, 1850)  
(Fig. 7C)

REFERRED MATERIAL. QMF44631-32.

DESCRIPTION. *Shell*. Elongate, dextrally coiled, robust, turreted, length to 30mm; 6-7 whorls, carinate, spiral ridges complemented with nodules; ovoid shaped aperture; inner lip thickened, outer lip thin. [Smith and Kershaw 1979]

Order PULMONATA Cuvier, 1817  
Family PLANORBIDAE Rafinesque, 1815

**Gyraulus** Charpentier, 1837  
**Gyraulus gilberti** (Dunker, 1848)  
(Fig. 7D).

REFERRED MATERIAL. QMF44574-79.

DESCRIPTION. *Shell*. Planispiral, diameter to 6.29mm; 4 whorls; spire sunken; umbilicus wide; last whorl with a peripheral keel; shell sculpture consists of fine transverse ridges; aperture keeled elongate; outer lip relatively thin and straight. [Brown, 1981]

Family RHYTIDIDAE Pilsbry, 1895

**Saladelos** Iredale, 1933  
**Saladelos** sp.  
(Fig. 7E)

REFERRED MATERIAL. QMF44956.

DESCRIPTION. *Shell* planispiral, diameter to 3mm; whorl count reduced, 2-3 whorls, last whorl capacious; spire slightly depressed; shell sculpture of fine radial ribs; umbilicus narrow; aperture ovate-lunate; lip simple. [Iredale, 1933]

**Strangesta** Iredale, 1933  
**Strangesta** sp.  
(Fig. 7F)

REFERRED MATERIAL. QMF44582-83.

DESCRIPTION. *Shell*. Planispiral, diameter to 6.82mm; 3-4 whorls; slightly depressed spire; apical sculpture of fine to medium coiled radial ribs; umbilicus narrow; aperture wide, ovate-lunate; lip simple. [Smith and Kershaw, 1979]

Family CHAROPIDAE Hutton, 1884.

**Coenocharopa** Stanisc, 1990  
**Coenocharopa** sp.  
(Fig. 7G)

REFERRED MATERIAL. QMF44584-89.

DESCRIPTION. *Shell*. Planispiral, diameter to 4.5mm; whorls coiled, last descending; apex and spire slightly elevated; apical sculpture of prominent coiled radial ribs; post-nuclear

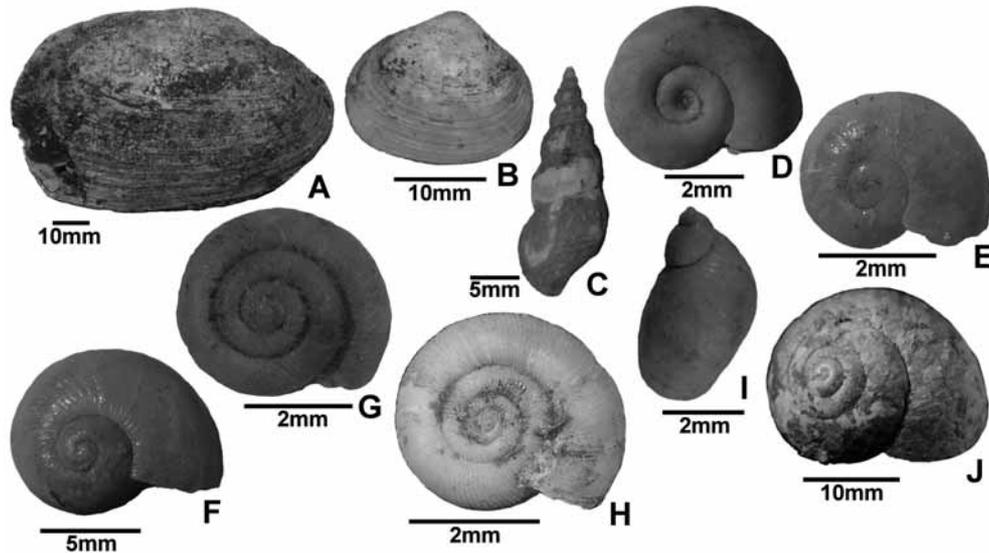


FIG. 7. A. *Velesunio ambiguus*; B. *Corbicula (Corbiculina) australis*; C. *Thiara (Plotiopsis) balonnensis*; D. *Gyraulus gilberti*; E. *Saladelos* sp.; F. *Strangesta* sp.; G. *Coenocharopa* sp.; H. *Gyrocochlea* sp.; I. *Austrosuccinea* sp.; J. *Xanthomelon pachystylum*.

sculpture moderately spaced; umbilicus wide and U-shaped; aperture ovate-lunate; lip simple. [Stanisic, 1990]

**Gyrocochlea** Hedley, 1924  
**Gyrocochlea** sp. 1 and 2  
 (Fig. 7H)

REFERRED MATERIAL. Sp. 1: QMF44590-95; Sp. 2: QMF44598-602.

DESCRIPTION. Shell planispiral, diameter to 4mm; moderately tightly coiled whorls, last descending more rapidly; apex slightly concave; apical sculpture of fine crowded spiral cords and weakly curved radial ribs; umbilicus wide and U-shaped; aperture ovately lunate; lip simple. [Stanisic 1990]

REMARKS. *Gyrocochlea* sp. 1 differs from *Gyrocochlea* sp. 2 by a smoother shell sculpture, and possessing a more closed umbilicus.

Family SUCCINEIDAE Beck, 1837

**Austrosuccinea** Iredale, 1937  
**Austrosuccinea** sp.  
 (Fig. 7I)

REFERRED MATERIAL. QMF44580.

DESCRIPTION. Shell elongate, dextrally coiled; shell height 10.65mm; 4 whorls present, last whorl large; spire short; fine growth lines on

shell; aperture ovate; inner lip relatively straight, outer lip thin and straight. [Smith & Kershaw, 1979]

Family CAMAENIDAE Pilsbry, 1895

**Xanthomelon** Martens, 1861  
**Xanthomelon pachystylum** (Pfeiffer, 1845)  
 (Fig. 7J)

REFERRED MATERIAL. QMF44581.

DESCRIPTION. Shell subglobose, diameter to 18.7mm; 4 whorls present, body whorl large; spire slightly elevated; shell sculpture relatively smooth; anomphalous; aperture ovate lunate; outer and inner lip simple, thin. [Solem, 1979]

Phylum CHORDATA Linnaeus, 1758  
 Class REPTILIA Laurenti, 1768  
 Order SQUAMATA Oppel, 1811  
 Family AGAMIDAE Hardwicke & Gray, 1827.

**Tympanocryptis** Peters, 1863  
**Tympanocryptis "lineata"** Peters, 1863  
 (Fig. 8H)

REFERRED MATERIAL. QMF44198-202, maxillary fragments; QMF44619, dentary.

DESCRIPTION. *Maxilla*. 4 foramen present; pleurodont teeth 2, acrodon teeth 12; 1st pleurodont tooth orientated mesiobuccally; 2nd pleurodont tooth caniniform; maxillary suture

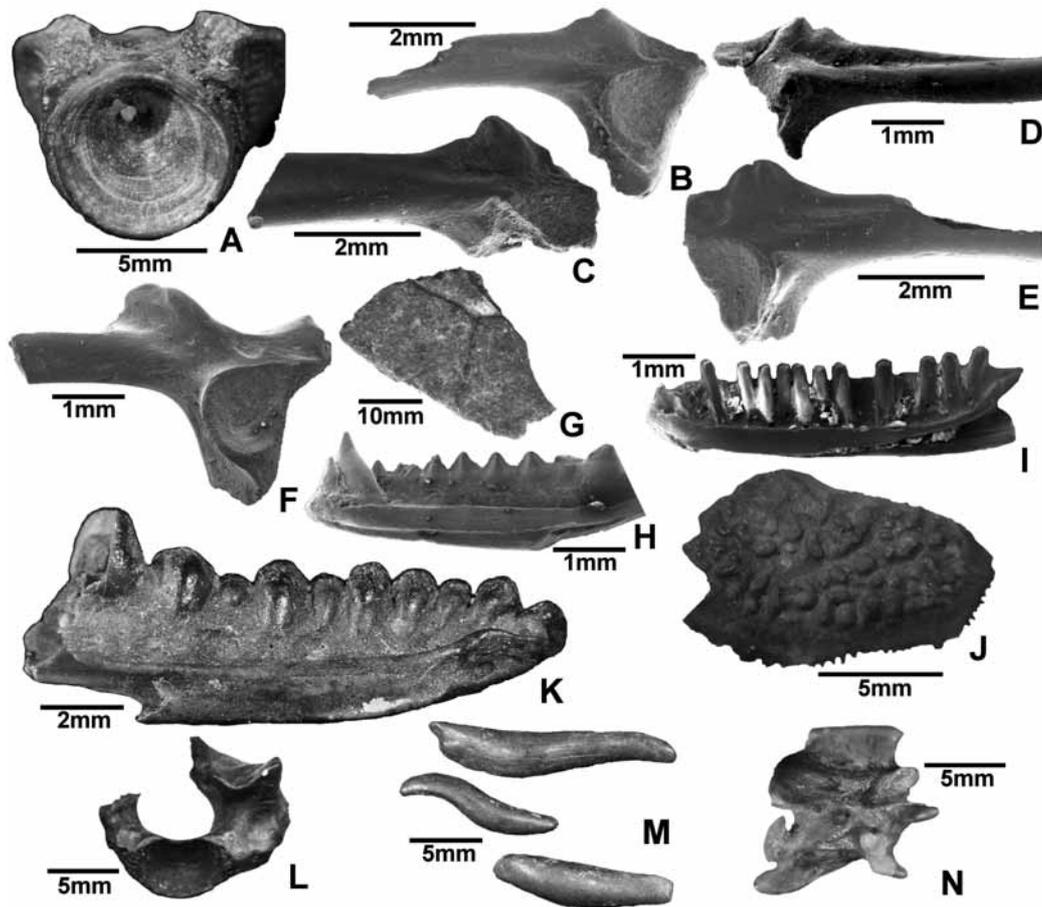


FIG. 8. A. Fish vertebra; B. *Limnodynastes tasmaniensis*, left ilium; C. *L. sp. cf. L. dumerili*, left ilium; D. *?Limnodynastes sp.*, right ilium; E. *Neobatrachus sudelli*, right ilium; F. *Kyarranus sp.*; G. Chelid plastron fragment; H. *Tympanocryptis "lineata"*, right dentary. I. "*Sphenomorphus Group*" sp., right dentary; J. *Tiliqua rugosa*, osteoderm; K. *Cyclodomorphus sp.*, left dentary; L. *Varanus sp.* vertebra; M. *Megalania prisca*, osteoderms; N. Elapid vertebra.

anterodorsal to pleurodont teeth; dorsal maxillary process narrow.

*Dentary*. Short; 3 mental foramina present; pleurodont teeth 2, acrodont teeth 12; pleurodont teeth closely positioned, 2nd pleurodont twice the size of the 1st; acrodont teeth sub-triangular with indistinct anterior and posterior conids; Meckel's groove parallel to dental sulcus, narrowed anteriorly. [Hocknull, 2002]

REMARKS. *Tympanocryptis lineata* is distinguished from other members of the genus by a combination of features including: 1) its

larger size, 2) 1st pleurodont tooth orientated mesiolabially, and 3) lower anterior hook.

#### Family SCINCIDAE Oppel, 1811

Skinks are the largest and most diverse squamate group in Australia (Greer, 1979; Hutchinson, 1993). Within the Scincidae, three distinct monophyletic groups are informally recognised: the *Egernia* group, *Eugongylus* group, and *Sphenomorphus* group (Greer, 1979, Hutchinson, 1993). Members allied to the *Sphenomorphous* Group and *Egernia* group are represented in the deposit.

“**Sphenomorphus** Group” sp. 1 and 2 (sensu Greer, 1979)  
(Fig. 8I)

REFERRED MATERIAL. Sp. 1: QMF44620-22, QMF44654, dentaries; Sp. 2: QMF44623-25, maxillae.

DESCRIPTION. *Dentary*. Tooth row bears up to 17 teeth or tooth loci; Meckel’s groove widely open along ventrolingual margin; internal septum poorly developed; up to 6 mental foramina present, last one positioned about the level of the 12<sup>th</sup> tooth; tooth crowns not flared or thickened; lingual face of each crown vertical. [Greer, 1979]

REMARKS. *Sphenomorphus* Group members are distinguished from the *Egernia* and *Eugongylus* Groups by possessing a Meckel’s groove that remains open along the length of the ventrolingual margin of the dentary (Hutchinson, 1993). Two distinct size classes of members representing the *Sphenomorphus* group were identified within the deposit. Hutchinson (1993) recognised that while sexual dimorphism is common in skinks, it is only subtle. The large size difference between the two size classes is considered here to represent distinct species.

Until the taxonomy of those two species is better known, their significance in Pleistocene Darling Downs will remain unclear.

“*Egernia* group” (sensu Greer, 1979)

**Tiliqua** Gray 1825a  
**Tiliqua rugosa** (Gray, 1825a)  
(Fig. 8J)

REFERRED MATERIAL. QMF44603-605, osteoderms.

DESCRIPTION. *Osteoderms*. Up to 10mm in diameter; thick, coarsely pitted; rugose surface.

REMARKS. The osteoderms of *Tilqua rugosa* differ from all other *Tiliqua* as they are generally thicker and more coarsely pitted, functioning to form an armoured shield (Hutchinson, 1993). [Smith, 1976]

**Cyclodomorphus** Fitzinger, 1843  
**Cyclodomorphus** sp.  
(Fig. 8K)

REFERRED MATERIAL. QMF44639, dentary.

DESCRIPTION. *Dentary*. Near complete with large hemispherical teeth and closed Meckel’s groove; ventral symphyseal crest extends to third tooth; ten teeth present in dentary with tenth tooth markedly larger than all anterior teeth; teeth variable in size, with acutely conical crowns;

specimen is adult as dental sulcus well defined, and dentary indicates cycles of tooth replacement.

REMARKS. *Cyclodomorphus* spp. are similar in size to *Tiliqua* spp., but are distinguished by a markedly larger tenth tooth in the dentary (Hutchinson, 1993). The fragmentary nature of the fossil remains precludes a full comparison to other members of the genus. [Shea, 1990]

Family VARANIDAE Hardwicke & Gray,  
1827.

**Varanus** Merrem 1820

**Varanus** sp.  
(Fig. 8L)

REFERRED MATERIAL. QMF48166, vertebra.

DESCRIPTION. Vertebra broken dorsally; condyle overhanging, oblique articulation; cotyle oblique; centrum broad; neural canal round.

REMARKS. The fragmentary nature of the vertebra, particularly the lack of neural spine, precludes a full comparison to other *Varanus* spp. [Smith, 1976].

**Megalania** Owen, 1860  
**Megalania prisca** (Owen, 1860)  
(Fig. 8M)

REFERRED MATERIAL. QMF44615-17, osteoderms.

DESCRIPTION. Small, worm shaped osteoderms to 8mm in length, 3mm in diameter; growth lines evident.

REMARKS. *Megalania prisca* osteoderms grow in the snout and nape regions of the lizard (Erickson et al., 2003). Growth lines present on the osteoderms may reflect the age of the individual (Erickson et al., 2003). [Hecht, 1975]

Family ELAPIDAE Boie, 1827  
gen. et sp. indet.  
(Fig. 8N)

REFERRED MATERIAL. QMF44606-08, vertebrae.

DESCRIPTION. Vertebrae with long, acute accessory processes; hypapophysis arises near lip of cotyle, extends posteriorly for half the length of centrum, then deepens to taper into a sharp point; parapophysial processes rounded anteriorly; neural spine low, laterally compressed, does not extend posteriorly; four pairs of foramina present.

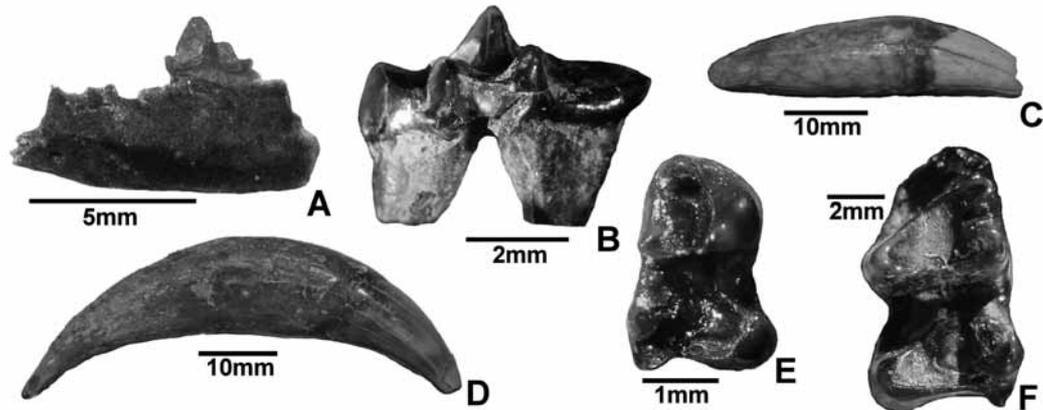


FIG. 9. A. *Sminthopsis* sp., left dentary; B. *Dasyurus* sp.,  $M^4$ ; C. *Sarcophilus* sp.,  $C_1$ ; D. *Thylacinus cynocephalus*,  $I_1$ ; E. *Perameles bougainville*,  $M_1$ ; F. *P. nasuta*,  $M_3$ .

REMARKS. Elapid vertebrae considered here are comparable in size to extant forms currently found on the Darling Downs today, such *Pseudechis australis* and *P. porphyriacus*. [Smith, 1976]. However, the fragmentary nature of the fossil material precludes a full comparison to other members of the family.

Class MAMMALIA Linneus, 1758  
Order MARSUPIALIA Cuvier, 1817  
Family DASYURIDAE Goldfuss, 1820; sensu  
Waterhouse, 1838

**Sminthopsis** Thomas, 1887  
**Sminthopsis** sp.  
(Fig. 9A)

REFERRED MATERIAL. QMF44637, dentary.

DESCRIPTION. *Dentary*. Small, gracile, deepest below  $M_1$ ; mental foramen posteroventral to root of  $M_1$ .  $P_3$  ovoid in occlusal outline; anterior cuspid reduced, lingual to midline, forming anterior margin; central cuspid massive, positioned one third from anterior margin; blade-like crest runs posteriorly to a small posterior cuspid.  $M_1$  anterior one-third triangular, remainder sub-rectangular in occlusal outline; talonid wider than trigonid; protoconid tallest cusp on crown, followed by metaconid, hypoconid, paraconid and entoconid; paraconid forms anterior margin slightly lingual to midline; protoconid posterobuccal to paraconid; metaconid transverse and slightly posterior to protoconid; hypoconid posterobuccal to protoconid; entoconid most posterior cusp forming posterolingual corner of crown; anterior and posterior cingula small but distinct;

metacristids and hypocristids transverse to long axis.

REMARKS. Identification to specific level is not possible due to insufficient preservation of diagnostic features. [Archer, 1981]

**Dasyurus** Geoffroy, 1796  
**Dasyurus** sp.  
(Fig. 9B)

REFERRED MATERIAL. QMF44597,  $M^4$ .

DESCRIPTION.  $M^4$ . Ovoid in occlusal outline; paracone tallest cusp on crown followed in descending order by stylar cusp B, metacone and protocone; paracone most anterior cusp, positioned in midline of crown; Stylar cusp B posterobuccal to paracone; metacone posterolingual to paracone; anterior cingulum absent.

REMARKS.  $M^4$  described above is much larger than the corresponding tooth in all species of *Dasyurus* excepting *D. maculatus*. It is well within the size range of extant *D. maculatus*, although differs in that: 1) it is not anteriorly concave in occlusal outline, 2) the metacone is positioned more lingually, and 3) the anterior cingulum is absent. [Ride, 1964].

**Sarcophilus** Cuvier, 1837  
**Sarcophilus** sp.  
(Fig. 9C)

REFERRED MATERIAL. QMF44640,  $C_1$ .

DESCRIPTION.  $C_1$ . Enamel constricted to anterior one-quarter of tooth; curved slightly in occlusal view and is deepest one-third from

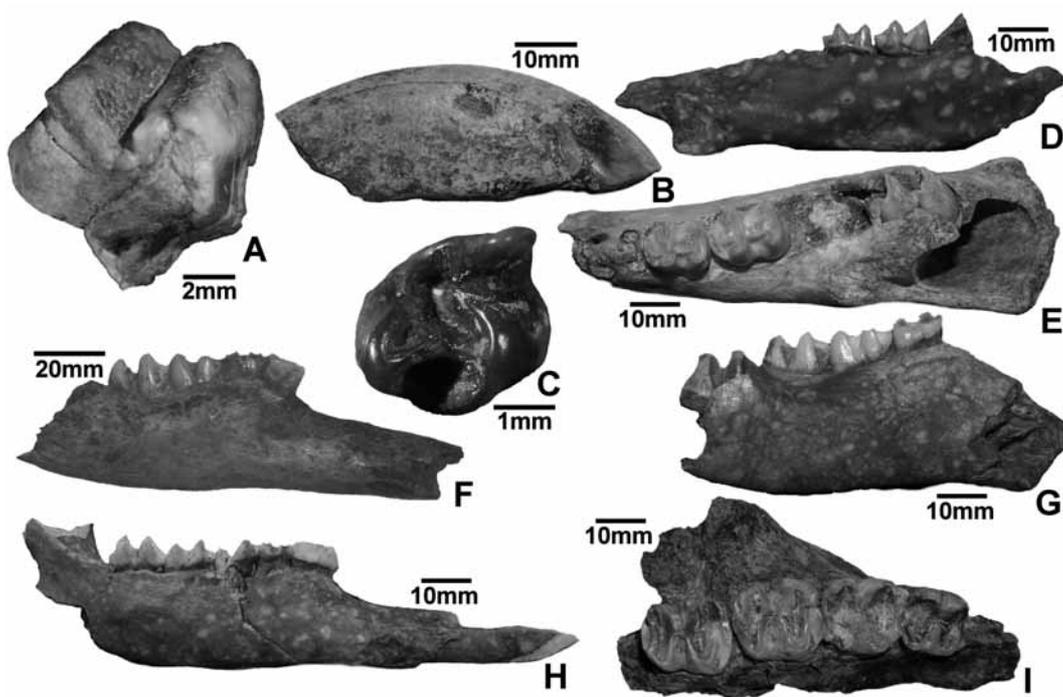


FIG. 10. A. *Diprotodon* sp.,  $P_3$ ; B. *Thylacoleo carnifex*,  $I^1$ ; C. *Aepyprymnus* sp.,  $M^3$ ; D. *Troposodon minor*, right dentary; E. *Procoptodon pusio*, left dentary; F. *Macropus agilis siva*, right dentary; G. *M. titan*, right dentary; H. *Protemnodon anak*, left dentary; I. *P. brehus*, right maxilla.

enamelised tip of tooth; root laterally compressed tapering to a blunt point.

REMARKS. QMF44640 compares well to the corresponding tooth of recent *Sarcophilus harissi* although is slightly larger and may represent the Pleistocene *S. lanianus*. [Ride, 1964]

Family THYLACINIDAE Bonaparte, 1838

**Thylacinus** Temminck 1824

**Thylacinus cynocephalus** (Harris, 1808)  
(Fig. 9D)

REFERRED MATERIAL. QMF44643,  $I_1$ .

DESCRIPTION.  $I_1$ . Markedly curved in lateral and occlusal view; enamel constricted to the anterior one-quarter of tooth and tapers to an acute point; deepest and broadest half way along length of entire tooth; root laterally compressed, deep, with posterior half tapering to an acute point.

REMARKS. QMF44643 is morphologically similar to the corresponding tooth of recent *Thylacinus cynocephalus*. [Ride, 1964]

Family DIPROTODONTIDAE Gill, 1872

**Diprotodon** Owen, 1838

**Diprotodon** sp.  
(Fig. 10A)

REFERRED MATERIAL. QMF44649,  $P_3$ .

DESCRIPTION.  $P_3$ . Sub-rectangular in occlusal outline; bilophid with lophs connected by a high lingual crest; anterior lophid markedly larger than posterior lophid; enamel thick with a worm-eaten punctate appearance.

REMARKS. *Diprotodon* sp. is distinguished from other diprotodontids by possessing a bilophodont lower premolar, with thick, punctated enamel. [Archer, 1977]

Family THYLACOLEONIDAE Gill, 1872

**Thylacoleo** Owen 1858

**Thylacoleo carnifex** Owen, 1858  
(Fig. 10B)

REFERRED MATERIAL. QMF44642,  $I^1$ .

DESCRIPTION.  $I^1$  markedly curved in occlusal view with enamel confined to anterior and lateral surface in a U shape; occlusal wear surface concave; root deep and laterally compressed.

REMARKS. *Thylacoleo carnifex* is distinguished from other members of the genus by its significantly larger size. [Wells et al., 1982]

Family POTOROIDAE Gray, 1821; sensu Archer & Bartholomai, 1978

**Aepyprymnus** Garrod, 1875  
**Aepyprymnus** sp.  
(Fig. 10C)

REFERRED MATERIAL. QMF44652,  $M^3$ .

DESCRIPTION.  $M^3$  metalophid low and very thin, but distinct; postmetacrista connects to posterior cingulum to form a very large and fairly deep pocket-like structure on posterior margin of tooth; premetacrista well defined.

REMARKS. Fragmentary material precludes a full comparison to *Aepyprymnus rufescens*, the only the only known member of the genus. [Tate, 1948]

Family MACROPODIDAE Gray, 1821  
Subfamily STHENURINAE Glauert, 1926

**Procoptodon** Owen 1874  
**Procoptodon pusio** (Owen, 1874)  
(Fig. 10E)

REFERRED MATERIAL. QMF44648, dentary.

REMARKS. *Dentary*. Short, deep and robust; buccal groove on ramus well defined.

*Lower molars*. Sub-rectangular in occlusal outline, with slight constriction in midvalley; base of molars swollen and lophids high, convex anteriorly; enamel crenulated, though smooth on lingual and buccal lateral surfaces; anterior cingulid is high, angled slightly lingually.

REMARKS. *Procoptodon pusio* is distinguished from other members of the genus by a combination of characters including: 1) its slightly smaller size, 2) lacking a distinct posthypocristid, and 3) less extensive transverse anterior portion of paracristid (Prideaux, 2004). The horizon from which the *P. pusio* material was collected is unknown. *Procoptodon* is restricted to Pleistocene deposits, though may have had its origins in the late Tertiary (Bartholomai, 1970; Prideaux, 2004). [Prideaux, 2004]

Subfamily MACROPODINAE Gray, 1821

**Troposodon** Bartholomai 1967  
**Troposodon minor** (Owen, 1877b)  
(Fig. 10D)

REFERRED MATERIAL. QMF44646-47, dentaries.

DESCRIPTION. *Dentary*. Shallow and gracile; symphysis elongate with ventral surface markedly lower than ventral surface of ramus. *Lower molars*. Subrectangular in occlusal outline, with slight kink in midvalley; lophids low, angled slightly lingually, and slightly concave anteriorly; preparacristid links to anterior cingulid; premetacristid descends anterolingually from metaconid to fuse with preparacristid.

REMARKS. *Troposodon minor* is placed within Macropodinae rather than Sthenurinae following Prideaux (2004). *T. minor* is easily distinguished from other members of the genus by being intermediate in size between the larger *T. kenti* and smaller *T. bowensis*. [Flannery and Archer, 1983]

**Macropus** Shaw 1790  
**Macropus agilis siva** (De Vis, 1895)  
(Fig. 10F)

REFERRED MATERIAL. QMF44638,  $I_1$ ; QMF44655, dentary; QMF44656-7, maxillary fragments.

DESCRIPTION. *Dentary*. Gracile, with groove on ventral surface of ramus extending from posterior of symphysis to below posterior root of  $M_2$ ; symphysis elongated and diastema long.  $I_1$ . Elongated and deeply rooted; slightly curved in both lateral and occlusal views.  $P_3$ . Elongated, blade-like; small ridges descend lingually and buccally from apex of longitudinal ridge.

*Lower molars*. Increase in size from  $M_{1-3}$ ; sub-rectangular in occlusal outline, with slight constriction in midvalley; hypolophid wider than protolophid; lophids high; cristid obliqua high; posterior cingulid absent.  $DP^2$  elongated, broad posteriorly; small ridges descend main crest; posterolingual fossette shallow.  $DP^3$  molariform; subrectangular in occlusal outline with slight constriction in midvalley; lophids low; metaloph wider than protoloph; posterior fossette moderately developed.  $M^1$  sub-rectangular in occlusal outline, with slight constriction in midvalley; high lophids; metaloph broader than protoloph; midlink moderately high; posterior fossette well developed.

REMARKS. *Macropus agilis siva* is distinguished from other members of the genus by possessing a combination of features including: 1) elongate diastema, 2) P<sub>3</sub> as long as M<sub>1</sub>, 3) lower molars high crowned, with high links, and lacking posterior cingula, 4) elongate upper premolars, and 5) upper molars elongated with high crowns, slight forelink and moderate midlink. [Bartholomai,1975]

**Macropus titan** Owen, 1838  
(Fig. 10G)

REFERRED MATERIAL. QMF44645, dentary.

DESCRIPTION. *Dentary*. moderately deep, the base of symphysis slightly lower than the base of horizontal ramus.

*Lower molars*. Sub-rectangular in occlusal outline, slightly constricted across talonid basin; lophids high and curved slightly anteriorly; forelink high, curving anteriorly to meet a high anterior cingulid; posterior fossette present on posterior loph.

REMARKS. *Macropus titan* is distinguished from other members of the genus by a combination of features including: 1) its large size, 2) elongate diastema, 3) high crowned, elongated lower molars with slightly curved lophids, high links and high anterior cingulum (Bartholomai, 1975). An additional dentary fragment, QMF44644, is referred to *M. sp. cf. M. titan*. The molars are within the size range of *M. titan*, however it differs in that: 1) the dentary is markedly more robust and deep, 2) forelink is slightly lower, 3) anterior cingulid broader, and 4) cristid obliqua is higher. [Bartholomai,1975]

**Protemnodon** Owen 1874  
**Protemnodon anak** (Owen, 1874)  
(Fig. 10H)

REFERRED MATERIAL. QMF44650, skull; QMF44658, dentary.

DESCRIPTION. *Dentary*. Moderately shallow, with elongated symphysis ascending anteriorly at low angle; mental foramen oval shaped, close to diastemal crest. P<sub>3</sub>. Elongated, blade-like; exceeds length of M<sub>1</sub>.

*Lower molars*. Sub-rectangular in occlusal view with slight constriction in midvalley; lophids high, concave anteriorly with high forelink; posterior cingulid small P<sub>3</sub>. Elongate; crown concave buccally; high longitudinal crest, slightly concave buccally; transected by four vertical blades.

*Upper molars*. Sub-rectangular in occlusal outline, slightly constricted across mid valleys; midlink strong; forelink absent; anterior cingulum slightly swollen.

REMARKS. *Protemnodon anak* is distinguished from other Pleistocene members of the genus by a combination of characters including: 1) small size, 2) P<sub>3</sub> elongate, concave buccally, with high longitudinal crest, and longer than M<sub>4</sub>, 3) M<sub>3</sub> and M<sub>4</sub> lacking cuspules in the lingual portion of the midvalley. [Bartholomai,1973]

**Protemnodon brehus** (Owen, 1874)  
(Fig. 10I)

REFERRED MATERIAL. QMF44627, maxilla.

DESCRIPTION. *Upper molars*. Sub-rectangular in occlusal outline, slightly constricted across midvalley; anterior cingula broad; forelink absent; strong ridge curves from paracone into crista obliqua.

REMARKS. *Protemnodon brehus* is distinguished from other members of the genus by: 1) its large size, and 2) lacking a lingual cuspule in the midvalley of M<sup>3-4</sup>. [Bartholomai,1973]

Order RODENTIA Bowdich, 1821.  
Family MURIDAE Illiger, 1811

**Pseudomys** Gray 1832  
**Pseudomys** sp. 1 & 2  
(Fig. 11A)

REFERRED MATERIAL. Sp. 1: QMF44609-10, maxillae; Sp.2: QMF48168, maxilla.

DESCRIPTION. *Maxilla*. Anterior portion of zygomatic arch not broadened; molar alveoli pattern 3(M<sup>1</sup>) 3(M<sup>2</sup>) 3(M<sup>3</sup>). M<sup>1</sup>. Relatively elongate; T7 absent; three rooted, with one lingual root.

REMARKS. *Pseudomys* sp. 1 and 2 could not be identified to specific level considering the nature of the fragmentary remains. *Pseudomys* sp. 1 fits within the size class of extant *P. australis*. *Pseudomys* sp. 2 is smaller, approximating the size of extant *P. delicatulus*. [Jones & Baynes,1989]

**Rattus** sp. (Fischer, 1803)  
(Fig. 11B)

REFERRED MATERIAL. QMF44611-12, isolated molars; QMF44613-14, maxillae.

DESCRIPTION. M<sup>1</sup>. Cusps rounded in occlusal outline; two lingual cusps; five rooted, with two

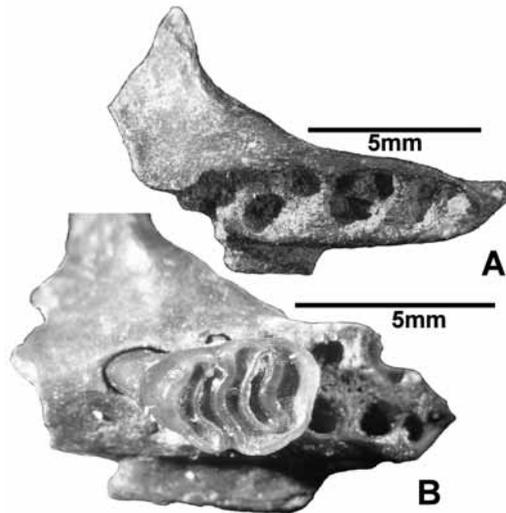


FIG. 11. A. *Pseudomys* sp. 1, left maxilla; *Rattus* sp., left maxilla.

lingual alveoli.  $M^2$ . Four rooted, arranged in a square pattern.

REMARKS. *Rattus* spp. are distinguished from other murid genera by possessing an  $M^2$  that has four roots, arranged in a square pattern (Knox, 1976). [Jones & Baynes, 1989]

#### MATERIAL ASSIGNED TO OTHER TAXA

Teleostei fam. gen. et sp. indet. (Fig. 8A); QMF44634-36, vertebrae.

*Limnodynastes tasmaniensis* (Gnther, 1858) (Fig. 8B); QMF43978-43985, ilia.

*L.* sp. cf. *L. dumerili* (Peters, 1863) (Fig. 8C); QMF43995-43997, ilia.

?*Limnodynastes* (Fitzinger, 1843)(Fig. 8D); QMF44000, ilium.

*Neobatrachus sudelli* (Lamb, 1911) (Fig. 8E); QMF44001-44002, ilia,

*Kyarranus* sp. (Fig. 8F); QMF44003, ilium.

Chelidae gen. et sp. indet. (Fig. 8G); QMF44626; QMF44641, carapace fragments.

*Perameles bougainville* (Quoy & Gaimard, 1824) (Fig. 9E); QMF44549,  $RM_1$ .

*Perameles nasuta* (Geoffroy, 1804) (Fig. 9F); QMF44566,  $LM_3$ .

#### ECOLOGICAL REMARKS

Elements of the fauna are here listed with minor pertinent ecological comments as appropriate.

MOLLUSCS. The invertebrate fauna is rich and diverse. Four families of land snails are represented, comprising seven species, as well as two families of freshwater snails, containing two species (J. Stanisic, pers. comm.). Freshwater bivalves are also common throughout the main fossiliferous units.

***Velesunio ambiguus*** (Philippi, 1847): This most common species of the Australian Unioniidea, occurs in coastal and interior rivers throughout South Australia, Victoria, New South Wales and Queensland (Lamprell & Healy, 1998). *Velesunio ambiguus* is a typical floodplain species commonly found in billabongs and creeks; it rarely occurs in large rivers, except in the vicinity of impoundments (Sheldon & Walker, 1989). The exclusion of *V. ambiguus* from larger rivers probably reflects its weak anchorage (Sheldon & Walker, 1989).

Extant populations of *Velesunio ambiguus* are common throughout the creeks and tributaries of the Darling Downs. Additionally, *V. ambiguus* has been recorded from the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

***Corbicula (Corbiculina) australis*** (Deshayes, 1830): *C. (C.) australis* occurs in coastal and inland rivers and streams. It is a hermaphroditic species that has a benthic crawling larva that makes it possible for *C. (C.) australis* to spread rapidly (Britton & Morton, 1982).

Extant *C. (C.) australis* are common throughout water courses of the Darling Downs. Additionally, *C. (C.) australis* has been reported from the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

***Thiara (Plotiopsis) balonnensis*** (Conrad, 1850): *T. (P.) balonnensis* was the most common identifiable species recovered from the deposit. It was collected in-situ from shell beds up to 10cm thick. It is the most widespread of the Australian thiraidids, common throughout the Murray-Darling River system.

Extant populations commonly occur in ponds, dams and rivers (Smith & Kershaw, 1979). Extant populations of *Thiara (Plotiopsis) balonnensis* are present on the Darling Downs. *Thiara (P.)* sp. has been reported from the fossil record of the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

***Gyraulus gilberti*** (Dunker, 1848): Planorbids are a common Australian family of freshwater snails. The Planorbidae are confined to waters with low salinity and are generally associated with macrophytes or algae. *Gyraulus* has been

## DARLING DOWNS PALAEOECOLOGY

reported in the Tertiary fossil record of northern Australia (McMichael, 1968).

**Saladelos** sp.: *Saladelos* sp. commonly occur in closed to open forest to vine thicketed habitats (J. Stanisic pers. comm.).

**Strangesta** sp.: *Strangesta* sp. commonly occur under dry, dense ground cover in dry forest to woodland scrub, and vine thickets (Smith & Kershaw, 1979; J. Stanisic pers. comm.).

**Coenocharopa** sp.: *Coenocharopa* sp. are generally found in warmer temperate forest thickets to cool, dry, sub-tropical notophyll vine forests from the central to north eastern coast of the Australian continent (Stanisic, 1990).

**Gyrocochlea** sp. 1 and 2: Members of *Gyrocochlea* typically inhabit dry to humid sub-tropical vine forests and prefer to live under logs (Stanisic, 1990). Like most charopids, *Gyrocochlea* sp. are common throughout central eastern Australia (Stanisic, 1990).

**Austrosuccinea** sp.: *Austrosuccinea* are land snails that are found in a variety of habitats ranging from marches and swampy environments, to sand dunes and seasonally dry stream basins (Solem, 1993).

**Xanthomelon pachystylum** (Pfeiffer, 1845): Camaenids are among the most diverse of Australian land snails. The Australian camaenid fossil record is scant with only a few known records (Ludbrook, 1978, 1984; McMichael, 1968; Kear et al., 2003). *X. pachystylum* is a herbivorous species associated with dense vine thickets (J. Stanisic, pers. comm.).

### AMPHIBIANS

**Limnodynastes tasmaniensis** (Gnther, 1858): Extant *L. tasmaniensis* populations are common over much of eastern Australia and have been recorded in a range of habitats ranging from wet coastal environments to dry, arid regions (Cogger, 2000).

Extant populations of *L. tasmaniensis* have been recorded from the Darling Downs (Ingram & Longmore, 1991).

**L.** sp. cf. **L. dumerili** (Peters, 1863): Extant populations have been recorded in most habitats, with the exception of alpine areas, rainforest, and extremely arid zones (Cogger, 2000).

Extant populations of *L. dumerili* have been recorded from the Darling Downs (Ingram & Longmore, 1991).

**Neobatrachus sudelli** (Lamb, 1911)

Extant populations of *Neobatrachus sudelli* occur throughout southeastern Australia, commonly occurring in open woodlands with grassy understories (Cogger, 2000).

**Kyarranus** sp.

Extant *Kyarranus* populations occur in areas of dense ground cover and thickets in isolated montane forest patches on the Great Dividing Range in southeastern Queensland and northeastern New South Wales (Tyler, 1991).

### REPTILES

**Tympanocryptis “lineata”** (Peters, 1863): Extant *T. lineata* populations occur in a variety of semi-arid to arid environments in central Australia. *T. lineata* commonly occur in earth cracks, grass or ground litter on desert sandhills, to black soil plains (Cogger, 2000).

Extant *T. lineata* populations have been recorded from the Darling Downs (Covacevich & Couper, 1991). Additionally, agamids have previously been recognised in the Darling Downs fossil record (Bennett, 1876; Lydekker, 1888; Molnar & Kurz, 1997).

“**Sphenomorphus** Group” sp. 1 and 2: The ecology of extant members of the *Sphenomorphus* group is varied and includes taxa that burrow in soil, burrow under leaf litter, have semi-amphibious lifestyles and others that are found in rocky arid environments (Cogger, 2000).

**Tiliqua rugosa** (Gray, 1825a): Extant populations of *T. rugosa* are found in a range of habitats including coastal heaths, dry sclerophyll forest, woodlands, mallee, and arid *Acacia* and eucalypt scrublands. *T. rugosa* shelters under fallen timber and leaf litter spinifex when inactive (Cogger, 2000).

**Cyclodomorphus** sp.: *Cyclodomorphus* spp. are ground dwelling skinks, although commonly climbs on low growing vegetation. Extant *Cyclodomorphus* populations have been recorded from wet to dry sclerophyll forest, commonly found under leaf litter or areas with low ground cover (Cogger, 2000).

**Varanus** sp.: Extant *Varanus* sp. populations have been recorded in a wide range of habitats from deserts to rainforest, and may have semi-aquatic, terrestrial, or arboreal locomotive strategies.

Extant *Varanus* populations have been recorded from the Darling Downs (Covacevich & Cooper, 1991). Additionally, *Varanus* sp. has

been recorded from the Pleistocene Darling Downs (Wilkinson, 1995).

**Megalania prisca** (Owen, 1860): Molnar (1990) suggested that *M. prisca* was unlikely to have been arboreal, though it may have had a semi-aquatic life style.

*Megalania prisca* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997).

**Other elements:** Indeterminate chelid and elapid remains have been found in the deposit.

#### MARSUPIALS

**Sminthopsis** sp.: Extant *Sminthopsis* spp. populations occur in open to closed habitats (Strahan, 1995).

Extant populations of *S. murina* have been recorded on the Darling Downs (Van Dyck & Longmore, 1991).

**Dasyurus** sp.: *Dasyurus maculatus* is the largest extant native mammalian carnivore on the mainland of Australia. *Dasyurus* spp. are partly arboreal and occur on the eastern margin of the continent and Tasmania in a wide range of wooded habitats including rainforests, open forests, woodlands, and riparian forest. Den sites commonly include caves, rock crevices and hollow logs.

**Sarcophilus** sp.: Once common over the central and eastern portions of the Australian continent, *Sarcophilus* is now restricted to Tasmania where it is abundant in dry sclerophyll forest and woodlands that are interspersed with grasslands (Jones, 1995).

**Thylacinus cynocephalus** (Harris, 1808): Prior to European arrival in Australia, extant *T. cynocephalus* was restricted to Tasmania before over hunting led to its subsequent extinction. *T. cynocephalus* was once common in open forest and woodland (Dixon, 1989).

**Perameles bougainville** (Quoy & Gaimard, 1824): Extant populations of *P. bougainville* are restricted to Bernier and Dorre Islands, Shark Bay, Western Australia, although once occurred over much of semi-arid Australia (Friend & Burbidge, 1995). Extinction on the mainland has been attributed to the effects of habitat disturbance and introduction of non-native predators by Europeans. *P. bougainville* was once common on the mainland in a range of habitats including dense scrub thickets, open saltbush plains and stoney ridges bordering scrubland (Friend & Burbidge, 1995).

**Perameles nasuta** (Geoffroy, 1804): Extant *Perameles nasuta* populations occur in a wide range of habitats including rainforests, wet to dry woodlands, and areas with very little ground cover (Stoddart, 1995). It is a common and widely distributed species with a wide range of habitat tolerances, and its presence in the fossil record is of little palaeoenvironmental significance.

Extant *Perameles nasuta* populations are common on the Darling Downs.

**Diprotodon** sp.: *Diprotodon* spp. are generally regarded browsers of shrubs and forbs and probably occupied an open woodland to savanna habitat (Murray, 1984).

**Thylacoleo carnifex** (Owen, 1858) : *T. carnifex* may have occupied an open forest habitat (Murray, 1984). *T. carnifex* filled the 'large cat' niche of the Australian Pleistocene, and may have had the ability to kill *Diprotodon*-sized animals (Wroe, et al., 1999). The lower incisor functioned as a stabbing or piercing tooth that occludes with the upper incisors where it acts as an anvil against which food is restrained (Wells et al. 1982).

*T. carnifex* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997).

**Aepyprymnus** sp.: Extant *A. rufescens* populations occur in a variety of habitats ranging from wet sclerophyll to dry open woodlands, but only occupy areas with sparse grassy understories commonly adjacent to areas of dense undergrowth (Dennis & Johnston, 1995).

**Procoptodon pusio** (Owen, 1874): *Procoptodon* spp. were adapted for a diet of highly fibrous vegetation (Prideaux, 2004).

*P. pusio* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997; Prideaux, 2004).

**Troposodon minor** (Owen, 1877b): *Troposodon minor* is generally regarded as a semi-browser (Bartholomai, 1967). Flannery & Archer (1983) suggested that at least two species of *Troposodon* occurred sympatrically at most Plio-Pleistocene localities. However, *T. minor* remains the only member of the genus recorded at QML1396.

*Troposodon minor* is relatively common in Pleistocene Darling Downs deposits (Molnar & Kurz, 1997).

**Macropus agilis siva** (De Vis, 1895): Extant *Macropus agilis* populations favour savannah woodland or open forest habitats (Bell, 1973).

*M. a. siva* was common and widespread on the Pleistocene Darling Downs (Molnar & Kurz, 1997).

**Macropus titan** (Owen, 1838): The high crowned molars *M. titan* are typical of grazing species (Bartholomai, 1975).

*M. titan* was one of the most common and widespread megafauna species on the Darling Downs, being recorded from 21 fossil deposits (Molnar & Kurz, 1997).

**Protemnodon anak** (Owen, 1874),

**Protemnodon brehus** (Owen, 1874): *Protemnodon* spp. are regarded as grazers (Bartholomai, 1973).

*P. anak* and *P. brehus* have been recorded from over 30 fossil localities on the Darling Downs (Molnar & Kurz, 1997).

#### RODENTS

**Pseudomys** sp. 1 & 2: Extant *Pseudomys* spp. populations occur in a wide variety of habitats from sparsely vegetated deserts to closed sclerophyll forests (Strahan, 1995). Until the taxonomy of the Pleistocene Darling Downs *Pseudomys* spp. is better known, their palaeoenvironmental significance will remain unclear.

*Pseudomys* spp. have been recorded from the Pleistocene Darling Downs (Archer & Hand, 1984).

**Rattus** sp.: In terms of abundance and diversity, *Rattus* is the most diverse extant murid genus in Queensland. Extant *Rattus* populations are found in a number of habitats including rainforests, woodlands, and savanna grasslands.

Extant *Rattus* spp. populations (native and introduced) have been recorded from the Darling Downs (Covacevich & Easton, 1974). Additionally, *Rattus* sp. has been reported from the Pleistocene Darling Downs (Archer & Hand, 1984).

#### DATING

The AMS<sup>14</sup>C dating results of freshwater bivalves and charcoal indicate that deposition of Horizon B occurred 44300±2200 to >49900 and Horizon D at 45150±2400 (Table 9). However, those results should be considered as minimum ages only considering the fact that the QML1396 assemblage appears to be close the limits of the AMS<sup>14</sup>C dating technique. Owing to the importance associated with dating late Pleistocene megafauna extinction and climate

TABLE 9. AMS <sup>14</sup>C dating results of charcoal and *Velesunio ambiguus* samples from QML1396. Ages quoted are radiocarbon ages, not calendar ages. Ages rounded according to Stuiver & Polach (1977)

ANSTO code	sample	horizon	conventional <sup>14</sup> C age ± 2σ error
OZG855	charcoal	D	45150 ± 2400
OZG547	bivalve	B	>49900
OZG548	bivalve	B	44300 ± 2200

change, it is desirable to further test the dating results presented here.

#### DISCUSSION

**SEDIMENTOLOGY.** The deposit represents both high velocity lateral channel deposition and low velocity vertical accretion. The lower fossiliferous unit, Horizon B, represents the most significant input of sandy deposits in the sedimentary environment. Horizon B is laterally continuous for more than 70 metres. However, the horizon is largely unexposed and positioned below the modern water table, therefore the precise lateral extent of Horizon B is unknown. Horizon B is characterised by: 1) abundant freshwater mollusc fossils, including large-sized bivalves; 2) vertebrate fossils; 3) fluviually transported sediments (including rounded basalt, calcrete and sandstone pebbles and cobbles); and 4) upwardly fining grain size. The geometry of Horizon B and the interpreted sedimentary processes suggest that deposition took place in the main channel. Horizon B accumulated under higher velocity deposition than Horizon D considering the significantly larger grain sizes and preponderance of larger-sized bivalves (Fig. 2, Table 1).

The fine brown-grey clay unit, Horizon C, suggests a period of low velocity deposition. Mollusc shells are rare, however, freshwater gastropods (*Thiara (Plotiopsis) balonnensis*) are slightly more common than freshwater bivalves. The presence of freshwater molluscs in the horizon are consistent with the proximity to the channel.

Horizon D is laterally continuous for approximately 30 metres. Horizon D is characterised by: 1) discontinuous lenticular sandy and shelly beds; 2) mud cracks in-filled with fine clays; 3) vertebrate fossils; and 4) fluviually transported sediments (including rounded basalt, calcrete and sandstone pebbles). The facies association of lenticular shelly beds

overlies the low velocity brown-grey clay unit (in continuity with the channel deposit). Freshwater gastropods in Horizon D show polymodal current directions indicating that they were not deposited as traction load in flowing water. The data suggest that deposition occurred as overbank deposits on the floodplain adjacent to the channel belt. A succession of several small overbank depositional events created superposed shelly lenses up to 100mm thick. The depositional setting of Horizon D is interpreted as representing a series of small crevasse splays and subsequent drying pools in the overbank that resulted from minor flood events. It is hypothesised that as the pools evaporated, stranded gastropods moved into the deeper parts of the pools (hence showing polymodal orientations) eventually dying when the pools evaporated.

Overlying fine-grained deposits of the upper units represent vertical accretion on the floodplain (Fig. 2, Table 1). The occurrence of iron nodule formation in the upper units of the profile reflect alternating periods of oxidation and reducing conditions due to watertable fluctuations. Additionally, in-situ, white to brownish-grey mottled calcrete formation in the upper units is related to similar watertable fluctuations. Mottled calcretes are chemically precipitated in the freshwater phreatic zone of the watertable, and are primarily related to the lateral movement and percolation of alkaline waters in the soil profile (Arakel & McConchie, 1982). The close association of the formation of in-situ mottled calcretes and ferruginous oxides are indicative of a response to an increasingly arid environment, subsequent to deposition of the major fossiliferous horizons.

#### TAPHONOMIC HISTORY OF BONES.

Numerous unidentifiable bone fragments recovered from the deposit exhibited a range of abrasion and weathering characteristics. However, the following taphonomic conclusions are largely based on identifiable vertebrate remains horizons B and D. Better preserved specimens may yield more accurate palaeobiological and palaeoecological information than unidentifiable fragments. However, it is recognised that some components of the assemblage may have had different taphonomic pathways leading to their final deposition.

It is unlikely that acidic ground waters have played a role in the diagenesis of fossil material

from either horizon, considering the high degree and diagenetically unaltered preservation of calcareous material (i.e. mollusc shell and calcrete) that has been identified in the deposit. Additionally, root etching of vertebrate fossil material was not observed. Few of the identifiable specimens indicate any significant pre-burial weathering (*sensu* Behrensmeyer, 1978).

There were several biases in the preservation of different faunal groups and skeletal elements observed in the deposit. For squamates, there was a noticeable lack of post-cranial material preserved in the deposit in comparison to mammals. Similar biases between terrestrial non-mammals and mammals have been identified within fossil deposits of the Koobi Fora Formation of Kenya (Behrensmeyer, 1975). Additionally, within the Agamidae and Scincidae, differences were observed in the preservability of cranial and dental elements. The differences may be related to minor differences in bone density or structure. However, few previous studies have addressed the causes of such preservational biases, focusing predominantly on the accumulation of fossil mammals. In the absence of comparative data on squamate transportability and preservability in fluvial systems, it is difficult to explain such biases in the fossil record.

Large-sized mammals are better preserved in Horizon B than Horizon D, but small-sized taxa are generally absent from Horizon B. Bones and shells act as sedimentary particles in fluvial systems and may have settling velocities that are related to equivalent-sized spherical quartz grains (Behrensmeyer, 1975). Therefore, if the size of bone and shells are relative to the size of the surrounding grains, then coarse-grained units such as Horizon B would be expected to contain larger-sized skeletal elements or species than finer-grained units such as Horizon D. That hypothesis may equally explain: 1) why large-sized bivalves are more common in Horizon B than Horizon D; 2) why the Horizon B assemblage is dominated by large-sized vertebrates, and Horizon D by small-sized vertebrates; and 3) the differences between the relative abundance of skeletal elements of large and small mammals within Horizon D.

Assemblages of both horizons are generally characterised by: 1) low levels of post-crania; 2) high degrees of bone breakage; 3) low degrees of abrasion; and 4) low degrees of weathering. A

comparison of the abundance of skeletal elements to experimental data of skeletal element transportability in fluvial systems indicates that both units contain elements that are among the last to be transported in flowing water. That suggests that horizons B and D represent bone lag deposits. The high degree of breakage of skeletal elements suggests that the vertebrate remains were subjected to considerable forces. Additionally, the loss of limb bone ends may reflect a density mediated destruction of lower-density bone (distal and proximal ends) and that the higher-density bone shafts were not destroyed (Rapson, 1990). The low degree of bone abrasion and low degree of pre-burial weathering indicate that the vertebrates died within close proximity to the final point of deposition and were probably buried rapidly after death. Additionally, no elements were recovered that show the effects of digestion, polishing or gnawing that may be attributable to predator accumulation (sensu Andrews, 1990; Sobbe, 1990). Collectively, the data indicate that the vertebrate material was accumulated and fluvially transported into the deposit from the surrounding proximal floodplain.

#### PALAEOENVIRONMENTAL INTERPRETATION

Megafauna species are less abundant and less well preserved in Horizon D (low-energy overbank deposition) than Horizon B (high-energy channel deposition), and all vertebrate taxa smaller than *Sarcophilus* sp. (~8 kg) are absent from Horizon B (Figure 6). Three hypotheses could explain the faunal differences: 1) Megafauna went locally extinct progressively between the time of deposition of Horizons B and D (the age of the two QML1396 assemblages may bracket the terminal extinction event of the Australian megafauna [~46ka; Roberts et al., 2001a]); 2) Sampling by the creek system was biased towards the collection of small-sized species in Horizon D; or 3) Larger-sized bones may not have been able to be transported into overbank deposits from flood events (large bones in the overbank deposits may be derived directly from the proximal floodplain rather than from fluvial transport). Additionally, a third of the large-sized taxa that are present in Horizon B, but absent from Horizon D, are carnivorous species (*Sarcophilus* sp., *Thylacinus cynocephalus* & *Thylacoleo carnifex*; Table 2). Hence, the rarity of carnivorous taxa in the Pleistocene Darling Downs might be assumed regardless. However,

TABLE 10. Preferred and inferred habitat types of extant and fossil taxa recorded from Horizon B. (\* Extinct on Darling Downs; \*\* Totally extinct).

Species	freshwater	open woodland	open grassland
<i>Velesunio ambiguus</i>	x		
<i>Corbicula (Cobiculina) australis</i>	x		
<i>Thiara (Plotiopsis) balonnensis</i>	x		
<i>Sarcophilus</i> sp.*		x	
<i>Thylacinus cynocephalus</i> **		x	
<i>Diprotodon</i> sp.**		x	x
<i>Thylacoleo carnifex</i> **		x	
<i>Troposodon minor</i> **		x	
<i>Macropus agilis siva</i> **		x	
<i>M. titan</i> **		x	x
<i>Protemnodon anak</i> **		x	x
<i>P. brehus</i> **		x	x

considering the taphonomic sampling biases of the Pleistocene channel, it is difficult to accurately compare habitat and species differences between the Horizon D and B assemblages, and hence, directly demonstrate the extinction of megafauna temporally based on data from QML1396.

Large-sized taxa previously used to make interpretations about Darling Downs Pleistocene palaeoenvironments are present in the Horizon B assemblage, thus in agreement with previous broad interpretations of a woodland and open grassland Pleistocene habitat (Table 10). All of the mammals recorded from Horizon B are either locally or totally extinct.

The Horizon D assemblage consists of large and small-sized taxa that are extant, locally or totally extinct. The small-sized faunas have revealed a series of increasingly complex terrestrial habitats, some that have not previously been documented in the Pleistocene Darling Downs. It appears that at the time of deposition of Horizon D, a suite of habitats existed that consisted of grasslands, open woodlands with grassy understories, and scrubby vine-thicketed habitats (Table 11). A scrubby vine thicketed habitat is indicated predominantly by the diverse land snail fauna. That interpretation is additionally supported by the presence of *Kyarranus*, a frog genus whose extant members are restricted to dense understories and thickets. Vine thickets are common on the Great Dividing

TABLE 11. Preferred and inferred habitat types of extant and fossil taxa from Horizon D. (\* Extinct on Darling Downs; \*\* totally extinct).

species	freshwater	vine-thicket	scrubland	closed woodland	open woodland	open/ grassland
<i>Velesunio ambiguus</i>	X					
<i>Corbicula (Cobculina) australis</i>	X					
<i>Thiara (Plotiopsis) balonnensis</i>	X					
<i>Gyraulus gilberti</i> *	X					
<i>Coencharopa</i> sp.*		X				
<i>Gyrocochlea</i> sp. 1*		X				
<i>Gyrocochlea</i> sp. 2*		X				
<i>Austrocccinea</i> sp.*	X				X	X
<i>Xanthomelon pachystylum</i> *		X				
<i>Strangesta</i> sp.*		X	X			
<i>Saladelos</i> sp.*		X				
Teleost	X					
<i>Limnodynastes tasmaniensis</i>		X	X	X	X	X
<i>L. sp. cf. L. dumerili</i>		X	X	X	X	X
? <i>Limnodynastes</i>		X	X	X	X	X
<i>Neobatrachus sudelli</i> *					X	X
<i>Kyarranus</i> sp.*		X		X		
Chelid	X					
<i>Tympanocryptis "lineata"</i> *						X
" <i>Sphenomorphus</i> Group" sp. 1		X	X	X	X	X
" <i>Sphenomorphus</i> Group" sp. 2		X	X	X	X	X
<i>Tiliqua rugosa</i> *			X		X	X
<i>Cyclodomorphus</i> sp.*		X	X	X	X	
<i>Varanus</i> sp.	X	X	X	X	X	X
<i>Megalania prisca</i> **	X				X	X
Elapid	X	X	X	X	X	X
<i>Sminthopsis</i> sp.		X	X	X	X	X
<i>Dasyurus</i> sp.				X	X	
<i>Perameles bougainville</i> *		X	X			
<i>Pe. nasuta</i>		X	X	X	X	X
<i>Aepyprymnus</i> sp.					X	
<i>Macropus agilis siva</i> **					X	
<i>M. titan</i> **					X	X
<i>Protemnodon anak</i> **					X	X
<i>Pr. brehus</i> **					X	X
<i>Pseudomys</i> sp.*		X	X	X	X	X
<i>Rattus</i> sp.		X	X	X	X	X

Range today and support a similar land snail fauna (J. Stanisc, pers. comm.). Additionally, scrubby and closed habitats have previously been suggested for late Pleistocene deposits of the

Kings Creek catchment (Price, 2004; Price et al., in press). Woodlands were likely to have been open sclerophyll, interspersed with sparse grassy understories. That interpretation is highlighted by the presence of taxa such as *Austrocccinea* sp., *Neobatrachus sudelli*, *Aepyprymnus* sp., and *Macropus agilis siva*. Grasslands were likely dominated by large browsing macropods including *Macropus titan* and *Protemnodon* spp. Small agamid lizards such as *Tympanocryptis lineata* probably occupied a similar open habitat, utilizing the earth cracks within black soils.

There are few modern analogues to explain the high habitat diversity indicated by the fauna represented in the Horizon D assemblage. However, considering the relatively constrained sampling area of the Kings Creek palaeo-catchment, it is unlikely that the diverse QML1396 assemblage resulted from the sampling of wide geographic areas outside the immediate catchment area (i.e. by long distance fluvial transport). Additionally, taphonomic data indicates that while the assemblage was hydraulically transported, the components were unlikely to have been transported over long distances. Collectively, those data suggest that a mosaic of grassland, sclerophyllous woodlands, and scrubby vine-thicketed habitats were present within the geographically small Pleistocene Kings Creek catchment. Non-analogue associations of taxa (sensu Lundelius, 1989, as 'disharmonious' associations) from other sites in the Kings Creek catchment (e.g. bandicoots from QML796) support the hypothesis that a vegetative mosaic of habitats was present during the late Pleistocene (Price, 2004).

Comparison of such Pleistocene habitats to those of the modern Kings Creek catchment is difficult considering extensive pastoral activities which have altered natural vegetation in the region since the early 1840's. Even where natural remnant vegetation survives, its current structure and floristics do not necessarily reflect its pre-settlement character. However, a review of over 5,000 land surveys from periods of the initial settlement of the Darling Downs indicates that the region surrounding the immediate area of deposition of QML1396 was dominated by grasslands, with *Eucalyptus orgadophila* woodlands with grassy or shrubby understories being found closer to the range (Fensham & Fairfax, 1997). Based solely on the numbers of different species representing the interpreted Pleistocene habitats of QML1396, it is evident that taxa indicating open grassland habitats are

the minority, and that species favouring woodlands and scrubby, vine thicketed habitats dominate the assemblage (Tables 10 & 11). It is hypothesised that the immediate area surrounding the Pleistocene watercourse was dominated by woodlands, scrublands and vine thickets, and that open grasslands were situated farther away from the creek. That interpretation suggests that there must have been significant environmental change between the time of deposition of QML1396 and present, and that would have reflected contraction of woodlands and vine thickets closer to the range, and expansion of grasslands in the catchment area.

Deposition of the QML1396 assemblage occurred around the time of the extinction of the Australian megafauna, i.e. ~46ka (Roberts et al., 2001a). Hence, it is an extremely important Pleistocene assemblage as it provides detailed information about habitats and environments during a critical period for Australian megafauna. The two major hypotheses surrounding the extinction of Australian megafauna are: 1) a naturally driven climate change that coincided with the last glacial maximum, and reduced viable habitats for megafauna, and 2) anthropogenic overkill of megafauna or modification of habitats during initial colonisation of the continent during the late Pleistocene (Martin & Klein, 1984; Diamond, 2001; Roberts et al., 2001a; Brook & Bowman, 2004; Barnosky et al., 2004; Wroe et al., 2004). While there are numerous examples documenting increasing aridity and less fertile habitats during the late Pleistocene (Ayliffe et al., 1998; Bowler et al., 2001; Field et al., 2002; Pack et al., 2003), there are very few examples linking early human artifacts directly to megafauna (Roberts et al., 2001a). One source of confusion has been that important archaeological sites such as Lake Mungo and Koonalda Cave have yielded meager faunal data. Cuddie Springs, New South Wales, is the only site in Australia that shows evidence of a dated association between human technology and megafauna (Dodson et al., 1993). Fossil bone exhibiting human processing marks were dated to 36-27 ka (Field & Dodson, 1999). However, the association between the artifacts and megafauna remains was questioned by Roberts et al. (2001a) who suggested: 1) that sediment mixing and re-deposition of bones from older to younger units had occurred, and 2) the cut marks on the bones relate to an extant species of kangaroo. Although there is little systematic evidence to suggest an anthropogenic component

to Australian megafauna extinction, Flannery (1990) argued that because of the rapid nature of an overkill 'blitzkrieg' extinction, kill sites are unlikely to be found. Additionally, timing the arrival of the first humans and extinction of the megafauna has been impeded by a lack of reliable dates (Baynes, 1999; Diamond, 2001; O'Connell & Allen, 2004). On the Darling Downs, there is no evidence of human occupancy prior to 12ka (Gill, 1978). From sedimentological and ecological data, it is evident that increasing aridity on the Darling Downs during the late Pleistocene may have led to woodland and vine thicket habitat contraction, and grassland expansion on the floodplain. Such habitat change was likely detrimental to the persistence of megafauna species on the Darling Downs during the late Pleistocene. However, at present there is no direct evidence to support a hypothesis of an anthropogenic component relating to the retraction of habitats on the Darling Downs between the Pleistocene and present.

## CONCLUSIONS

Systematic collecting targeting both large and small-sized species has facilitated the recovery of a wide variety of fossil taxa, many previously unknown in the Darling Downs fossil record. First Pleistocene Darling Downs records include: pulmonates (7 terrestrial species, 1 aquatic species), *Tympanocryptis "lineata"*, scincids (4 species), and *Sminthopsis* sp. Additionally, several of those new records indicate Pleistocene geographic range extensions.

It has been assumed that the Pleistocene Darling Downs represents a single local fauna with no faunal regionalisation (Molnar & Kurz, 1997). That may appear to be true for larger megafauna taxa, but the small-sized fossil faunas are poorly known at most sites owing to the lack of systematic treatment. Hence, additional systematically collected and dated sites are required to test the hypothesis proposed by Molnar and Kurz (1997), that the Darling Downs represents a single local fauna.

The habitats deduced for the time of deposition of Horizon D appear to be more floristically complex than that of Horizon B. However, analysis of the Pleistocene channel deposits have revealed several taphonomic biases relating to the preservation of large- and small-sized taxa within and between those horizons. Such biases limit palaeoenvironmental comparisons between those two units.

It is evident that there was major habitat change in the Kings Creek floodplain post-deposition of the two major fossiliferous horizons at QML1396. That habitat change likely reflected the contraction of woodlands, vine thickets and scrublands, and expansion of grasslands on the floodplain. Sedimentological and ecological data suggest that that habitat change was climatically driven and occurred irrespective of potential human occupation of the region during the late Pleistocene.

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