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Taphonomy of Oligo-Miocene fossil sites of the Riversleigh World Heritage Area, Australia

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Abstract. Taphonomic analyses were carried out on six sites from the Riversleigh World Heritage Area fossil deposits of northwestern Queensland, Australia. The six sites range in age from late Oligocene to late Miocene and possibly younger. A diverse fossil fauna has been found at these sites, but in this study, only mammalian remains were considered. The aim was to assess the biological and ecological information obtainable from these sites in anticipation of a palaeoecological study of the sites. To determine if fossils from each site were locally derived, specimens were examined for abrasion, breakage, weathering, evidence of digestion or scavenging, and skeletal part representation. Age-class distribution analysis of several peramelemorphians and a subfamily of macropodids was carried out for one of the sites to determine if the mortality profile might be attritional or catastrophic. Vertebrate remains from the six sites are disarticulated and, in combination with the lack of bone weathering, this suggests rapid burial in moist conditions. The majority of specimens are unweathered, unabraded, have a wide range of transport potentials and, at this stage, are not suspected to have significant predator/scavenger biases. These sites are therefore interpreted to be autochthonous assemblages. The age-class distribution analysis indicates attritional accumulation, however exact duration of accumulation can not be ascertained.

Resumen. TAFONOMÍA DE LOS SITIOS FÓSILES DEL ÁREA DE RIVERSLEIGH WORLD HERITAGE (OLIGOCENO-MIOCENO), AUSTRALIA. Se realizó un análisis tafonómico en seis sitios de los depósitos del área Riversleigh World Heritage en el noroeste de Queensland, Australia. Los seis sitios abarcan edades desde el Oligoceno tardío al Mioceno tardío y posiblemente más jóvenes. Se ha encontrado allí una diversa fauna fósil pero en este estudio solamente los mamíferos son considerados. El objetivo fue evaluar la información biológica y ecológica quese podía obtener para esos sitios antes de llevar a cabo un estudio paleoecológico. Para determinar si los fósiles de cada sitio fueron derivados localmente, se examinó el material en busca de evidencias de abrasión, fractura, meteorización, digestión o carroñeo y representación de partes esqueléticas. El análisis de distribución de varios peramelemórfidos y una subfamilia de macropódidos fue realizado para cada uno de eses sitios para determinar si el perfil de mortalidad puede ser atricional o catastrófico. Los restos de vertebrados de los seis sitios están desarticulados y, en combinación con la falta de meteorización de los huesos, esto sugiere un rápido enterramiento en condiciones húmedas. La mayoría de los ejemplares no está meteorizado ni presenta abrasión, tiene una amplio espectro de potenciales de transporte y, en esta etapa, no se sospecha que tengan un sesgo especial por depredadores o carroñeros. Por lo tanto, se los interpreta como conjuntos autóctonos. La distribución de las clases etarias indica una acumulación atricional pero su exacta duración no puede ser establecida.

Key words. Mammalian. Autochthonous. Age-class distribution. Attritional. Australia.

Palabras clave. Mamíferos. Autóctonos. Distribución edad-clase. Atrición. Australia.

Introduction

The Riversleigh World Heritage Area is located near Riversleigh Station homestead on the Gregory River, approximately 200 km north-west of Mount Isa, in north-western Queensland, Australia (Archer *et al*., 1996; figure 1). Over 300 fossil sites, or assemblages, have been identified at Riversleigh, spanning at least the last 25 million years (Archer *et al*., 1996). The sites occur in Tertiary limestones and were formed in fluvio-lacustrine, cave, sinkhole, or fissure fill situations (Archer *et al*., 1989). Most of the sites occur on two plateaus, D-site Plateau and Gag Plateau. Determination of absolute ages of Riversleigh sites has been a major challenge. Radiometric dating of Riversleigh fossil sites, using U/Pb from calcites, is currently underway (Archer *et al*., 1997). Temporal relationships of the sites have been determined through biocorrelation studies (Archer *et al*., 1989; Woodburne *et al*., 1994; Archer *et al*., 1997; Black 1997a; Cooke 1997a) and stratigraphic analyses (Creaser, 1997).

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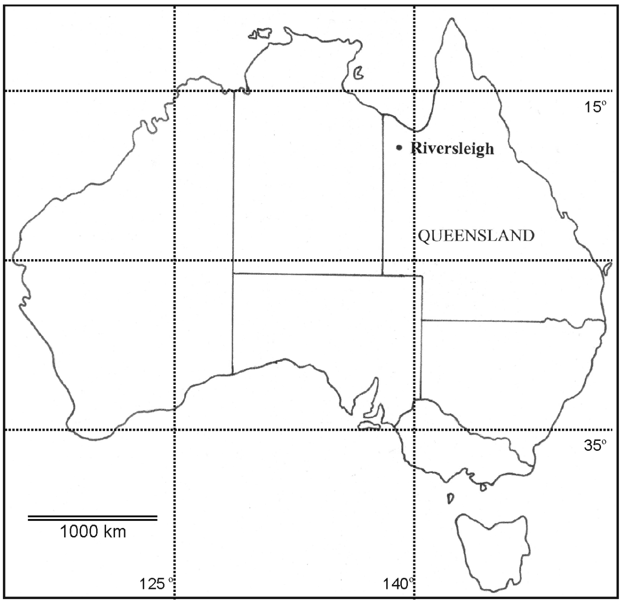


Figure 1. Map of Australia showing location of Riversleigh (19°2′, 138°45′) / *Mapa de Australia mostrando la ubicación de Riversleigh (19°2′, 138°45′)* .

Riversleigh sites preserve a great diversity of fauna, including insects (Arena 1997; Duncan *et al.*, 1998), molluscs, amphibians, fish, reptiles, birds and mammals (Archer *et al.*, 1989, 1996). Taphonomic analyses were carried out on six sites, believed to range in age from late Oligocene to late Miocene or possibly younger, in anticipation of a palaeoecological study of these sites. Only mammalian cranial and skeletal fossils were used for this study. The major aims of the taphonomic analyses were to determine whether the sites represent allochthonous or autochthonous assemblages and, where possible, whether accumulation was attritional or catastrophic. These aims were addressed through investigation of taxonomic presence and relative abundance at the sites; the extent of exposure of specimens prior to burial; skeletal element representation at sites; extent of predator/scavenger activity; analysis of skeletal completeness according to potential for water transport and sorting of bone elements; and age class distributions of taxa.

Table 1. The chosen sites and their ages (site ages from Archer *et al.* 1997 and Creaser 1997) / *Sitios seleccionados y sus edades (edades tomadas de Archer* et al. *1997 y Creaser 1997).*

Age (millions of years)	Epoch	Sites
2	Pleistocene	Encore
3.4	Late Pliocene	
5.2	Early Pliocene	
6	Late Miocene	
8		
10.4		
12	Middle Miocene	Ringtail
14		
16.3		
18	Early Miocene	Bitesantennary, Camel Sputum, Mike's Menagerie
20		
22		
23.3		
24	Late Oligocene	Quantum Leap
26		
28		
29.3		

The sites

The sites in this study were chosen to cover the widest period of time represented at Riversleigh (table 1). Quantum Leap and Bitesantennary Sites are located on northern D-site Plateau, separated by a distance of approximately 500m; Camel Sputum and Mike's Menagerie Sites are on central D-site Plateau, situated 5.4 m apart from each other; Ringtail Site is on northern Gag Plateau; and Encore Site is on southern Gag Plateau. Dimensions of the excavations at the sites are as follows: Camel Sputum is approximately 25 m^2 with an average depth of 2 m; Mike's Menagerie is approximately 9 m^2 with an average depth of 0.3 m; Encore is approximately 6 m^2 and 0.64 m deep; Bitesantennary is approximately 5 m^2 and 0.7 m deep; all fossil material from Quantum Leap Site was obtained from a boulder approximately 1m in diameter (A. Gillespie pers. comm.); and the dimensions of Ringtail Site could not be measured because the excavation boundaries have become obscured over time, although its depth does not exceed one metre.

Because of severe problems with vandalism at localities adjacent to Bitesantennary Site in the Riversleigh World Heritage Property, precise localities are provided via permit from the Queensland Museum and the Queensland National Parks and Wildlife Service, Brisbane. All locality data available on permit from these two Queensland Government institutions have been determined using a differential global positioning system and logged as part of a database that records localiy and taxic data for all sites at Riversleigh. The longitude and latitude of Riversleigh Station is 19° 02′, 138° 45′.

Bitesantennary Site is interpreted to be a cave deposit because of the diversity and the huge number of microchiropteran specimens preserved, and also, there is a flowstone floor with a stalagmite at the base of the deposit (Hand, 1997). Mike's Menagerie Site may have belonged to the same subterranean system as Camel Sputum because they are linked by lithologically similar fossiliferous deposits. The Ringtail Site local fauna contains the monotreme *Obdurodon dicksoni*. It also contains the crocodilian *Trilophosuchus rackhami* (Willis, 1993) and other aquatic

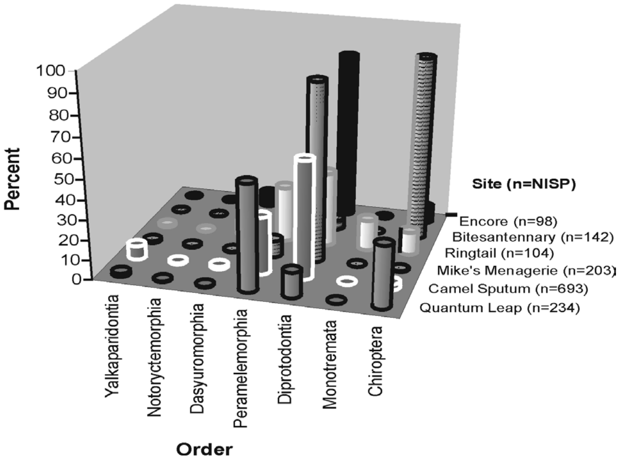


Figure 2. Relative abundance of taxa at each site / *Abundancia relativa de taxones de cada sitio.*

taxa, for example, lungfish, molluscs and frogs. The fossils at this locality and also at Quantum Leap are considered to have been deposited under low energy fluvial conditions, probably in a tufa barrage pond (Arena, in prep.). The Encore Site deposit may have been formed in a shallow pool (Creaser, 1997).

Methods

Taxa found at each site were noted for an indication of taxonomic diversity (table 2). Myers *et al.* (2001) provide more details on the fauna of Encore Site. To estimate the relative abundance of taxa at each site (figure 2), dental specimens were counted using the NISP method (Grayson, 1984; Badgley, 1986). Postcranial elements were not used in the NISP count because it was not possible to assign them to a taxon with certainty in this study. The reason for this is that many Riversleigh species- and generic-level taxa, described chiefly from craniodental specimens, are so far unknown from anywhere else and skeletal remains at Riversleigh sites are, in most cases, disassociated.

All specimens were put into size groups (small, medium or large) because taphonomic processes may affect small and large bones in different ways. All fossil specimens were assigned to a size group by comparison to corresponding elements of a potoroo (*Potorous tridactylus*; av. 1.1 kg, Johnston, 1998) and a swamp wallaby (*Wallabia bicolor*; av. 15 kg, Merchant, 1998). Dimensions measured were length and circumference for limb bones and other elongated elements; occlusal length and width for teeth; and maximum width, length and height for vertebrae, pelves, scapulae, crania and dentaries. Specimens the same size or smaller than corresponding elements of the potoroo were grouped as small, those intermediate in size between the potoroo and wallaby were grouped as medium, and those larger than the wallaby were grouped as large.

Weathering and breakage patterns reveal the extent of aerial exposure of bones prior to fossilisation. Specimens from each site were scored for six categories of bone surface deterioration (adapted from Behrensmeyer, 1978 and Coombs and Coombs, 1997). To determine when bones from each site were broken (fresh, after aerial exposure, or after fossilisation), breakage of limb bones was categorised into groups (adapted from Shipman, 1981 and Coombs and Coombs, 1997). Although it is arguable that fracture shapes indicate when breakage occurred (Shipman, 1981), spiral fractures are more common in fresh bones, transverse and longitudinal fractures occur on mineralised bones, and stepped fractures develop after long aerial exposure (Andrews, 1990; Behrensmeyer, 1991; Coombs and Coombs, 1997).

To determine if fossils from each site were locally derived, they were examined for: abrasion; evidence of predator/scavenger activity; skeletal element representation; and association of elements. Also, specimens were grouped on the basis of their potential for hydraulic transport. These hydraulic transport potential groups (referred to as 1, 2 and 3) are based on the findings of Voorhies (1969), Behrensmeyer (1975), Dodson (1973) and Korth (1979) for medium and small sized mammals. The groups combine the information from these authors but, where appropriate, certain elements are excluded (for example, ribs were removed as there is likely to be a sorting bias against them in the laboratory because they are not taxonomically informative and are hard to recognise when broken). Group 1 includes vertebrae, sacra and sternums - those elements most easily transported by water; group 2 includes scapulae, limbs, foot/hand bones and teeth - elements that are intermediate in their water transport potential; and group 3 includes dentaries - the element most resistant to water transport. The distributions of fossil specimens (within their size categories) amongst these groups were compared to the numbers expected for no hydraulic transport. These expected numbers were obtained by calculating the average number of elements in each group from marsupial skeletons (these numbers are generally close to numbers for the average michrochiropteran; there is further discussion of this, with respect to bat remains at Bitesantennary Site, below).

An age-class distribution analysis was performed in an attempt to determine if assemblages exhibit attritional or catastrophic mortality profiles. An attritional mortality profile indicates an assemblage accumulated over time and reflects the number of individuals in each age class that are dying. Catastrophic

Table 2. Taxonomic representation at the sites (grey shading refers to presence of taxa) / *Representación taxonómica en los sitios (sombreado gris: presencia de taxones)* Q = Quantum Leap; C = Camel Sputum; M = Mike's Menagerie; R = ringtail; B = Bitesantennary; E = Encore. Number in brackets indicates the reference where the species is described / *Número entre paréntesis indica las referencias donde las especies están descriptas.*

Order	Sub order	Superfamily	Family	Sub family or tribe	Genus	Species	Q	C	M	R	B	E
Yalkaparidontia		Yalkaparidontoidea	Yalkaparidontidae		*Yalkaparidon*	*coheni* (1)	▨	▨	▨	▨		
Notoryctemorphia			Notoryctidae				▨	▨	▨			
Dasyuromorphia		Dasyuroidea	Dasyuridae		*Barinya*	*wangala* (2)					▨	
					Ganbulanyi	*djadjinguli* (3)						▨
			Thylacinidae		*Wabulacinus*	*ridei* (4)		▨				
					Ngamalacinus	*timmulvaneyi* (4)		▨				
					Maximucinus	*muirheadae* (5)				▨		
					Thylacinus	*macknessi* (6)			▨			
						sp. cf. *T. macknessi*						▨
			Incertae sedis		*Mayigriphus*	*orbus* (7)						▨
Peramelemorphia		Yaraloidea					▨	▨	▨	▨	▨	▨
			Yaralidae		*Yarala*	*burchfieldi* (8)		▨				
			Incertae sedis		*Genus* 1	sp.		▨				
					Genus 2	sp.		▨				
					Genus 3	sp.		▨				
			V-Didae				▨			▨		
Diprotodontia	Vombatiformes		Wynyardiidae					▨	▨			
			Phascolarctidae		*Litokoala*	*kanunkaensis* (9)						▨
					Nimiokoala	*greystanesi* (10)		▨				
					Phascolarctos	sp.						▨
			Vombatidae		cf. *Warendja*	sp.						▨
			Thylacoleonidae		*Wakaleo*	*vanderleuri* (11)						▨
					Priscaleo			▨				
		Diprotodontoidea	Diprotodontidae				▨	▨	▨	▨		▨
				Zygomaturinae	*Nimbadon*	*lavarackorum* (12)				▨		
					Neohelos	sp.		▨	▨			▨
						tirarensis (12)		▨	▨			
			Palorchestidae		*Propalorchestes*	*ponticulus* (13)		▨				
					Palorchestes			▨	▨			▨
						anulus (14)						▨
						sp.						▨
	Phalangerida	Phalangeroidea	Phalangeridae							▨		
					Strigocuscus	*reidi* (15)		▨				
					Wyulda	*asherjoli* (16)		▨	▨			
					Trichosurus	sp.					▨	▨
			Pilkipildridae				▨	▨	▨			
		Tarsipedoidea	Acrobatidae					▨	▨	▨		
		Burramyoidea	Burramyidae		*Burramys*	*brutyi* (17)		▨		▨		▨
					Cercatetus					▨		
		Petauroidea	Petauridae				▨			▨		
			Pseudocheiridae		*Pseudochirops*					▨		▨
					Marlu	cf. *kutjamarpensis* (18)		▨		▨		
					Paljara	*maxbourkei* (19)		▨				
						nancyhawardae (19)		▨				
					Pildra	sp. 2		▨				▨
			Incertae sedis		*Djaludjangi*	*yadjana* (20)		▨	▨			
		Macropodoidea	Macropodidae	Macropodinae				▨	▨			
				Bulungamayinae	*Wabularoo*	*naughtoni* (21)		▨	▨			
					Nowidgee	*matrix* (22)		▨				
					Bulungamaya	*delicata* (23)	▨	▨				
					Gangaroo	*bilamina* (22)		▨	▨		▨	
						sp. nov.						▨

Order	Sub order	Superfamily	Family	Sub family or tribe	Genus	Species	Q	C	M	R	B	E
Diprotodontia	Phalangerida	Macropodidea	Macropodidae	Bulungamayinae	*Warburoo*	*hilarus* (24)						■
						sp.						■
					Gumardee			■				
				Sthenurinae	*Hadronomas*	cf. *Hadronomas* sp.						■
			Potoroidae	Potoroinae				■				
			Hypsiprymnodontidae	Hypsiprymnodontinae	*Hypsiprymnodon*		■	■	■			
				Propleopinae	*Ekaltadeta*	*ima* (25)		■	■			■
						jamimulvanegi (26)						■
			Balbaridae	Nambarinae	*Ganawamaya*	*acris* (27)		■				
					Balbaroo	*gregoriensis* (23)		■				
					Wururoo	sp.		■				
					Nambaroo	sp. 5		■				
						sp. 3	■					
Monotremata			Ornithorhynchidae		*Obdurodon*	*dicksoni* (28)				■		
Chiroptera	Microchiroptera	Rhinolophoidea	Hipposideridae	?	*Xenorhinos*	*halli* (29)					■	
					Riversleigha	*williamsi* (30)					■	
				Rhinonycterini	*Brachipposideros*			■	■	■	■	
						watsoni (31)					■	
					Rhinonicteirs	*tedfordi* (31)					■	
						Bitesantennary sp. 1					■	
						Bitesantennary sp. 3					■	
						Bitesantennary sp. 4					■	
						Bitesantennary sp. 5					■	
						Bitesantennary sp. 6					■	
						Bitesantennary sp. 7					■	
						Bitesantennary sp. 8					■	
						Bitesantennary sp. 9					■	
			Megadermatidae		*Macroderma*			■	■	■	■	■

1. Archer *et al.* (1988); **2.** Wroe (1999); **3.** Wroe (1998); **4.** Muirhead (1997); **5.** Wroe (2001); **6.** Muirhead (1992); **7.** Wroe (1997); **8.** Muirhead and Filan (1995); **9.** Springer (1987); **10.** Black and Archer (1997); **11.** Clemens and Plane (1974); **12.** Hand *et al.* (1993); **13.** Murray (1990); **14.** Black (1997b); **15.** Flannery and Archer (1987); **16.** Crosby *et al.* (2001); **17.** Brammall and Archer (1997); **18.** Woodburne *et al.* (1987); **19.** Bassarova *et al.* (2001); **20.** Brammall (1998); **21.** Archer (1979); **22.** Cooke (1997b); **23.** Flannery *et al.* (1982); **24.** Cooke (1999); **25.** Archer and Flannery (1985); **26.** Wroe (1996); **27.** Cooke (1992); **28.** Archer *et al.* (1992); **29.** Hand (1998a); **30.** Hand (1998b); **31.** Hand (1997).

mortality profiles may result from instantaneous mortality events. Some assemblages, however, may exhibit a catastrophic mortality profile but may have been accumulated over a long period of time, for example, pitfall trap and owl pellet deposits which sample randomly from the living population and reflect the proportion of individuals in each age class in that living population.

The age classes used for the fossils in this study are arbitrary categories determined from the extent of tooth wear (see appendix) and are based on the assumption that teeth wear down at a constant rate over time. Only first lower molars were used in assigning fossils to an age class so as to overcome the problem of differential wear of teeth in the tooth row of individuals. Peramelomorphians (bandicoots) and a subfamily of macropodids (kangaroos) were examined only from Camel Sputum, because of sample size limitations at the other sites. Catastrophic and attritional death curves for extant bandicoots were constructed for comparison, using the data of Dufty (1994). Also for comparison, dasyurids from Jurien Caves owl deposit, Western Australia, were examined, as an example of a fossil catastrophic mortality profile.

Results and discussion

There appears to be a bias in the size of the specimens preserved at most sites. Most numerous are the specimens in the small size category. This is most likely a result of animals with smaller body sizes generally having faster turnover rates and larger populations. However, the preservation of a high proportion of small specimens is unusual because small material is very fragile. This preservation is therefore interpreted to be the result of a low energy depositional regime combined with a lack of aerial exposure (see below for discussion of weathering patterns). Mike's Menagerie is the only site to have produced

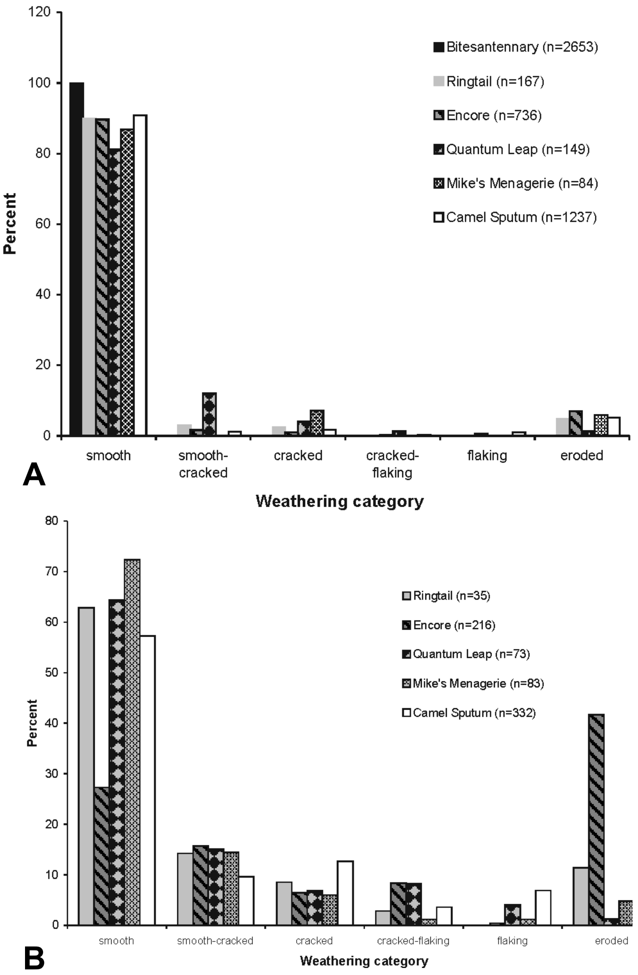


Figure 3. Percentages of various levels of bone weathering for **A,** small size category; and **B,** medium size category. Behrensmeyer's (1978) weathering categories 0, 1, 2 and 2-3 correspond to smooth, smooth-cracked and cracked, cracked-flaking, and flaking respectively, but are possibly not equivalent in exposure time / *Porcentajes de varios niveles de desgaste de hueso para* ***A,*** *categorías de tamaño pequeño;* ***B,*** *categorías de tamaño medio. Las categorías 0, 1, 2 y 2-3 de desgaste de Behrensmeyer (1978) corresponden a lisa, lisa-quebrada y quebrada, quebrada-escamada y escamada respectivamente, pero posiblemente no son equivalentes en el tiempo de exposición.*

greater numbers of specimens in the medium size category than in the small size category. At this stage, the Mike's Menagerie situation can only be explained by the fact that it has not been sampled as extensively as the other sites.

Examination of weathering patterns reveals that all sites have a predominance of smooth bone for the small size category (figure 3.A), indicating minimal aerial exposure. The medium size category shows a greater variance of weathering states (figure 3.B). Encore Site has a majority of medium-sized specimens in the "eroded" category. The interpretation of the "eroded" state is uncertain but it may possibly represent the effect of chemical reactions. It appears that medium sized elements have had slightly longer aerial exposure prior to fossilisation than small elements. This may be because larger bones last longer unprotected and, of the small elements, only those that were quickly buried survived.

Breakage patterns (figure 4) reveal that the majority of limb bones, from all sites, were broken either fresh (spiral breaks) or after fossilisation (tranverse breaks). Relatively few were broken after long aerial exposure (stepped breaks). This is consistent with the extent of weathering. In Riversleigh deposits, post-fossilisation breaks may occur in situ when erosion creates fissures through the limestone, or as a result of the collection process.

Fossils from none of the sites show sufficient surface abrasion to indicate significant fluvial transport. For example, from Quantum Leap only 3 specimens out of 1107 exhibit abrasion, with two being slight and one moderate.

Vertebrate remains from the six sites are disarticulated, except for one snake vertebral column from Camel Sputum. The separation of all vertebrae normally indicates exposure prior to burial (Behrensmeyer, 1975; Hill, 1979). However, in combination with the predominance of smooth bones, the extent of disarticulation suggests moist conditions created by microhabitats or standing water. Such conditions have been found to accelerate disarticulation and lead to rapid burial and therefore, good preservation (Coe, 1980). The bat deposit at Bitesantennary Site probably occurred in water rather than guano, based

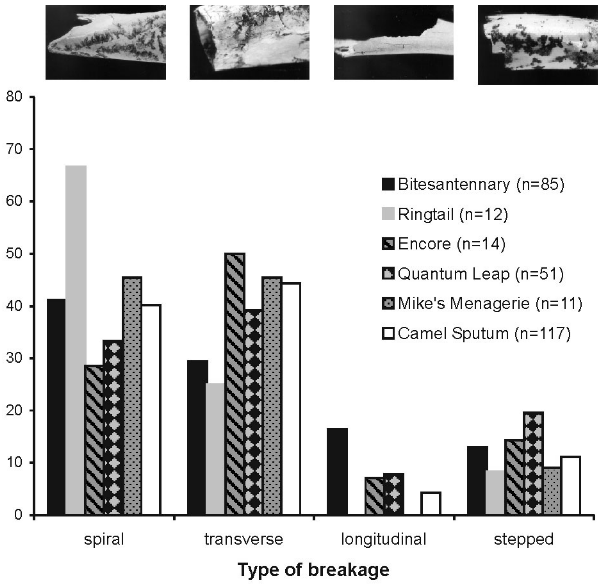


Figure 4. Percentages of various break shapes on limb bones for all size categories (break shape above corresponding to breakage type) / *Porcentajes de varias formas de fractura de huesos de los miembros para todas las categorías de tamaño (las formas de las fracturas arriba mencionadas corresponden a un tipo de rotura).*

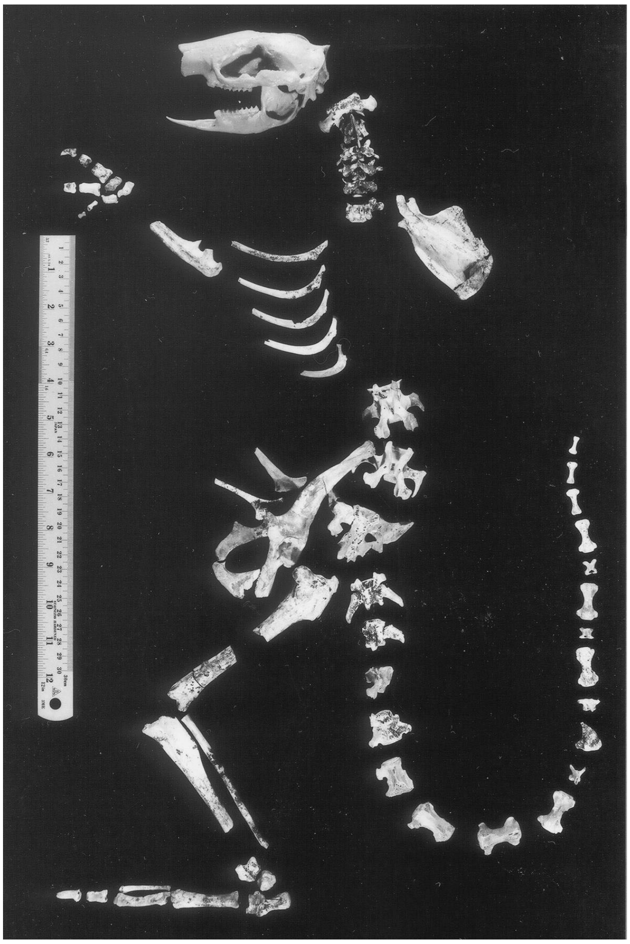


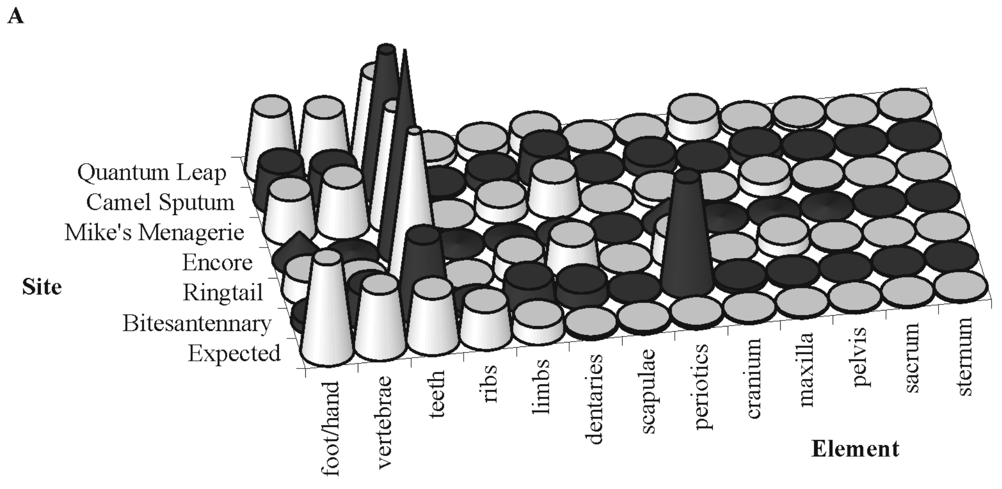
Figure 5. *Nambaroo* sp. 3 from Quantum Leap (scale = 30 cm) / *Nambaroo sp. 3 de Quantum Leap (escala: 30 cm).*

on the fact that biodegradation would be expected in guano and also, ostracod and fish fossils are found there (Hand, 1997). From Quantum Leap there is one almost complete kangaroo skeleton (figure 5) but the bones are associated, not articulated. Also, Encore Site has produced associated skull and postcranials of *Wanburoo* sp. (Kear *et al.*, 2001). This is further evidence that, for these sites, bones were not exposed to significant fluvial transport. Aside from these associated elements, most of the sites have produced disassociated elements indicating some non-transport post-mortem disturbance, such as bioturbation.

Elements in the medium and large size categories, on the whole, are represented in similar proportions to the expected for an unbiased sample (figure 6.B; only medium category is shown). The expected proportions of elements are the relative numbers of each element type in an average marsupial skeleton. Medium elements from Mike's Menagerie and small elements from most sites have a higher than expected proportion of teeth and dentaries and fewer foot/hand bones, ribs and vertebrae than expected (figure 6.A). A possible explanation is that ribs, vertebrae and foot/hand bones are not as robust as dental elements and therefore have a greater chance of being broken beyond recognition, especially if they are in the small category and thus, very fragile. Also, a collecting/sorting bias may result from the fact that dental elements, even if broken, are more easily recognisable and more taxonomically informative than broken postcranial pieces.

Hydraulic transport potential groupings are shown only for the small and medium size categories (figure 7); the sample size for the large category was too small for most sites. The Quantum Leap medium category exhibits almost identical distribution amongst the groups to the expected for no fluvial transport ($0.5<P\{\chi^2$ $(0.7\}<0.75$). Quantum Leap small category also comes close to this pattern. Ringtail medium, Encore medium, Bitesantennary small, Mike's Menagerie small and Camel Sputum small categories deviate slightly from the expected in having fewer group 1 elements. Dental elements make up the greater numbers in groups 2 and 3 for those categories. The majority of elements from Bitesantennary are from bats. Certain bat vertebrae are fused, so the proportion of vertebrae in a bat skeleton would be slightly less than in the average marsupial skeleton (which is what the expected numbers are based on). Also, bat vertebrae are very small and taxonomically uninformative so there may be a collection bias against them. This may explain the slight underrepresentation of group 1 elements from Bitesantennary. For the other sites, this may be due to a collection/sorting bias again, or may reflect the varying susceptibilities of skeletal elements to destruction rather than indicating fluvial transport (see below for further discussion of the extent of fragmentation of different elements). If, however, the lower-than-expected number of group 1 elements is taken as evidence of fluvial transport, then what we are seeing in the fossil samples from these sites is the untransported, or lag, component which is autochthonous.

Encore small, Ringtail small and Mike's Menagerie medium categories show a considerable underrepresentation of group 1 elements. In the case of Encore and Ringtail, both interpreted at this stage to be pool deposits, this may be explained by their environment of deposition. These pool deposits potentially had a weak flow of water, affecting mainly small sized elements. In this case, the Encore and Ringtail small categories represent the lag deposit and therefore, are autochthonous. The Mike's Menagerie situation is harder to explain because evidence from the medium category is not consistent with the small category. If water moves group 1 elements of the medium size category, it would surely



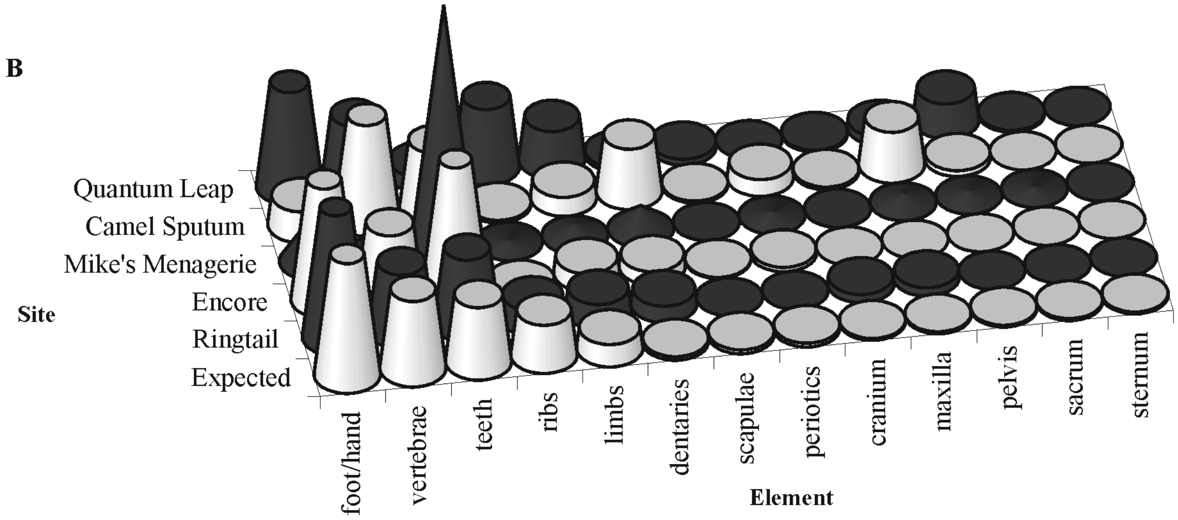


Figure 6. Skeletal representation for: **A,** small size category and **B,** medium size category / *Representación esqueletaria para* ***A****, categoría de tamaño pequeño y* ***B****, categoría de tamaño mediano.*

move group 1 elements of the small size category to a greater extent. Perhaps there is a link with Camel Sputum's medium category which has more elements in group 1 than expected. As previously mentioned, Mike's Menagerie and Camel Sputum are in close proximity and are linked by a continuous fossiliferous deposit. Work currently in progress is investigating whether these two sites are in fact part of the same deposit. If this is the case, deviations exhibited by Camel Sputum and Mike's Menagerie medium size categories will not be so large when data for the two sites are combined. Further sampling of Mike's Menagerie site may also shed some light on this problem.

The extent of fragmentation of skeletal elements is shown only for Ringtail Site, for the small size category (figure 8). Small elements from all sites follow a similar pattern, from teeth, foot/hand bones and periotics being mostly unbroken or entire, to pelves, dentaries, maxillae and crania being mostly fragmented (ribs are ignored because of the small sample size). The medium size category follows a similar pattern in all cases, but with a smaller proportion of entire elements. This again, may be due to longer exposure of larger elements prior to burial.

Riversleigh Oligocene-Pliocene terrestrial predators include mammalian and reptilian taxa (Wroe, 2002) and birds of prey (Boles, 1993). There are con-

Table 3. Percentage of specimens (of all size categories) exhibiting evidence of possible digestion or tooth marks / *Porcentaje de especímenes (de todas las categorías de tamaño) que exhiben evidencia de posible digestión o marcas de dientes.*

Site	%digestion	% tooth marks	Total sample size
Camel Sputum	0.23	0.51	3550
Mike's Menagerie	1.72	0.86	581
Ringtail	0.12	0.5	806
Quantum Leap	1.36	1.36	1107
Encore	0.4	0.43	3001
Bitesantennary	0	0.01	8086

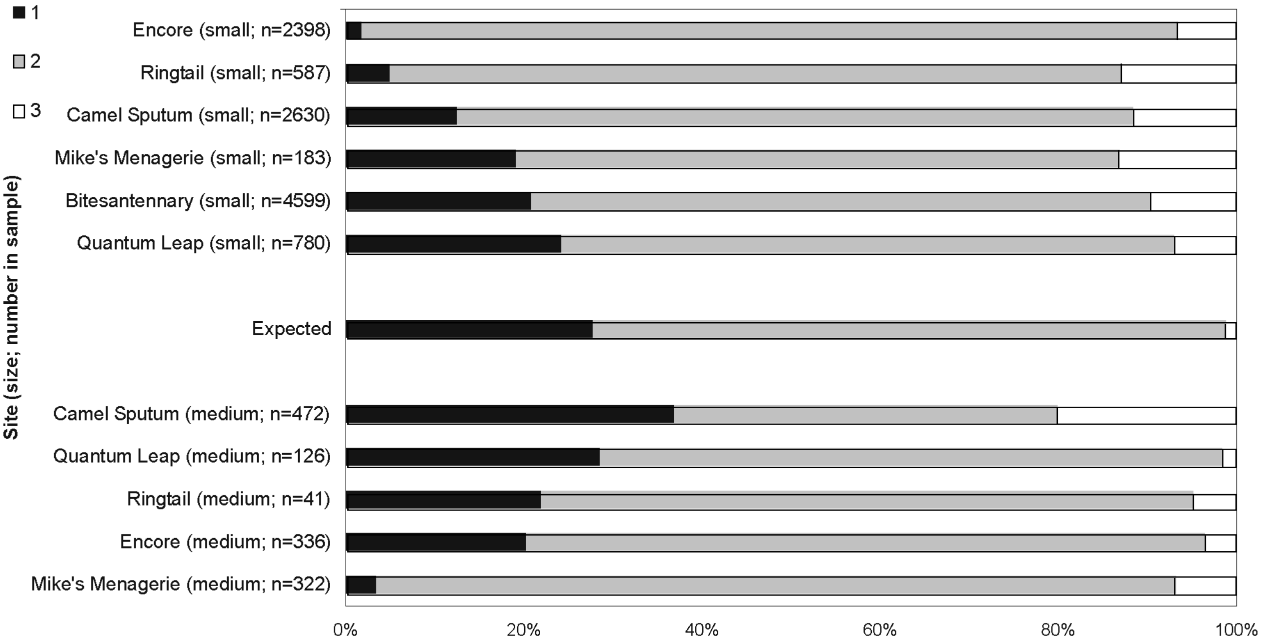


Figure 7. Hydraulic transport potential groupings for elements from fossil sites / *Agrupamientos potenciales de transporte hidráulico para los elementos de los sitios fósiles.*

siderably fewer terrestrial reptilian predator species than there are mammalian predator species (Wroe, 2002) and reptilian predators are less likely to leave evidence of their predation. Prey assemblages may be recognised by the size of prey, species composition, and modification of the bones of prey, which may all be predator-specific (Andrews, 1990). At this stage, the six fossil sites are not interpreted to be the result of predator accumulations based on lack of bone modification (such as rounding, digestion and tooth marks), skeletal representation, and taxonomic and size variation. There is no evidence of digestion or obvious tooth marks on the majority of specimens from the six sites (table 3). Taxonomic diversity and size range at each site is broad (for example, Camel Sputum mammals vary in size from the tiny *Burramys brutyi* with an approximate body mass of 21g, through to *Neohelos tirarensis* with a body mass of approximately 124kg, estimated using the body mass equations of Myers, 2001). Boles (2000) has found no evidence of owl predator accumulations at Riversleigh. Also the age-class distribution of bandicoots at Camel Sputum (figure 9.A) does not follow the pattern for owl prey accumulation shown by the Jurien Caves dasyurids. For medium- to large-sized mammals, the assemblages preserve many long bones with their shafts intact and with epiphyses present; skeletal representation is not consistent with that found at the kill sites of medium- to large-sized mammalian predators, which leave mostly phalanges, metapodials/tarsals, teeth and fragments of shafts of long bones (Haynes, 1982); and skeletal representation is not consistent with that found at carnivore feeding places and dens, which preserve a majority of limb and girdle bones (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001) and display a high frequency of gnawing marks on cranial, limb and girdle elements, and on preserved epiphyses (Palmqvist *et al.*, 1996).

Further work is necessary to determine if *Macroderma* (genus of predatory bat) was involved in accumulation of small taxa at the six sites. The modern ghost bat, *Macroderma gigas*, is opportunistic in its hunting habits, taking as many as 40 species of bird (Boles, 1999), a broad range of small mammals (Douglas, 1967), and other vertebrates and invertebrates to be eaten in roost caves (Boles, 1999). Very few specimens of *Macroderma* have been identified from the six Riversleigh sites (maximum of three specimens at each site), suggesting the sites do not represent *Macroderma* roosts. To determine if *Macroderma* is in fact responsible for accumulation of any remains at the sites, fossils of birds, frogs and reptiles -potential prey for *Macroderma*- will need to be examined in addition to mammalian fossils.

Results of the age-class distribution analysis for Camel Sputum bandicoots (figure 9.A) are shown along with the age-class distribution for dasyurids (several species of varying sizes) from Jurien Caves owl pellet accumulation. The dasyurids exhibit a cata-

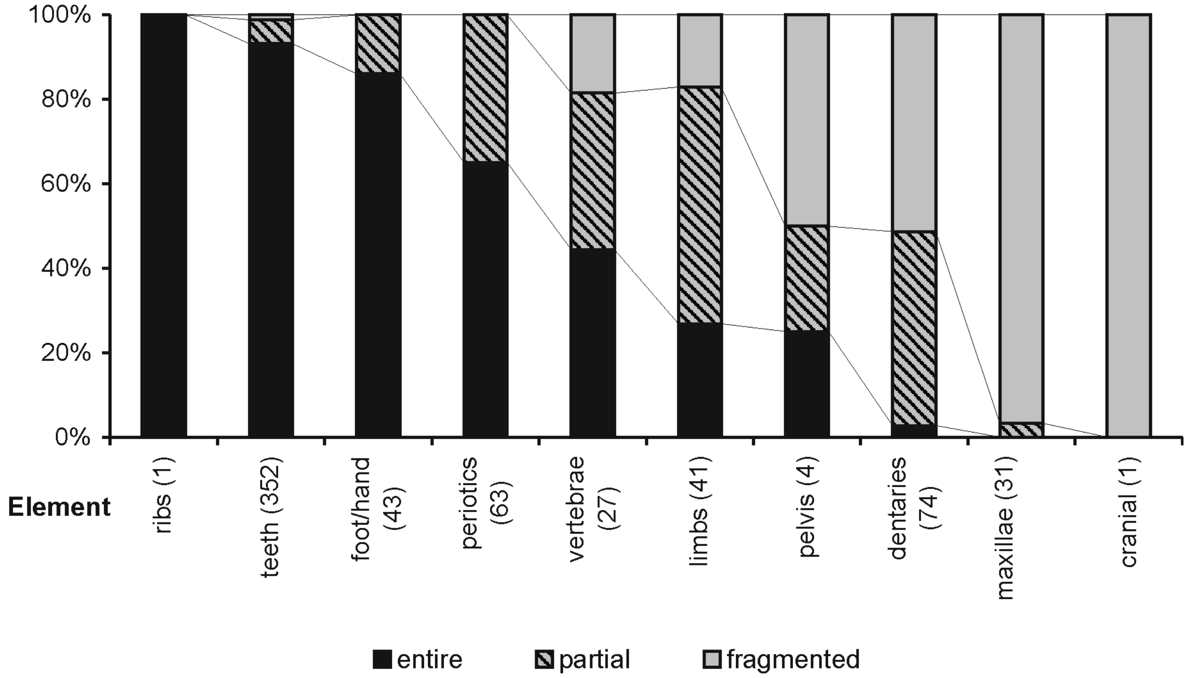


Figure 8. Completeness of skeletal elements for small size category, from Ringtail (number in brackets is sample size) / *Integridad de los elementos esqueletarios por categoría de tamaños pequeños del sitio Ringtail (número entre paréntesis indica tamaño de muestra.*

strophic mortality profile because their predator would have selected for size, not for age of individuals, thus taking a random sample from the living population. Catastrophic death curves reflect the numbers of living individuals for each age class in the population. Attritional death curves, on the other hand, reflect the number of individuals for each age class of a population, that are dying - i.e. there is high mortality of juveniles, mortality decreases for adults and then increases for aged individuals - (Voorhies, 1969; Lyman, 1994). Camel Sputum bandicoots seem to follow the pattern of attritional mortality, with a high proportion of juveniles (tooth wear category 1), a relatively low proportion of adults (categories 2-4), an increase from adults to aged individuals (category 5), and total die off (category 6); also see figure 9.B for comparison, but note that age classes do not correspond directly to tooth wear categories for figure 9.A. An age-class distribution analysis of the kangaroos from Camel Sputum revealed a similar pattern (not shown here).

Assemblages accumulated over long time periods (attritional mortality profile), that are not the result of predator activity, typically exhibit high taxonomic diversity (Varricchio and Horner, 1993); assemblages with a catastrophic mortality profile may or may not exhibit high taxonomic diversity, depending on whether accumulation was instantaneous, over a period of time such as for pitfall trap deposits, or the result of certain predators. Instantaneous, mass mortality events are often taxon-specific in their preservation (Behrensmeyer *et al.*, 2000); pitfall trap accumulations may exhibit high taxonomic diversity; and owl pellet accumulations, for certain species, do not exhibit high taxonomic diversity (Dodson and Wexlar, 1979; Andrews, 1990). Due to high taxonomic diversity, Ringtail, Encore, Bitesantennary, Quantum Leap and Mike's Menagerie deposits are presumed to have accumulated over time and not to be due to instantaneous mortality events. It is expected that Ringtail and Encore Sites, being pool deposits, will not exhibit the catastrophic mortality profile of a pitfall trap, but a greater sample size from both sites is necessary for this to be demonstrated. The fauna from Camel Sputum Site exhibits an attritional mortality profile and suggests Camel Sputum is not a pitfall trap deposit and this perhaps also will apply to Mike's Menagerie if it is shown to be a part of the same deposit. Creaser (1997) states that the lithology of the sediments and fossils at Camel Sputum and Mike's Menagerie suggest that these deposits accumulated over a period of time.

Time-averaging at the six sites is not expected to be long-term because animals at different evolutionary stages are not mixed and preservation quality is consistent within each site. Short-term time-averaging is possible, in the order of up to several thousand years (Fürsich and Aberhan, 1990), but it is difficult to determine exactly to what extent the sites are time-averaged.

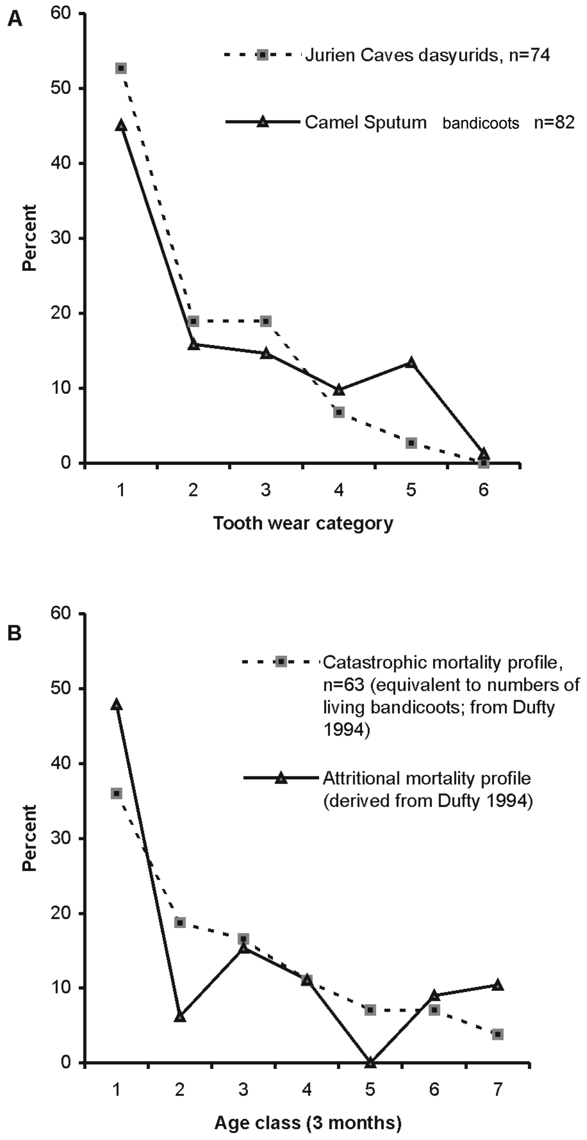


Figure 9. Mortality profiles for: **A,** dasyurids from Jurien Caves owl pellet material and bandicoots from Camel Sputum; and **B,** *Perameles gunii* from Hamilton, Victoria / *perfiles de mortalidad para* ***A,*** *dasiúridos de Jurien Caves tomados de egragópilos de lechuzas y bandicoots de Camel Sputum; y* ***B,*** Perameles gunii *de Hamilton, Victoria.*

Summary

Palaeoecological studies of the local faunas from Camel Sputum, Mike's Menagerie, Ringtail, Encore, Quantum Leap and Bitesantennary Sites can be carried out in future with consideration of the taphonomic biases affecting remains at each site.

The Bitesantennary local fauna is taxonomically biased, containing mostly bats, so further palaeoecological study will have to be restricted to bat communities.

Skeletal element associations at Quantum Leap and Encore, and lack of abrasion of specimens from all sites suggest that water is not a significant transport agent for these samples of specimens. The general over-representation of dental elements for all sites may be the result of a collecting or sorting bias and/or may reflect the lower susceptibility of these elements to destruction; if in any case it is due to water flow, the sample represents the untransported component so palaeoecological studies will not be affected.

The lack of surface deterioration and the break patterns of limb bones from all sites indicate minimal aerial exposure of bones prior to burial and therefore reduced risk of bones being moved considerable distances. Burial of bones at all the sites is likely to have occurred in wet or moist conditions (either underwater or in wet microenvironments), as suggested by the extent of disarticulation combined with minimal weathering. Disassociation of the majority of elements at all sites suggests bioturbation of pre-fossilised burial sediment by churning or mixing caused by the movement of live organisms (Behrensmeyer *et al.*, 1989).

The involvement of Macroderma as an accumulator of small vertebrates seems unlikely due to the small number of Macroderma specimens recovered from the sites, however, further analysis is required to completely rule out this possibility. At this stage there appear to be no significant predator/scavenger-caused biases.

Bandicoots from Camel Sputum Site exhibit an attritional mortality profile and the remaining sites are presumed to have accumulated over time and not to represent instantaneous mortality events. Accumulation at all sites is considered to be autochthonous, but exact duration of accumulation can not be ascertained.

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Appendix

Bandicoot tooth wear categories for lower first molar, adapted from Morrell (2002).

Wear category	Life stage	Features
1	Juvenile	Totally unworn to slight exposure of dentine on tips of cuspids
2	Sub-adult	Dentine exposed along length of cests
3	Adult	Dentine exposed within talonid basin; cuspids worn to 90% of their original height
4	Adult	Cuspids worn to 75% of their original height
5	Aged	Cuspids worn to 50% of their original height; cuspids are same height as interconnecting crests
6	Very old	Trigonid and talonid basins worn smooth; crown almost entirely worn away