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Holocene avian assemblage from Skull Cave (AU-8), south-western Western Australia.

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Abstract

The avian assemblage from Skull Cave is composed of a minimum of 10 species. It is dominated by a single species, *Glossopsitta porphyrocephala*, which comprises up 58% of the total number of individuals recorded from the deposit (68), *Atrichornis clamosus* makes up a further 19%, and the last eight species cover the rest of the total (33%). The species which dominate this assemblage are non-terrestrial/diurnal/gregarious species, which are irruptive in nature. Terrestrial forms are also important to the composition of the assemblage. The assemblage was probably accumulated by *Tyto alba*. A palaeoenvironmental intrepretation based upon this assemblage indicates the presence of forest throughout the period of deposition.

Introduction

Until recently birds have been largely ignored or overlooked in the fossil vertebrate assemblages of Australia although they are useful in determining palaeoenvironments (Baird 1989) and could provide baseline data for biogeography and biostratigraphy (Baird in press a). The fossil material in Skull Cave (AU-8: Matthews 1985) includes one of the few avian assemblages associated with radiocarbon dates of Holocene age in Australia (Baird in press a). Although the Leeuwin/Naturaliste Penninsula has a proponderance of fossil localities (Porter 1979), because of the cavernous limestones in that region (Baird in press b), few have either radiocarbon dates or significant avian assemblages (Baird in press a). Information from the study of this assemblage, combined with the palaeoenvironmental information from the fossil avian assemblage of Devil's Lair (Baird in press e), could provide a hypothesis on a pattern of regional changes in climate over the past 35,000 years for the southwest of Western Australia.

Several studies on fossil vertebrate material from Skull Cave have been published, including mammals (Porter 1979) and frogs (Tyler 1985). This paper will provide identifications and discussion of the significance of the avian assemblage from Skull Cave.

Skull Cave occurs on the Leeuwin/Naturaliste Peninsula approximately 10 km west-north-west of the township of Augusta, Western Australia (115°05'S and 34°17'E). The local topography consists of hills with a relief of 30-90 m composed of sandstone and conglomerate (Laut *et al.* 1975). The vegetation surrounding Skull Cave consists of a forest of *E. diversicolor* to the east and north, open scrub merging to low open scrub to the west and low open woodland to the south (Smith 1973).

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The cave is a collapse doline, whose longest axis is in an east-west direction (approximately 40 m x 25 m) and an apical entrance (Figure 1). There is a pile of rubble which stands 13 m high, whose peak is 10 m below the entrance.

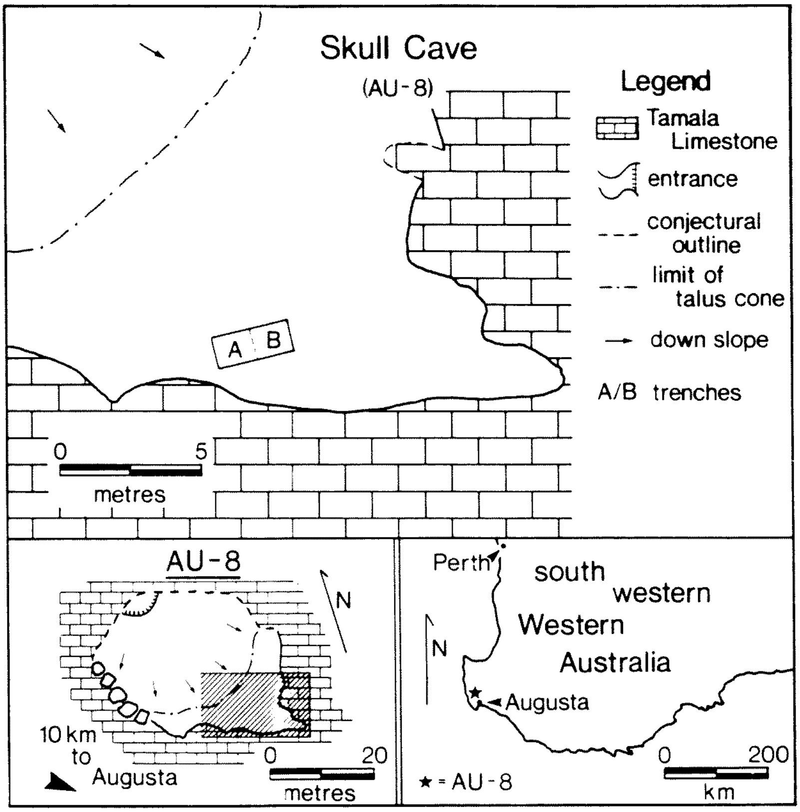

Figure 1. Plan view of Skull Cave demonstrating the position within the feature from which the fossil material was excavated.

The deposits in Trenches A and B consist of "thin interfingering bands of brown, orange and sometimes whitish coloured sediments" Porter (1979). A time transgressive chronology of deposition is corroborated by the radiocarbon dates on charcoal from two different levels within the stratigraphy (see Table 1).

No figure was offered to display the distribution of the layers. The vertebrate remains were labelled by excavation level not sedimentary unit. Therefore, except for the depth of the spits involved, there is no stratigraphic information for the specimens. The minimum number of individuals (MNI) calculated, then, will be lower than that which might have been possible if discrete sedimentological units had been identified.

Table 1. Radiocarbon dates, in y.B.P., completed on charcoal associated with excavations in Skull Cave, accomplished by J.R. Porter between 1969 and 1975 (from Porter 1979). SUA = University of Sydney, Australia.

Trench/Unit	Date	Reference #
B 4	2,900 ± 80	SUA 227
A 12	7,875 ± 100	SUA 228

Porter (1979) stated that the bulk of the small animals (undefined) were brought into the cave by owls, and the large animals, like *Macropus fuliginosus*, were trapped in the cave as a result of falling through the apical opening which created an effective pitfall trap. The evidence for the taphonomic scenario comes from the size and relative complete nature of the elements of smaller animals and the undamaged elements of the larger animals, except for broken limb-bones, which could be effectively argued as evidence for a pitfall origin of the material. There is little evidence for human involvement in the deposit, and no occupational evidence has been uncovered (*e.g.* hearths, shelly fauna, burnt bone, numerous artifacts, etc.).

The proposed palaeoenvironmental sequence for the time period covered by the deposit is as follows (from Porter 1979): that the area surrounding the cave must have been forested for much of the Holocene, based on the presence of *Potorous tridactylus*, whose undamaged remains are interpreted as being pitfall in origin. In addition most of the other animals included in the deposit include forest in their repertoire of habitats. Porter (1979) also suggested that the disappearance of the heath and scrub dwelling animals from the deposits represents the contraction of local pockets of these habitats as a "culmination of trends begun in late Pleistocene times perhaps initially influenced by marine transgression".

Materials and Methods

Material available for study included all avian elements excavated from trenches A and B (Figure 1). Of the available material there is still a moderate amount of passeriform elements which are as yet unidentified (Appendix IV). This is largely due to their fragmentary nature and the uniformity of most postcranial elements across the order, therefore hindering determinations.

All of the material discussed in the section on Skull Cave will be deposited in the palaeontological collection of the Western Australian Museum (WAM).

The scientific names used in each account follow Condon (1975) and Schodde (1975). Minimum numbers of individuals were determined by the standard method of counting the most abundant element from a particular side from each excavation level. This may lead to an overestimate of the MNIs due to mixing of the excavation layers (the levels do not necessarily correspond to discrete stratigraphic layers), although this is considered to by minor, because the deposit is largely time transgressive.

Geographical ranges for each species are here assumed to be the same as the current range, unless otherwise noted. Anatomical terminology follows Baumel *et al.* (1979). All measurements in the text are in millimetres. Standard measurements in the text are indicated in brackets and follow the guidelines in von den Driesch (1976) unless stated otherwise. All measurements were taken with vernier calipers accurate to 0.05 mm and were rounded to the nearest 0.1 mm. Species determination is based upon mensural criteria in every species account except where otherwise stated. Botanical nomenclature follows the guidelines of Specht (1981). Abbreviations used in the text and figures are listed in Appendix I. Material identified as juvenile is based upon the criteria of having a "pitted appearance of the surface of the bone and incomplete ossification of the articular facets" (Campbell 1979: 17). Morphological characters for determinations higher than species level are included in Appendix II, unless only one element is considered, in which case they are included in each species account (see Baird in press c for detailed methods).

Accounts of Species

Family: Phasianidae

Coturnix sp.

Material

Incom. right hum. (74.8.64), 2 huml end left ccd (86.7.398, 86.7.399), com. left tmt. (76.10.83).

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the genus *Coturnix.*

The larger species of *Coturnix* cannot be separated by size or morphology (see Baird 1986).

Remarks

Coturnix pectoralis and *C. australis* are both considered likely for this material, based on biogeographic probability. Both of these species are irruptive, dispersing when food becomes scarce, and *C. pectoralis* will invade inland areas after substantial rains (Frith *et al.* 1977, Frith & Waterman 1977). The range of habitats covered by these species includes EOFF, EWF, HF, MOSF and ATSF.

Family: Columbidae

Phaps elegans

Material

Com. right ulna (76.10.126).

Characters

See van Tets and Rich (1980) for the suite of characters considered diagnostic for the family Columbidae and the genus *Phaps.*

The one specimen referred to *P. elegans* has a total length [GL] of 43.5 mm. This measurement falls within the range of total lengths for *P. elegans* and outside those for its cogeners (van Tets & Rich 1980).

Remarks

"Throughout its [*P. elegans*] range, it maintains this preference for healthland and other vegetation with a heath-like structure" (Frith 1982), particularly around swamps and coastal and near-coastal country. Although this species is not exclusively dependant on heaths, where it is sympatric with *P. chalcoptera* it seems to have a strong preference for this type of habitat.

Family: Loriidae

Glossopsitta porphyrocephala

Material

See Appendix III.

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Glossopsitta.*

G. porphyrocephala is intermediate in size between *G. pusilla* and *G. concinna* and the fossil material falls within the range of variation for *G. porphyrocephala* (see Baird in press e for an example of this).

Remarks

Mensurally the specimens of *Glossopsitta porphyrocephala* from this deposit are very similar to those from Devil's Lair (Baird in press e). There does not seem to have been any changes in the species, either mensural or morphological, throughout the span of time covered by the deposit.

The species is of little use in palaeoenvironmental interpretation, as it is nomadic and ranges over very large areas. It is considered irruptive and requires flowering plants, mainly eucalypts, for its food.

Family: Platycercidae

Platycercus icterotus

Material

Com. cran. (76.10.45), two dist. end right hum. (76.1.377, 86.7.501), two com. left hum. (75.10.25, 76.1.36), incom. right cmc. (86.7.498), dist. end right tmt. (86.7.500), com. left tmt. (86.7.499).

Characters

See Baird (in press c) and Appendix II for the suite of characters considered diagnostic for the family Platycercidae.

Within the south-west the family can be divided into a large species (*Barnardius zonarius*), a medium sized species (*Purpureicephalus spurius*) and a small species (*Platycercus icterotus*). Within this context, the fossil material falls into the range of variation exhibited by *Platycercus icterotus.*

Remarks

Habitats covered by this species include EOFF and EWF, particularly "open and partly cleared eucalypt woodland and forest but not heath" (Blakers *et al.* 1984).

Family: Aegothelidae

Aegotheles cristatus

Material

Prox. end left fem. (86.7.502), dist. end left tmt. (86.7.503).

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Aegotheles.*

Remarks

In most deposits *Aegotheles* material is usually considered to have had lived in the caves in which their remains are found but the condition, e.g. their incomplete nature and acute fractures, of the specimens in this deposit, would suggest that they were collected by *Tyto* sp. instead of being part of the autochthonous speleobiocenose fauna.

Aegotheles cristatus inhabits a broad range of habitats including EOFF, EWF, MOSF, and ATSF (Schodde & Mason 1980, Morris *et al.* 1981).

Family: Atrichornithidae

Atrichornis clamosus

Material

Two incom. rost. (76.7.228, 86.7.524), dist. end rost. (86.7.513), com. right hum. (72.8.120), incom. right hum. (74.8.45), dist end right hum. (86.7.507), com. left hum. (75.7.228), two prox. end left hum. (76.1.296, 86.7.508), com. right ulna (86.7.509), com. left ulna (86.7.525), com. right cmc. (86.7.519), com. left cmc. (86.7.520), two com. right ccd (76.10.262, 76.10.263), com. left ccd (86.7.526), incom. stm (86.7.517), incom. right fem. (74.1.70), prox. end right fem. (76.10.25), dist. end right fem. (86.7.510), two com. left fem. (86.7.504, 86.7.521) in com. left fem. (86.7.515), two prox. end right tbt. (86.7.516, 86.7.521), com. left tbt. (86.7.518), incom. left tbt. (86.7.505), two prox. end left tbt. (86.7.506, 86.7.514), com. left tmt. (86.7.523), dist. end left tmt. (86.7.511).

Characters

See Appendix II for the suite of characters considered diagnostic for the genus *Atrichornis* and refer to Rich *et al.* (1985) for plates on all elements.

Species-determination is based on both mensural and morphologic characters. *A. clamosus* is larger than *A. rufescens* (see Table 2, Baird in press d, Baird in press e, and Rich *et al.* 1985). All elements not included in the tables are considered to fall within the range of variation for *A. clamosus.* Unusual among these are the femora, which are considerably smaller than the one specimen of *A. clamosus,* but also far larger than the one specimen of *A. rufescens.* From the table of tarsometatarsal lengths (Baird in press d) it is apparent that the comparative specimen of *A. clamosus* is on the extreme upper end of the range of variation for this species. Therefore, because of the small sample size of fossil material, the difference between the fossil material and the comparative material is considered to be a result of sampling at either end of the range of variation. Extrapolating the size of femora from the fossil sample of tarsometatarsi (Table 2) demonstrates that both modern and fossil samples could fall within the total range of variation for *A. clamosus*.

Remarks

The material from Skull Cave was evenly distributed throughout the deposit. Mensurally, some of the elements have a wider range than would be expected for a single species, but I have no other reason to suspect that there are more than one. Measurements from specimens of this species from Skull Cave, and Devil's Lair versus modern specimens of both *A. clamosus* and *A. rufescens* are shown in Table 2.

Burbidge *et al.* (1986) described the habitat of *A. clamosus* in the following way: "Examination of the habitat at Two Peoples Bay, and other locations where Noisy Scrub-birds are known to have occurred, indicates that they were confined to the wetter area within the distribution of the Jarrah/Marri (*Eucalyptus marginata*/*E. calophylla*) forest, in particular to the ecotone between forest and swamp vegetation".

This species apparently requires sedges and/or shrubs in the understorey as well.

Table 2. Length measurements of femora of both species of *Atrichornis* and all referred material. The last set of data is extrapolated from tarsus lengths, from fossil material, multiplied by a factor of 1.0383 (the factor of difference between the femur and tarsus of the comparative specimen) to test the range or variation possible for this material.

	μ	σ 1	OR	N
A. rufescens (M)	>20.4			1
A. clamosus (M)	27.1		—	1
A. clamosus (AU-8)	24.4	0.4	24.0 - 24.9	4
A. clamosus (extrap.)	26.2	1.6	23.7 - 27.2	4

Family: Hirundinidae

undetermined

Material

Dist. end right hum. (86.7.533).

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the family Hirundinidae.

Generic — and specific — determinations are not possible for the Australian members of this family because of their extreme morphological uniformity (Baird 1985).

Family: Maluridae

Malurus sp.

Material

Com. right hum. (76.1.35).

Characters

The suite of characters considered diagnostic for the family Maluridae includes: **Humerus,** (proximal end), 1. *caput humeri* flattened proximally but has a centrally located distal extension (in palmar view), 2. *tub. dorsale* large, 3. *cta bicipitalis* convex proximally, 4. transition from *caput humeri* to *cta pectoralis* is abrupt (90^0), 5. single *fossa pneumotricipitalis*, 6. *crus dorsale fossae* attaches to shaft distally, 7. *cta pectoralis* proximodistally short, 8. *inc. capitis* broad, deep and extends to, midline of shaft, 9. *fossa pneumotricipitalis* not incised into shaft; (distal end), 1. whole end proximodistally flattened, 2. *proc. flexorius* extends furthest distally, 3. distal end of *proc. flexorius* rounded, 4. *proc. flexorius* forms a smooth transition with curve of shaft. The suite of characters considered diagnostic for the genus *Malurus*, includes: **Humerus,** 1. palmar face of *cta pectoralis* swollen, 2. *cta bicipitalis* not as reduced proximally, 3. sulcus for attachment of *M. pectoralis* not deep, 4. *cta pectoralis* ends abruptly distally, 5. medium size.

The total length of the specimen [G.L. = 11.5] falls within the range of variation for the species *M. elegans* and outside that for *M. splendens*, although there is an additional species of *Malurus* within which this specimen also falls, *M. leucopterus*. Although biogeographic probability suggests that this is referrable to *M. elegans*, the determination will be left at *Malurus* sp. until specimens of *M. pulcherrimus*, which also occur in this region, become available.

Family: Acanthizidae

Dasyornis longirostris

Material

Com. right hum. (86.7.528), com. left hum. (86.7.527), incom. right fem. (76.1.70), incom. left fem. (76.10.192)

Characters

See Baird (in press c) for the suite of characters considered diagnostic for the genus *Dasyornis*.

Dasyornis longirostris is the smallest of the three species in the genus *Dasyornis*. The fossil specimens are considered to fall within the range variation for *D. longirostris* and outside that for fossil specimens of *D. brachypterus* and both fossil specimens and modern material of *D. broadbenti* (see Baird in press c). Assignment only confers the fossil material to *D. longirostris* because of the lack of an adult comparative specimen of *D. longirostris* to confirm the identification.

Remarks

The range of *Dasyornis longirostris* at the time of European contact, as discerned through skins and sightings, has been figured and discussed in Smith (1977). Although it had not been recorded from the Cape Leeuwin/Naturaliste Peninsula, the author did demonstrate that the species was known from the area around Perth, to the north, and extensively around Albany, to the east. Smith (1977) mentions that the habitat in which the species is currently recorded is coastal heath.

Ford (1965) provides a more precise habitat of *D. longirostris* as, "although the Bristlebird frequently occurs in the same habitat as the Noisy Scrub-bird *Atrichornis clamosus*, at Two Peoples Bay, it prefers the margins of swamp heath and the dune valleys where the vegetation is only a few feet high. Sword grass, *Lepidosperma gladiatum* and *augustatum*, and saw grass, *Gahnia trifida*, are common elements of its habitat which is usually overgrown with an entanglement of dodder, *Cassytha racemosa*, and *Agrostis aemula*, mat grass, *Hemarthria uncinata*, spear grass, *Diplogon setaceus* and rushes which often include *Anarthria prolofera*, *Hypolaena gracillima*, *H. fasciculata* and *Loxocarya flexuosa*".

Family: Artamidae

Artamus cyanopterus

Material

Incom. left hum. (76.1.194).

Characters

The suite of characters considered diagnostic for the genus *Artamus* includes: **Humerus,** (proximal end) 1. single *fossa pneumotricipitalis*. 2. *cta bicipitalis* does not extend beyond *tub. ventrale* laterally, 3. *cta bicipitalis* not greatly expanded laterally, 4. *inc. M. supracoracoideus* and *M. pectoralis* restricted to distal end of *cta pectoralis;* (distal end), 1. *fossa M. brachialis* shallow; (whole), 1. element very stout.

The specimen (76.1.194) is referred to the species *A. cyanopterus* based on its total length [T.L.=20.5], which falls within the range of variation for this species and outside that for all other Australian artamid spp. (see Baird 1986).

Remarks

Artamus cyanopterus is largely restricted to EWF and EOFF (Morris *et al.* 1981), but can occur in wetter areas (*i.e.* ETOFF) particularly where dry ridges support a drier vegetation type (*i.e.* EOFF) than the surrounding gullies (Loyn 1980, Smith 1984).

Non-Passeriformes

Family: Undetermined

Material

Dist. end right ulna (76.1.163), incom. right cmc. (86.7.530), shaft frag. right cmc. (86.7.529), incom. left ccd (86.7.532), dist end left fem. (86.7.531).

Passeriformes

Family: Indeterminate

Material

Com. right hum. (74.8.19), incom. right hum. (74.8.20), incom. right fem. (86.7.534), two incom. left fem. (86.7.535).

Aves

Order: Indeterminate

Material

14 vertebrae (86.7.634, 86.7.636, 86.7.637, 86.7.638, 86.7.640), two acet, frag. pel. (86.7.635, 86.7.639).

Table 3. List of avian species identified from the Skull Cave deposit, with both common and scientific names, number of specimens (N), and minimum number of individuals (MNI) based on the total number of elements in the deposit.

	MNI	N
Phasianidae		
Coturnix sp. (Quail sp.)	4	5
Columbidae		
Phaps elegans (Brush Bronzewing)	1	1
Loriidae		
Glossopsitta porphyrocephala (Purple-crowned Lorikeet)	39	161
Platycercidae		
Platycercus icterotus (Western Rosella)	5	8
Aegothelidae		
Aegotheles cristatus (Australian Owlet-nightjar)	1	2
Atrichornithidae		
Atrichornis clamosus (Noisy Scrub-bird)	13	32
Hirundinidae		
indeterminate (Swallow sp.)	1	1
Maluridae		
Malurus sp. (Fairy-wren sp.)	1	1
Acanthizidae		
Dasyornis longirostris (Western Bristlebird)	2	3
Artamidae		
Artamus cyanopterus (Dusky Woodswallow)	1	1

Discussion

The avian assemblage from Skull Cave is composed of a minimum of 10 species. It is dominated by a single species, *Glossopsitta porphyrocephala,* which makes up 58% of the total number of individuals recorded from the deposit (68: Table 3). The MNI from *Atrichornis clamosus* make up a further 19%, and the last eight species cover the rest of the total (33%). The species which dominate this assemblage are non-terrestrial/diurnal/gregarious species, which are irruptive in nature (Figure 4). Terrestrial forms are also important to the composition of the assemblage.

The stratigraphic distribution of the species in the two trenches and their corresponding MNIs are demonstrated in Table 4. There are no extinct taxa currently recognized in the assemblage.

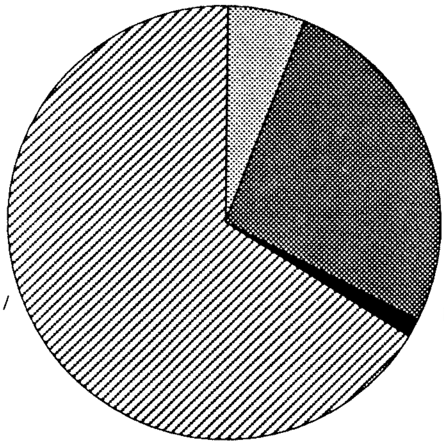

Figure 4. Percentages from total fauna (based on MNI=67) of various avian behavioural groups demonstrating that the non-terrestrial, diurnal, gregarious group dominate this assemblage (figures in brackets are the MNIs for each group).

Taphonomy

The condition of the avian material is good, with large percentages of complete and incomplete elements and crania present. Coloration ranges from white to light brown and increases in intensity with depth.

In the analysis of the distribution of weights of the avian taxa represented in the Skull Cave assemblage I have included all material except the hirundinid material, which is considered to be an allochthonous speleophile (Table 5). Incongruent to the rest of the material is the single specimen of *Phaps elegans,* whose weight of 212 g. is far outside of the mean for the bulk of the other specimens. A summary of the weight distribution can be seen in Figure 2. The bulk of the material (99%) falls below the 100 g level, with the greatest percentages within the 20-40g and 40-60g classes. The mean body weight for this material is 49g.

Sums of complete and incomplete elements barely outnumber those of the terminal ends (Figure 3). The pattern of element abundance for *G. porphyrocephala* is similar to that in Devil's Lair and to those of *Coturnix* and *Turnix* spp. in many of the other

Table 4. Stratigraphic distribution of MNI for avian species identified from sediments excavated from Trenches A and B of Skull Cave.

Depth from Surface (cm)	*Coturnix* sp.	*Phaps elegans*	*Glossopsitta porphyrocephala*	*Platycercus icterotus*	*Aegotheles cristatus*	*Atrichornis clamosus*	Hirundinidae indet.	*Malurus* sp.	*Dasyornis longirostris*	*Artamus cyanopterus*	Non-passerines unident.	Passerines unident.
0 — 7			2	1		1						3
7 — 14	1		2			2			1			4
14 — 21		1	2									2
*A 21 — 28	1		3	1		1						6
28 — 35			3									3
35 — 42			3			1			1			2
42 — 63			2	1		2						3
63 — 70	1		1			1						2
70 — 80			3								1	3
80 — 90	1		5	2		1		1				2
90 — 100			2			1						1
*B 100 — 115			4								1	2
115 — 127			2		1	1				1	1	2
127 — 137			4			1						5
137 — 144			2			1						1
144 — 150							1					2
150 — 160			1									
160 — 170												
170 — 180												1
180 — 190												

*A = 2900 ± 80 y.B.P. *B = 7875 ± 100 y.B.P.

deposits across southern Australia, despite the differences in element lengths and structure (Baird in press b). The only aberrant figure for this material is for the number of carpometacarpi, which is unusually low.

The Skull Cave avian assemblage is characterized by relatively good preservation, body size distribution under 100 g, and a large percentage of terrestrial species and gregarious/non- terrestrial/diurnal species which are irruptive in nature (Figure 4). These characters indicate tytonid owls as the accumulators of the avian assemblage (except for *P. elegans*). The tytonid species involved is indicated by the low value for mean body weight (*i.e. T. alba*). This interpretation corroborates the hypothesis of

Table 5. Avian taxa from excavations of Skull Cave and their proposed taphonomic accumulators.

Taphonomic group	Taphonomic agent	Species associated
Autochthonous /speleophiles		
		Hirundinidae
Allochthonous/avian		
	Tyto alba	
		All other species
	Unknown	
		Phaps elegans

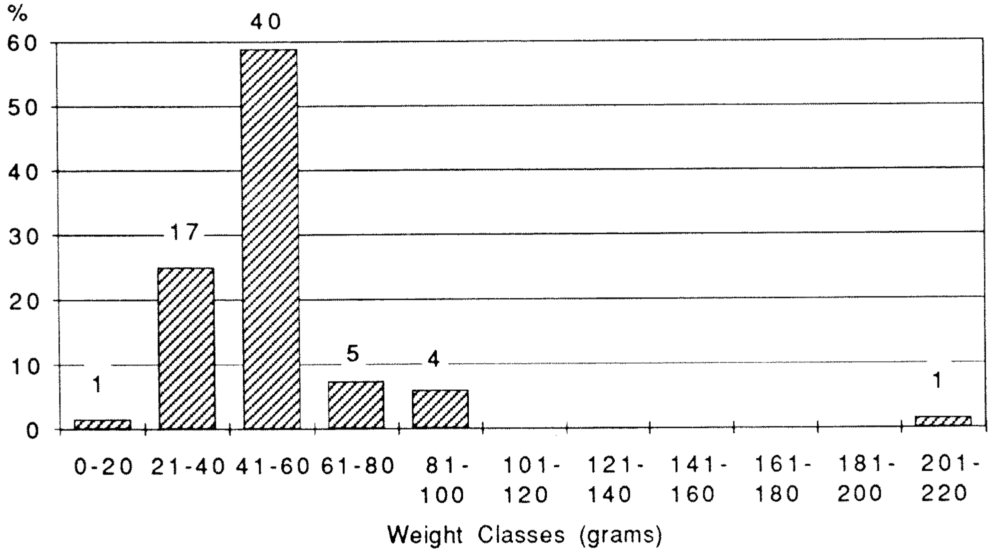

Figure 2. Percentage contribution of weight classes of bird species making up the Skull Cave assemblage (except the hirundinid material) showing the concentration of individuals below the 100 g class. Numbers above the columns represent MNI from a total of 67.

Porter (1979: see Introduction) for an owl accumulated assemblage and is consistant with the microvertebrate assemblage reported to date in that *Tyto alba* includes birds, mammals and amphibians in its diet (Baird in press b, Morgan 1977).

Palaeoenvironmental interpretation.

Although changes in the avian assemblage do not occur throughout the period of deposition, there are some indicators of habitats, which suggest that the environment was largely similar to that of today with a mixture of EOFF and HF, combined with a local wetland dominated by sedges (Table 6). This interpretation corroborates the hypothesis of Porter (1979) for the presence of forest throughout the period of deposition but fails to corroborate the loss of heath or scrub.

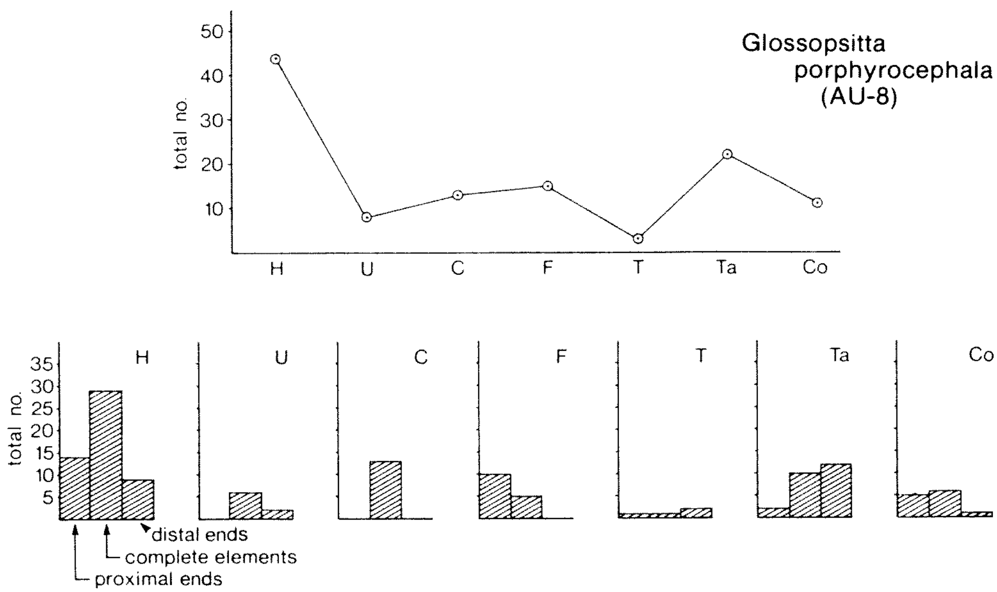

Figure 3. Abundances of seven commonly represented post-cranial elements of *Glossopsitta porphyrocephala* from the excavation of Skull Cave, Western Australia. Included are the sums of complete and most common terminal ends (Top: data points connected to facilitate visual cognition of changes), and the proportions of fragmentary specimens relative to complete (and incomplete) specimens (Bottom). H=humerus, U=ulna, C=carpometacarpus, F=femur, T=tibiotarsus, Ta=tarsometatarsus and Co=coracoid.

Table 6. Groups of avian taxa based on their usefulness in palaeoenvironmental interpretation (habitat specificity (exact/wide ranging)/habitat distribution (patchy/regional)).

Wide ranging/Regional
ETOFF, EOFF, EWF, HF, and MOSF
Coturnix sp.
Glossopsitta porphyrocephala
EOFF and EWF
Playtcercus icterotus
Artamus cyanopterus
HF
Phaps elegans
Exact/Patchy
HF/Wetlands
Dasyornis longirostris
Ecotone between EOFF and Wetlands.
Artichornis clamosus

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Appendix I

List of abbreviations and contractions used in text, figures and appendices.

acet.	*acetabulum*
ATSF	*Acacia* tall scrub formation
ccd	coracoid
cmc.	carpometacarpus
com.	complete
cond.	*condylus*
cot.	*cotyla*
cran.	cranium
cta	*crista*
dist.	distal
EOFF	*Eucalyptus* open forest formation
ETOFF	*Eucalyptus* tall open forest formation
EWF	*Eucalyptus* woodland formation
fac.	*facies*
fem.	femur
frag.	fragment
HF	heathland formation
hum.	humerus
huml	humeral
imp.	*impressio*
inc.	*incisura*
incom.	incomplete
juv.	juvenile
lig.	*ligamenta*
M.	*musculus*
mand.	mandible
MNI	minimum number of individuals
MOSF	mallee open scrub formation
N	number of elements in the statistical population
OR	observed range
pel.	pelvis
proc.	*processus*
prox.	proximal
rost.	rostum
scap.	scapula
σ	standard deviation
stm	sternum
stnl	sternal
sul.	*sulcus*
symph.	*symphysis*
syn.	synsacrum
tbt.	tibiotarsus
tmt.	tarsometatarsus
troc.	*trochlea*
tub.	*tuberculum*
μ	mean
y.B.P.	years Before Present

Appendix II

Suites of characters considered diagnostic for those taxa included in this study. Only those elements for which representatives occur in the cave deposit are included. The sequence of elements is standardized for ease of reference and includes the following: rostrum, cranium, mandible, humerus, ulna, carpometacarpus, coracoid, scapula, furcula, sternum, pelvis, synsacrum, femur, tibiotarsus and tarsometatarsus. For each of the long bones separate sections are provided for the proximal end, shaft and distal end (except for the coracoid, which is divided into humeral end, shaft and sternal end), and each character is numbered. Not included in the analysis were the vertebrae, costal elements and phalanges.

Order Psittaciformes

See Baird (in press c).

Family: Loriidae

Rostrum, 1. not strongly decurved, 2. culmen a sharp, well defined ridge extending distally, 3. external nares located proximally on rostrum, 4, thin nasal septum (W. Boles, pers. comm.); **Humerus,** (proximal end), 1. broad based *caput humeri,* 2. no distal extension of *caput humeri* on palman face, 3. second *fossa pneumotricipitalis* present, 4. *cta bicipitalis* not greatly expanded laterodistally but gradually slopes to shaft distally; **Ulna,** (shaft), 1. stout, 2. large curvature; (whole), 1. medium to small size (this suite of characters also present in *Lathamus*): **Coracoid,** (humeral end), 1. *proc. acrocoracoid* flattened humerally, not bulbous; (shaft), 1. intermediate between being gracile and stocky; (sternal end), 1. broad sternal base, 2. *imp. M. sternocoracoidei* shallow; **Femur,** (proximal end), 1. *cta trochanteris* does not surpass *caput femoris* proximally, 2. *fac ventralis* excavated; (distal end), 1. medial edge tends strongly distomedially; **Tibiotarsus,** (distal end), 1. very deep *sul. cartilaginis tibialis,* 2. *cond. medialis* much larger than *cond. lateralis,* 3. distal end shaft broad; **Tarsometatarsus,** (proximal end), 1. one large enclosed canal in hypotarsus; (shaft), 1. short and stout; (distal end), 1. *fac. dorsalis* flat, 2. ventral extension of *troc. metatarsi IV* appears further distally due to lack of distal extension of *troc. metatarsi III.*

Glossopsitta

Rostrum, 1. proximodistally short, 2. small size; **Cranium,** 1. area between orbit and proximal end wide (viewed laterally): **Humerus,** (proximal end), 1. *cta pectoralis* lacks medially projecting proc. on distal-most tip; **Carpometacarpus,** (proximal end), 1. facet for insertion of *lig. radiocarpometacarpale* more lateral on *troc. carpalis,* 2. more distally located *proc. pisiformis,* 3. T.L. less than 20mm; **Coracoid,** (proximal end), 1. shallow groove present in anteromedial face of acrocoracoid; **Tarsometatarsus,** (proximal end) 1. *cot. lateralis* not as distorted laterally; (whole), 1. total length less than 15.5 mm.

Family: Platycercidae

Carpometacarpus, (proximal end), 1. *proc. extensiorius* tends proximolaterally, 2. *proc. extensorius* gracile, 3. proximal end, as a whole, relatively small; (shaft), 1. gracile; **Tarsometatarsus,** (proximal end), 1. hypotarsus with one large unenclosed canal, ventrally, and rimmed, dorsally, by numerous small enclosed canals; (shaft), 1. long and gracile; (distal end), 1. *troc. metatarsi III* not greatly expanded distally, 2. *fac. dorsalis* flat (except in *Pezoporus, Geopsittacus* and *Neophema).*

Family: Aegothelidae

Tarsometatarsus, (distal end), 1. troc. with very little splaying laterally, 2. distal foramen in a deep groove extending between *troc. metatarsi III* and *IV,* 3. trochleae laterally compressed with narrow intermetacarpal spaces.

Family: Atrichornithidae

Atrichornis

Humerus, (proximal end), 1. insertion of *M. scapulohumeralis* anterior distally extending and pointed, 2. *caput humeri* flattened and at an angle greater than 90 degrees from shaft (measured internally), 3. *tub. ventrale* reduced, 4. *cta pectoralis* strongly arcuate; **Tarsometatarsus,** (distal end), 1. sulci present on all three *troc. metatarsi,* 2. *tub. M. tibialis cranialis* not pronounced, 3. *inc. intertrochlearis* restricted to extreme distal end (they do not pass middle of *troc. metatarsi* proximally, in dorsal view), 4. outer edges of *troc. metatarsi III* taper together distally, in ventral view, 5. inner edge of *troc. metatarsi II* tends proximomedially, in ventral view, 6. *troc. metatarsi II* and *III* equal in size and larger than *troc. metatarsi IV.*

Appendix III

Loriidae

Glossopsitta porphyrocephala

Material

com. rost. (76.10.227), 3 incom. rost. (71.10.158, 75.10.22, 86.7.480), 2 incom. mand., (71.10.184, 76.10.358), 14 incom. right hum. (74.8.43, 74.8.66, 74.8.122, 74,8,125, 74.8.126, 76.1.254, 76.1.263, 76.7.420, 76.10.392, 86.7.432, 86.7.450, 86.7.463), 7 prox. end right hum. (74.8.44, 74.8.68, 76.1.260, 86.7.409, 86.7.416, 86.7.421, 86.7.451), shaft frag. right hum. (86.7.433), dist. end right hum. (86.7.464), com. left hum. (75.10.26), 16 incom. left hum. (74.8.65, 74.8.145, 74.8.197, 74.8.198, 75.10.28, 76.1.137, 76.1.138, 76.1.191, 76.1.192, 76.10.412, 86.7.400, 86.7.417, 86.7.468, 86.7.482, 86.7.490), 7 prox. end left hum. (74.8.18, 74.8.21, 76.10.311, 76.10.356, 76.10.357, 76.10.414, 86.7.418), shaft frag. left hum. (86.7.452), 2 dist. end left hum. (75.10.29, 86.7.426), 3 incom. right ulna (86.7.453, 86.7.491), 4 incom. left ulna (86.7.434, 86.7.492), dist. end left ulna (86.7.435), 3 incom. right cmc. (86.7.407, 86.7.422, 86.7.483), prox. end right cmc. (86.7.401), 4 dist. end right cmc. (86.7.410, 86.7.436, 86.7.469), 2 com. left cmc. (86.7.427, 86.7.437), 7 incom. left cmc. (76.1.210, 86.7.411, 86.7.419, 86.7.470, 86.7.493), 2 prox. end left cmc. (86.7.412, 86.7.479), 4 dist. end left cmc. (86.7.402, 86.7.428, 86.7.471, 86.7.494), com. right ccd (86.7.481), 3 incom. right ccd (86.7.423, 86.7.438, 86.7.472), 5 huml end right ccd (86.7.440, 86.7.449, 86.7.454), stnl end right ccd (86.7.439), com. left ccd (86.7.484), 2 incom. left ccd (86.7.441), 6 huml end left ccd (86.7.442, 86.7.455, 86.7.486) 3 com. right fem. (76.8.97, 86.7.403, 86,7.456), incom. right fem. (86.7.473), 3 prox. end right fem. (86.7.414, 86.7.429, 86.7.465), incom. left fem. (76.1.69), 7 prox. end left fem. (86.7.404, 86.7.430, 86.7.443, 86.7.474, 86.7.487), 2 dist. end right tbt. (86.7.457, 86.7.477), incom. left tbt. (86.7.424), prox. end left tbt. (86.7.425), 3 dist. end left tbt. (86.7.444, 86.7.458), 12 incom. right tmt. (86.7.405, 86.7.415, 86.7.431, 86.7.445, 86.7.459, 86.7.475, 86.7.478, 86.7.488, 86.7.495), prox. end right tmt. (86.7.476), 3 dist. end right tmt. (86.7.446, 86.7.460), com. left tmt. (86.7.447), 8 incom. left tmt. (86.7.406, 86.7.448, 86.7.461, 86.7.466, 86.7.485, 86.7.489), 7 dist. end left tmt. (86.7.408, 86.7.462, 86.7.467, 86.7.495, 86.7.497).

Appendix IV

Unidentified passeriform material from Skull Cave.

incom. rost. (86.7.536), 2 dist. end rost. (86.7.578, 86.7.599), 2 mand. symph. (86.7.537, 86.7.607), right ramus mand. (86.7.628), left ramus mand. (86.7.620), mand. syph. frag. (86.7.627), com. right hum. (86.7.547), 11 incom. right hum. (74.8.46, 74.8.167, 74.8.178, 74.8.179, 76.1.261, 76.1.262, 86.7.566, 86.7.594, 86.7.597, 86.7.608), 10 prox. end right hum. (74.1.259, 74.8.48, 74.8.49, 76.1.193, 76.1.195, 76.1.257, 76.1.258, 86.7.548, 86.7.559, 86.7.600), prox. end frag. right hum. (74.8.168), shaft frag. right hum. (86.7.560), 6 dist. end right hum. (74.8.47, 74.8.197, 86.7.556, 86.7.567, 86.7.579, 86.7.629), 3 com. left hum. (74.8.144, 76.1.321, 86.7.538), 10 incom. left hum. (74.8.67, 74.8.69, 74.8.70, 74.8.71, 74.8.123, 76.10.125, 76.10.312, 86.7.539, 86.7.580, 86.7.604), incom. left hum (juv.) (74.8.121), 6 prox. end left hum. (74.8.72, 74.8.146, 76.1.136, 86.7.581, 86.7.617), prox. end frag. left hum. (76.1.135), 8 dist. end left hum. (75.10.30, 75.10.31, 76.1.320, 76.10.413, 86.7.540, 86.7.545, 86.7.557, 86.7.582), com. right ulna (86.7.583), 2 incom. right ulna (86.7.618), incom. left ulna (86.7.561), prox. end left ulna (86.7.595), com. right cmc. (86.7.562), 7 incom. right cmc. (86.7.584, 86.7.609, 86.7.621, 86.7.630), 10 incom. left cmc. (76.1.277, 86.7.568, 86.7.585, 86.7.605, 86.7.610, 86.7.619, 86.7.622, 86.7.625, 86.7.631), 2 com. right ccd (76.10.263, 86.7.623), 2 incom. pel. (86.7.549, 86.7.569), acet. frag. pel. (86.7.612), 2 com. syn. (86.7.601, 86.7.611), 2 incom. syn. (86.7.551, 86.7.632), 3 com. right fem. (74.8.95, 74.8.98, 76.1.368), 9 incom. right fem. (74.8.99, 76.1.68, 76.10.46, 76.10.193, 86.7.541, 86.7.552, 86.7.563, 86.7.570, 86.7.586), 2 prox. end right fem. (86.7.587, 86.7.606), shaft frag. right fem. (86.7.588), 2 dist. end right fem. (86.7.558, 86.7.571), com. left fem. (86.7.550), 8 incom. left fem. (86.7.543, 86.7.553, 86.7.554, 86.7.564, 86.7.589, 86.7.613, 86.7.694), prox. end left fem. (86.7.576), 4 dist. end left fem. (86.7.544, 86.7.590, 86.7.598, 86.7.614), 3 prox. end right tbt. (86.7.577, 86.7.596, 86.7.615), 4 dist. end right tbt. (86.7.555, 86.7.565, 86.7.572, 86.7.591), 2 incom. left tbt. (86.7.546, 86.7.573), incom. left tbt. (juv.) (86.7.616), 4 prox. end left tbt. (86.7.542, 86.7.574, 86.7.592, 86.7.602), 6 dist. end left tbt. (86.7.575, 86.7.593, 86.7.626), com. right tmt. (86.7.603), dist. end left tmt. (86.7.633).

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