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Avian Fossils from Quaternary Deposits in 'Green Waterhole Cave', South-eastern South Australia

R.F. BAIRD

Department of Earth Sciences, Monash University,
Clayton, Victoria 3168, Australia

ABSTRACT. Sixteen species of birds have been identified from Quaternary-aged deposits in 'Green Waterhole Cave' (L-81 of the Cave Exploration Group of South Australia cave classification) approximately twenty-four kilometres west of Mt Gambier, south-eastern South Australia. All but three species are referable to modern species. The exceptions are a new accipitrid (to be described by Drs P.V. Rich and G.F. van Tets), a new species of coucal, and a new species of passeriform. It is suggested that one of the extant species and all of the new taxa are examples of Pleistocene gigantism. Geographic range extensions are demonstrated for *Gallinula mortierii, Calyptorhynchus lathami* and the genera *Centropus* and *Orthonyx*. Taphonomic study of the deposit, using faunal composition as the main indicator, implies that water was the accumulating agent. Relative dating of the locality has been made by using sea level curves (last sea level transgression over the present eustatic high) and the presence of megafauna. Dating of the last sea level transgression suggests a maximum age of 125,000 years before present (y.B.P.) for the opening of the cave to the surface, because the cave lacks marine influence. The maximum age of accumulation is anytime before 15,000 y.B.P., which is the time of last occurrence of most mammalian megafauna.

'Green Waterhole Cave' (L-81 of the Cave Exploration Group of South Australia cave classification) is a drowned cave in the Tantanoola district of south-eastern South Australia, about twenty-four kilometres west of Mount Gambier (Fig. 1). The host rock is the Gambier Limestone of the Oligo-Miocene-aged Glenelg Group. L-81 lies on the border of the Kongorong Shank and Mt Gambier sections of Marker (1975). Karst production in this area, according to Marker, "has been promoted by late Quaternary marine fluctuations...". The cave shows no marine influence. The last marine incursion into the area at 124,000 y.B.P., therefore, may be taken as a maximum age for the opening of the cave (Shackleton & Opdyke, 1973; Bloom *et al.*, 1974). Karst development would have been aided by subsequent marine fluctuations, increased rainfall and greater seasonal temperature variations, especially during the last glacial (Sweeting, 1973: 156–157), therefore making it likely that the cavern opened to the surface sometime after the last interglacial.

The cavern probably opened in the latter half of the last glacial, based on the large proportion of extant species in the fossil avifauna. The floral history should give an idea of environmental changes during that time. The floral history of south-eastern South Australia and western Victoria is deduced from work on pollen-bearing sediments covering the past 50,000 y.B.P. collected within Lake Leake, S.A. and Lake Keilambete, Vic. (Dodson, 1974a, b, 1975). Briefly, the area was dominated by *Eucalyptus* woodland and heath before the oldest date of 50,000 y.B.P. (the limit of radiocarbon dating) up to 39,000 y.B.P. At this time, there was an ephemeral change to open formation that suggested dryer times. The flora reverted back to *Eucalyptus* woodland and heath understory at 38,000 y.B.P. After 35,000 y.B.P. the precipitation decreased. At about the same time, the coastline migrated further south as a result of the lowering of sea level synchronous with the last glaciation. It is assumed that, from then on, the area was drier than it had been at any other time in the last 50,000 years. *Casuarina* pollen, with
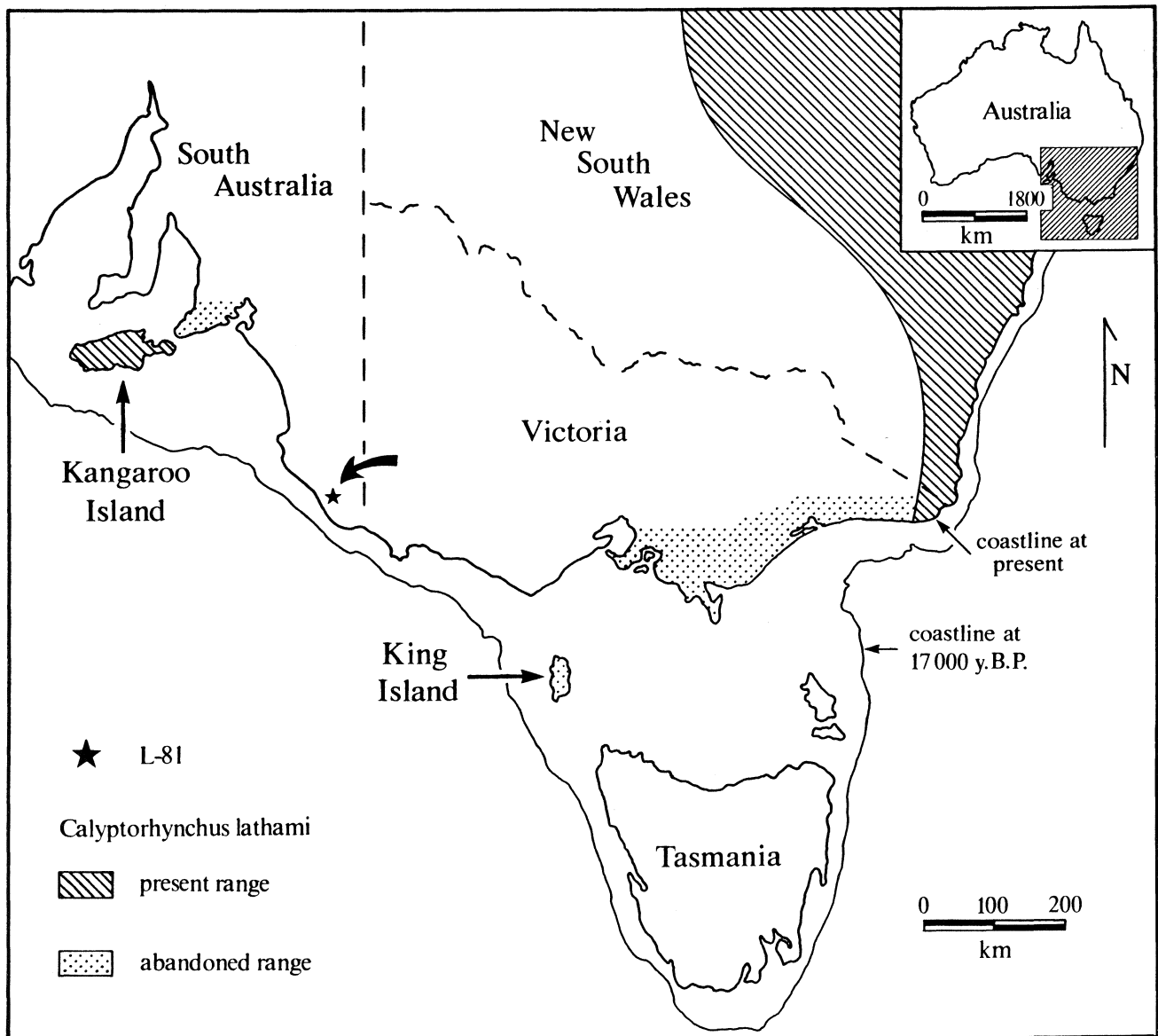
Fig. 1. Distribution of *Calyptorhynchus lathami* in south-eastern Australia including fossil locality, historical geographic range and present day geographic range.

diameters equal to or less than 24μm, dominates the microfloral assemblages continually from this time until approximately 10,000 y.B.P., when *Casuarina* greater than 28μm becomes dominant and continues so until the advent of European settlement. The *Casuarina* species with pollen diameters greater than 28μm is most likely to be *C. stricta*, due to its propensity to forming dense stands, therefore allowing its pollen to dominate microfloral assemblages, and its affinity to coastal and subcoastal areas (Kershaw, pers. comm.). Dodson suggested that, between 6,900 and 5,000 y.B.P., the area between Melbourne and Adelaide was wetter than the same area today, coinciding with the return of sea level to its current position (Thom & Chappell, 1975). The same scenario was suggested for the vegetation of the Nullarbor Plain where, during sea level regression, the

vegetation would have changed from eucalypt scrub to treeless plain. Upon sea level transgression, the eucalypts became locally dominant once again (Martin, 1973). This sequence of events corresponds to the movement of the humid zone associated with the coastline. Since European settlement, most of the forest cover has been removed, a process advanced even by 1915 (Marker, 1975).

The dimensions and early history of excavation of 'Green Waterhole Cave' are described and figured by Pledge (1980). Additional material has since been collected under the supervision of Dr R. Wells in a series of trips between 19 January 1979 and 6 March 1979. Large amounts of postcranial material have been retrieved by Dr Wells, and the bulk of the avian material, here discussed, has come from his excavations.

Pledge found the mammalian assemblage to be of mixed age, with both extant and extinct taxa represented in a deposit which had lent itself to the mixing of noncontemporaneous material. Though there is a definite stratification to deposits at this site, interpretation is difficult due to post-depositional slumping of the talus cone and the constraints of underwater excavating (Wells, pers. comm.). The mode of accumulation, as hypothesized by Pledge, was through drowning and subsequent settling of the corpses. Hypotheses concerning the cause for the initial drowning vary, and in this paper another scenario is offered.

Prior lists of the avian species in 'Green Waterhole Cave' were correct in most of their higher taxa determinations. Incorrectly identified were the specimens referred to *Genyornis* and *Dromaius* mentioned in Williams (1980) and Rich & van Tets (1982), respectively. Both records are most probably referable to a single specimen of a juvenile macropod right femur. The *Megapodius* of Rich & van Tets (1982) was also misidentified and is, in actual fact, *Gallinula mortierii*.

ACCOUNT OF SPECIES

The scientific names used in each account follow Condon (1975) and Schodde (1975), except in the case of the fossil taxa, where I follow Brodkorb (1971). Taxa previously unknown from subfossil and fossil deposits are also noted. Inclusions in the faunal lists of Rich & van Tets (1982) are not considered to be 'formally confirmed records' as no full diagnoses were put forward. Minimum numbers of individuals were determined by the standard method of counting the most abundant element from a particular side.

Geographic ranges given for each extant species are from Wheeler (1967), Condon (1969), Green (1977), Parker & Reid (1983) and Blakers *et al.* (1984) and are here assumed to be the same as the present range, unless otherwise noted.

Specimens and specimen numbers belong to the South Australian Museum.

All measurements in the text are in millimetres (mm). Standard measurements are indicated in brackets and follow the guidelines in von den Driesch (1976). All measurements were taken with vernier calipers accurate to 0.05 mm and were rounded to the nearest 0.1 mm.

ACCIPITRIFORMES

Accipitridae

new species

Material. Complete left and right ulnae (P.24324 & 24323), complete left and right radii (P.24325 & 24326), complete left and right carpometacarpi (P.24327 & 24328), all from site 07. In addition, there is a fourth thoracic vertebra (P.24329), site unknown, which seems

referable to this taxon. The specimens represent a minimum of 1 individual.

Remarks. This form will be fully described at a later date by Drs P.V. Rich and G. van Tets.

Interestingly, the left and right radii are completely different in colour, one being dark brown and the other being light tan. In all other respects the elements seem to be identical. This should be kept in mind when other composite skeletons from the deposit are being considered for it suggests that the coloration of each element may not be a reflection of its relative time of deposition.

Falconidae

Falco cf. *berigora*

Material. Incomplete right femur (P.24330).

Remarks. The specimen is assigned to this species on the basis of overall length measurement and slenderness. As compared with other Australian falconids of similar size (*F. peregrinus* and *F. subniger*), *F. berigora* has the most slender limb elements (Rich, van Tets & McEvey, 1982). Usually slenderness in postcranial elements varies concurrently with overall size and would not be a reliable character to base species identification on. But because *F. berigora* is unusual in that it is so consistently gracile through its size range, I have referred the element to this species.

GRUIFORMES

Rallidae

Gallinula mortierii

Material. Complete (P.24236) and incomplete (P.24237) right femora, incomplete left tibiotarsus (P.24238), proximal end of a left tibiotarsus (P.24234), 3 complete right tibiotarsi (P.22951, 24232 & 24233), incomplete right tibiotarsus (P.24239), incomplete left fibula (P.24235), and first phalanx for digit II (P.17349). The 10 specimens represent a minimum of 4 individuals.

Remarks. The main diagnostic features used in the identification of *Gallinula mortierii* are the large size and stoutness of its postcranial elements, whose dimensions are greater than those of all other Australian rallids (Olson, 1975). Measurements of *G. mortierii* material from Late Pleistocene-aged deposits are presented in Baird (1984).

The continental Pleistocene distribution for *G. mortierii* ranged from Kangaroo Island to Queensland. The largest concentration of fossil sites containing this species are centred about the Glenelg River region (Baird, 1984). The material from L-81 included the smallest tibiotarsus from any site in continental Australia, but its measurements could not be included in the statistics of Baird (1984) due to its incompleteness. Several of the *G. mortierii* elements from L-81 were larger than average, so a normal size distribution can be assumed for the fossil population from this site. The species is currently restricted to the island of Tasmania.

COLUMBIFORMES

Columbidae

Phaps chalcoptera

Material. Two incomplete left tibiotarsi (P.24331 & 24332).

Remarks. Three species of large columbid currently occur in south-eastern South Australia, *Phaps chalcoptera, P. elegans* and *Ocyphaps lophotes. Ocyphaps lophotes* is considered to be a relatively recent immigrant to the south-east, having colonized within the last 30 years (Parker & Reid, 1983). These three species exhibit considerable overlap in tibiotarsal lengths. The smallest and largest species can be identified beyond the areas of overlap with some certainty, but the median species cannot, on length measurements alone (see Table 1). The lengths of the fossil specimens (P.24331 & 24332) are 51.0 mm and 55.0 mm, respectively. Although the larger specimen may be reasonably referred to *P. chalcoptera*, the smaller is essentially indeterminate by size and, therefore, can only be referred to *Phaps* sp.

Table 1. Tibiotarsi length measurements [La] of the large columbid species presently inhabiting the area around L-81, south-eastern South Australia.

	mean	S.D.	min	max	N
Phaps chalcoptera	54.2	1.8	51.0	56.3	10
P. elegans	51.0	1.6	47.8	53.1	10
Ocyphaps lophotes	46.6	2.0	43.9	49.5	10

PSITTACIFORMES

Cacatuidae

Calyptorhynchus magnificus

Materials. Incomplete cranium (P.24333), incomplete left humerus (P.24335), distal end of a right radius (P.24336) and complete right femur (P.24337). The 4 specimens represent a minimum of 1 individual. Neither the genus nor species have been recorded previously in the fossil record.

Remarks. Characters distinguishing *Calyptorhynchus* from the larger species of *Cacatua* are listed in Table 2. Most apparent are the differences in the crania, with the crania of calyptorhynchids being anteroposteriorly elongate and dorsoventrally flattened. The cranial lengths and widths vary greatly among species in *Calyptorhynchus*, and the incomplete cranium (P.24333) falls well within the range of *C. magnificus* (Fig. 2). The cranium of *Callocephalon* exhibits features similar to those seen in *Calyptorhynchus*, although such modifications are probably correlated with feeding mechanics. Because of the convergent characters in the skulls of *Callocephalon* and *Calyptorhynchus*, postcranial characters, rather than cranial characters, appear to be more reliable for generic level identification because of their uniformity within each genus. This is due to the fact that feeding mechanisms may exhibit considerable plasticity intragenerically in the Cacatuidae, while locomotor mechanisms within generic groups remain essentially unvaried. Therefore, at the species level, both cranial and postcranial elements are useful for identification but, at the generic level, postcranial elements are more reliable due to their intrageneric uniformity. *Calyptorhynchus magnificus, C. funereus* and *C. lathami* differ considerably in size (see Appendix), and the fossil humerus (GL = 80.6) and femur (GL = 58.1) fall only within the size ranges of these elements for *C. magnificus*.

Calyptorhynchus lathami

Material. Incomplete rostrum (P.24334). Species previously unrecorded in the fossil record.

Remarks. Identification of *Calyptorhynchus* species can be easily accomplished using characters of the rostrum (Fig. 3). In *C. lathami*, the rostrum is antero-posteriorly short, laterally broad, with a diagnostic swollen dorsal surface and external nares that are level with the surface. In *C. funereus*, the rostrum is anteroposteriorly long, laterally flattened and with external nares that are level with the surface. In *C. magnificus*, the anteroposterior length of the rostrum is intermediate between that of *C. funereus* and *C.*
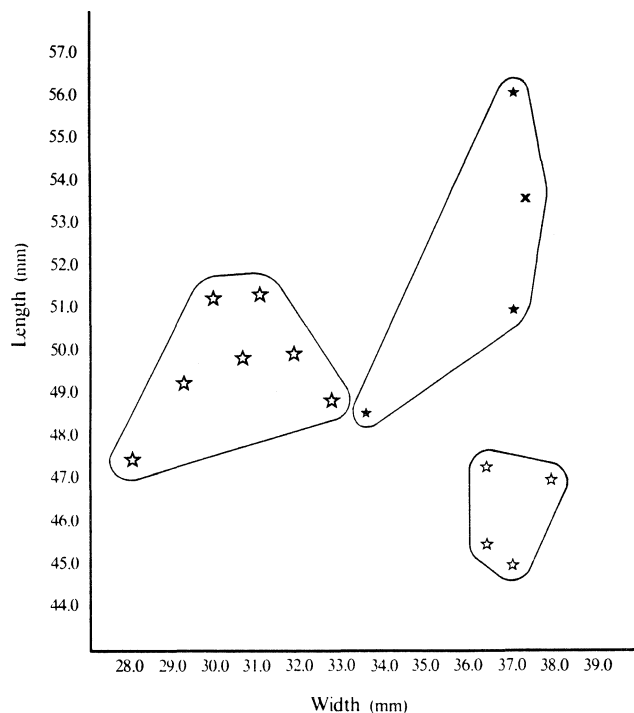

Fig. 2. Plot of cranial measurements (length [LP] and width [SBO]) of extant species in the genus *Calyptorhynchus*, including *C. lathami* (small open stars), *C. funereus* (large open stars) and *C. magnificus* (small closed stars). The X denotes the position of the fossil cranium (P.24333) on the plot.

Table 2. Morphological characters separating *Calyptorhynchus* from all other Australian cacatuids.

	Calyptorhynchus	Other cacatuids
Rostrum		
• external nares	• very small	• very large
Cranium		
• temporal foramen	• very large	• small
• temporal fossa	• proximodistally and dorsolaterally expanded	• proximodistally short and dorsolaterally narrow
• occiput	• displaced distally (not beneath the braincase)	• positioned beneath braincase
• tympanic wing of the exoccipital	• occupies a vertical plane	• occupies a horizontal plane
Humerus		
• bicipital crest	• gently slopes into shaft distally	• abruptly joins shaft distally
• pneumatic fossa	• shallow	• deep
• angle between the shaft axis and capital groove axis	• small	• large
• ventral tubercle	• proximodistally facing	• ventrally facing
Coracoid		
• brachial tuberosity	• extends further humerally	• extends humerally to a lesser degree
• impressio M. sternocoracoidius	• is more elongate humerosternally	• is less elongate humerosternally
Femur		
• fossa just below the antitrochanter articular facies on ventral side	• shallow	• deep
Tarsometatarsus		
• sulcus on the trochlea for digit three	• very shallow	• very deep

lathami. Calyptorhynchus magnificus also has a diagnostic ridge running dorsally between the two external nares, and external nares that are not level with the surface, but raised on small pedestals. Many workers have noted differences in the shape of the rhamphotheca in *C. magnificus, C. funereus* and *C. lathami* (Forshaw, 1969:51), but no-one has correlated these with equally large differences in the rostra. The form of the rhamphotheca depends upon the particular species' diet and can even vary between different populations of the same species. Ford (1980) demonstrated that the variation in the rhamphotheca in *C. magnificus* is correlated with the diet of the different populations. Populations in mid-western Western Australia have a large rhamphotheca and are ground feeders, concentrating on the large seeds of *Emex australis.* Populations in south-eastern South Australia and western Victoria have relatively small rhamphotheca and feed arboreally on seeds of *Eucalyptus baxteri* and *E. macrorhyncha.* Similar variability exists in south-western populations of *C. funereus sensu lato* (Saunders, 1974). Although the ramphethecae vary greatly between these populations, the rostra demonstrate less variability and are markedly constant within a species, while quite different between species.

Calyptorhynchus lathami, unlike its congeners, has a strong dependence upon seeds of one genus of plant throughout its range, *Casuarina* (including *Casuarina stricta, C. littoralis* and *C. torulosa;* Cleland & Sims, 1968). This relationship was first noted some time ago (North, 1896) and has been substantiated by recent studies of the species' ecology (Joseph, 1982). Of the species in the genus *Casuarina* with pollen diameters over 28μm (Kershaw, 1970), it is important to note that *C. stricta* is assumed to be the species of *Casuarina* dominating microfloral assemblages for the region from 10,000 y.B.P. to the present (Dodson 1974a, b, 1975;

Kershaw, pers. comm.).

The range of *C. lathami* has contracted since European settlement of south-eastern Australia (North, 1896; Backhouse, 1843; Lendon, 1968). Given the geographical position of L-81 (see Fig. 1), the evidence strongly suggests that the species once had a continuous distribution at least as far west coastally as Kangaroo Island. Hypothetically, the last glacial lowering of the sea, which reached its lowest level around 15,000–18,000 y.B.P. (Martin & Peterson, 1978), would have allowed the range of *C. lathami* to be extended south and west of its present eastern limits, along the expanded coast and possibly onto the coastal plain exposed between Tasmania and the mainland. It is possible that the distribution from the east coast of Australia to Kangaroo Island could have been complete from as early as 18,000 y.B.P. As *Casuarina stricta* is a coastal species, the distribution of *Calyptorhynchus lathami* would have fluctuated back and forth with the changes of the coastline. This type of change would have left relict populations of *Calyptorhynchus lathami* on all those islands capable of supporting large stands of *C. stricta.* This hypothesis is to some extent corroborated by Green & McGarvie's (1971) report that *Calyptorhynchus lathami* may have occurred on King Island. It is proposed that the ultimate prehistoric distribution, which was presumably continuous to Kangaroo Island, was split by the sea level rising into the volcanic region of Victoria's western districts. The habitat on the volcanic plains, savannah grassland, is regulated not by precipitation but by the volcanic rock substrate, and hence tends to resist changes in the vegetation during climatic amelioration (Dodson, 1974a). This would have effectively fragmented *C. lathami's* habitat, leaving disjunct distributions to the west and east. These populations have since been separated even further through land clearance
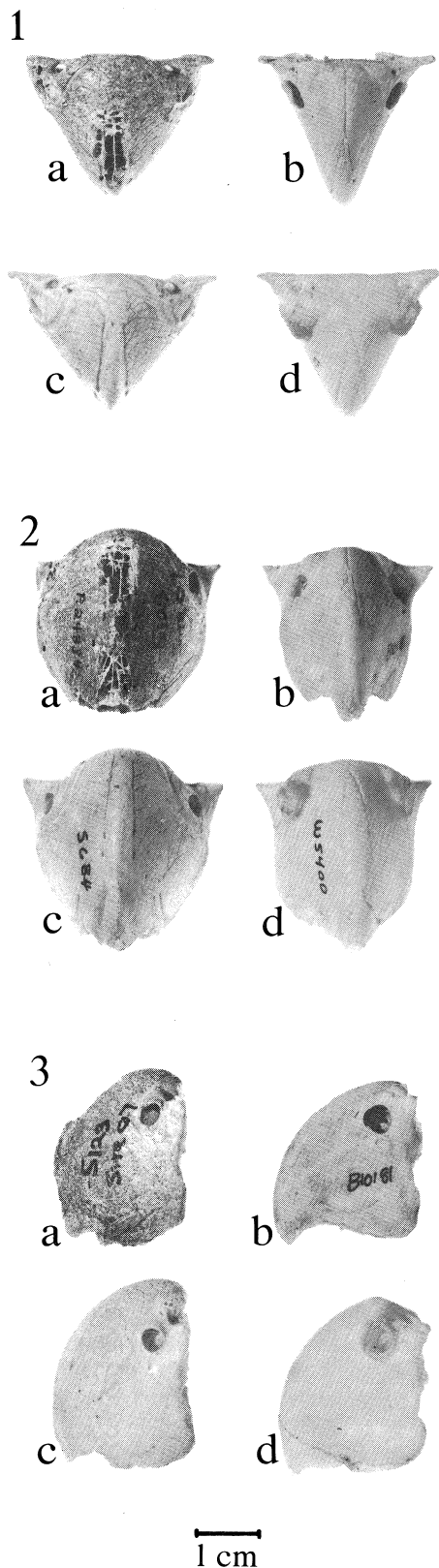
Fig. 3. Rostra of the three species of *Calyptorhynchus* inhabiting south-eastern Australia, *C. lathami* (AM S684) [1c, 2c, 3c], *C. funereus* (MV B10181) [1b, 2b, 3b], *C. magnificus* (MV W5400) [1d, 2d, 3d], compared with the fossil *Calyptorhynchus* rostrum (P.24334) [1a, 2a, 3a]: 1, dorsal views; 2, anterior views; 3, lateral views.

accompanying European settlement, eventually restricting the populations to the far east coast of the Australian mainland and to Kangaroo Island, South Australia.

Callocephalon fimbriatum

Material. Complete cranium (P.24338). Genus previously unrecorded in the fossil record.

Remarks. The skull of *Callocephalon*, with its less domed cranium (due to the distended occiput), large temporal fossa and diminutive size, is remarkably similar to the skulls of *Calyptorhynchus* spp.. Both are quite distinct from those of all other Australian cockatoos (see Appendix). An additional distinctive character in *Callocephalon* is the narrow bridge between the orbit and the anterior-most point of the cranium, as viewed laterally, which distinguishes this species from those of *Calyptorhynchus*.

Callocephalon fimbriatum was probably removed from its former range throughout the south-east of South Australia by the extensive land clearance during the initial stages of European settlement. At present, *C. fimbriatum* is quite abundant in the Lower Glenelg National Park along the Victorian and South Australian border and, given sufficient forest expansion, would probably frequent the south-east of South Australia (see Condon, 1969).

Cacatua tenuirostris

Material. Three incomplete crania (P.18301, 24339 & 24340), incomplete rostrum (P.24341), 11 complete or partial left humeri (P.18320, 24342-24351), 31 complete or partial left humeri (P.17287, 17311, 17322, 17323, 18334, 24352-24364), 10 complete or partial left ulnae (P.17332, 17333, 18340, 24365-24370), 11 complete or partial right ulnae (P.17324, 17325, 18340, 24371-24380), 3 incomplete left radii (P.24390-24392), 2 distal fragments of left radii (P.18318 & 18318), 7 complete right radii (P.24381-24389), 2 proximal fragments of right radii (P.24388 & 24389), distal end of a right radius (P.18318), 7 complete or partial left carpometacarpi (P.17336, 17337, 18321, 18338, 24393, 24394), 5 complete or partial right carpometacarpi (P.17327, 17342, 24395-24397), 3 complete right coracoids (P.17346 & 18336), 3 partial sterna (P.24398-24400), 7 complete or partial left femora (P.17329, 17339, 17340, 24401-24403), 3 complete or partial right femora (P.24404-24406), 5 complete or partial left tibiotarsi (P.17330, 24416-24419), 8 complete or partial right tibiotarsi (P.24407-24415), incomplete left tarsometatarsus (P.17344), 2 incomplete right tarsometatarsi (P.24420 & 24421) and incomplete synsacrum (P.17328). The 127 specimens represent a minimum of 31 individuals. Species previously unrecorded in the fossil record.

Remarks. *Cacatua* can be distinguished from *Calyptorhynchus* by the characters set out in Table 2. Therefore, the determination of *Cacatua tenuirostris* need involve only the genus *Callocephalon* and other species in the genus *Cacatua*.
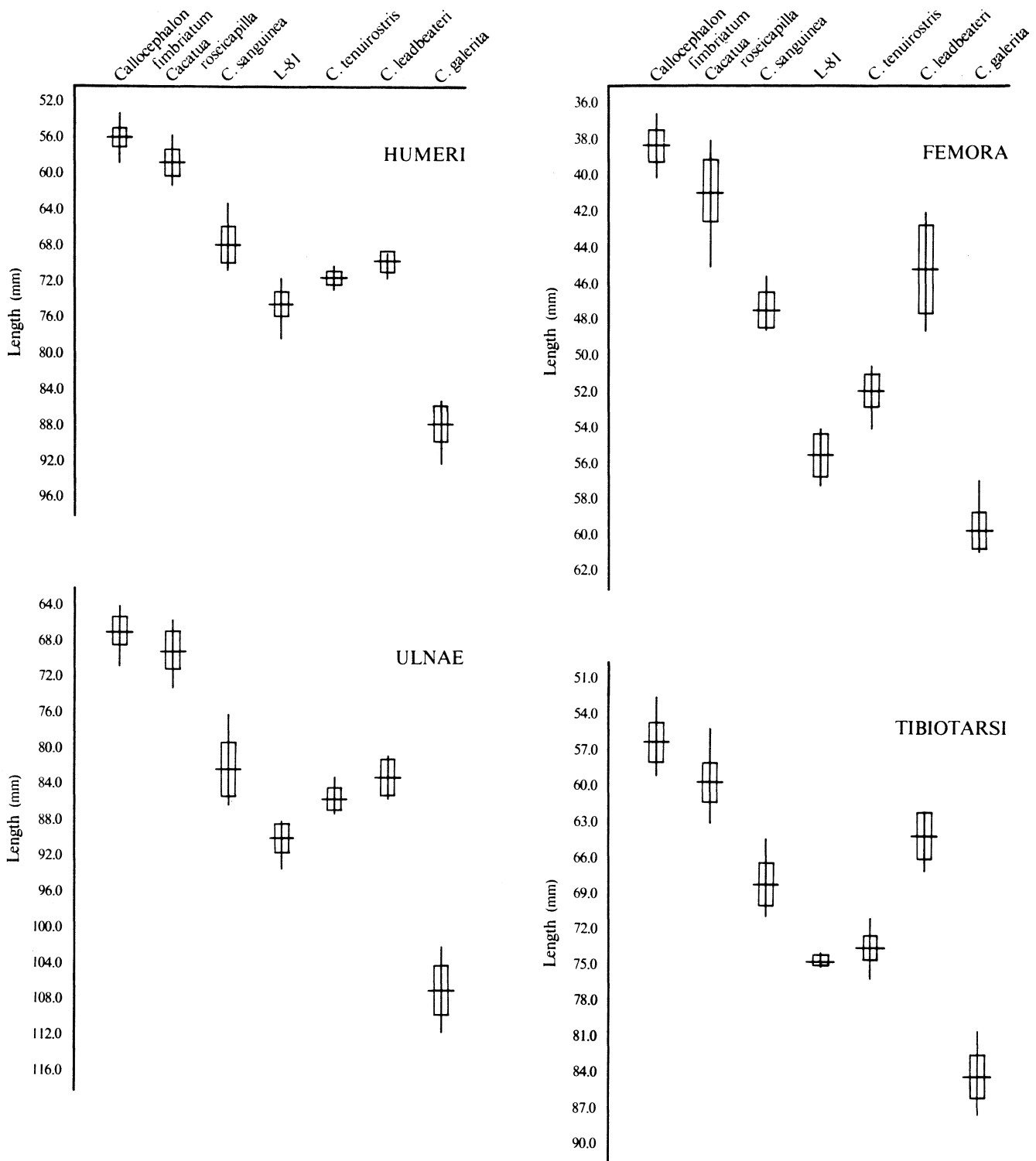
Fig. 4. Length measurements of humeri, ulnae, femora and tibiotarsi of *Cacatua* specimens from L-81 compared with those for all other south-eastern Australian representatives of the genera *Cacatua* and *Callocephalon*. Horizontal line is the mean, vertical the range and open box 90% of the population.

For conservation of space I will deal only with the most abundant element of *C. tenuirostris* in the deposit, the humerus: the distinguishing characteristics for all other elements can be seen in Figure 4. For the species of cockatoo involved, there can be designated three groups of humeral lengths, i.e., small, medium and large (see Fig. 4 and Appendix). The small-size group includes *Callocephalon fimbriatum* and *Cacatua*

roseicapilla. Humeri of *C. fimbriatum* are most similar to calyptorhynchids in that the bicipital crest gently slopes into the shaft distally, the pectoral crest is positioned further distally than that of other cacatuids, and the pneumatic fossa is shallow. The humerus of *C. roseicapilla* differs from that of *C. tenuirostris* in having a small pneumatic fossa, and in its diminuitive size.

The large-size group consists of only *C. galerita*,

Table 3. Morphological characters separating the south-eastern populations of *C. tenuirostris* from *C. sanguinea* (for specific length measurements see Appendix).

	C. tenuirostris	C. sanguinea
Rostrum		
• diameter of external nares	• greater	• lesser
• width between external nares	• greater	• lesser
• culmen curvature	• lesser	• greater
• distinct tomial notch	• lacking	• present
Humerus		
• on the anterior face of the pectoral crest	• small posterior groove	• no groove
• pneumatic fossa	• deep	• shallow
• angle between the capital groove and the shaft axis	• greater	• lesser
Ulna		
• length	• greater	• lesser
Carpometacarpus		
• length	• greater	• lesser
Coracoid		
• length	• greater	• lesser
Femur		
• fossa just below the antitrochanter articular facies on the ventral side	• double	• single
Tibiotarsus		
• length	• greater	• lesser
Tarsometatarsus		
• length	• greater	• lesser

whose humerus differs from that of *C. tenuirostris* in having a less attenuate pectoral crest. Because of the lack of dorsal expansion, the pectoral crest slopes distally with a lesser angle into the shaft. The humeral shaft in *C. galerita* is also relatively stouter.

Of the medium-size group. *C. sanguinea* and *C. tenuirostris* differ from *C. leadbeateri* in their laterally expanded pectoral crests (*C. leadbeateri* is similar to *C. galerita*), and their prominant ventral midshaft ridge. This last feature is lacking in both *C. leadbeateri* and *C. galerita. Cacatua sanguinea* and *C. tenuirostris* can be separated by characters given in Table 3.

The fossil material conforms to all aforementioned characters of *Cacatua tenuirostris*, although, as can be seen in Figure 4, for the fossil elements considered, most are clearly larger than the sample population of *C. tenuirostris*. The average difference between the mean values of the fossil and modern populations is four percent. This is considered to constitute an avian example of Late Pleistocene gigantism similar to that seen in Victorian samples of the kangaroo species *Macropus giganteus* (Flannery, 1981). Therefore, the fossil material is here still considered referable to the extant species, *Cacatua tenuirostris*.

As with other large species in the order Psittaciformes, *Cacatua tenuirostris* has had a history of range contractions and expansions (Jarman, 1979). The species has been ubiquitous in south-eastern South Australia since European settlement (Parker & Reid, 1983).

Cacatuidae indeterminate

Material. Anterior cranial fragment (P.24422), 5 right humeral fragments (P.24423–24427), 2 left ulnal fragments (P.17331 & 17334), right ulnal fragment (P.17289), 4 left tibiotarsal fragments (P.24429–24432)

and 5 right tibiotarsal fragments (P.17326, 24433–24436). The 18 specimens represent a minimum of 5 individuals.

Remarks. All of these specimens are deficient in the regions where diagnostic characters occur, but most are sufficiently intact to be placed within the Cacatuidae on morphology and size.

Platycercidae

Platycercus sp.

Material. Incomplete rostrum (P.17345). Family previously unrecorded in the fossil record.

Remarks. The specimen has a tomial notch and a width of 11.2 mm (measured ventrally at the midpoint between the external nares). The presence of a tomial notch rules out the Australian species in the genera *Trichoglossus* and *Glossopsitta*. The size of the rostrum precludes its placement in any genus except *Platycercus*, since *Apromiscus* and *Barnardius* are too large, and all others are too small. The local representatives of *Platycercus, P. elegans* and *P. eximius*, have similar-sized rostra, even though the postcranial elements of *P. eximius* are 10% smaller, on average, than those of *P. elegans*. The determination will, therefore, be made as *Platycercus* sp.

CUCULIFORMES

Cuculidae

Centropus colossus n. sp.

Materials. Slightly damaged left humerus (P.24240)

Diagnosis. The characters of the proximal end (e.g., small pneumatic foramina with little or no pneumatic fossa, and head tilted backwards and rotated clockwise)

1 cm

Fig. 5. Stereoviews of the type specimen of *Centropus colossus* (P.24240): 1, anconal view; 2, palmar view.

and those of the distal end (e.g., the impression of the M. brachilis anticus being restricted to the extreme distal end, the ectepicondylar prominence located further proximally, and the distal end not flared laterally), distinguish this humerus from those of members of the Strigiformes and Caprimulgiformes and place it in the Cuculidae. It is here allocated to the Centropodinae, containing the type-genus *Centropus*, not for any single character but for its suite of characters (see Table 4). These characters include: shaft swollen where it contacts the humeral head ventrally; dorsal fossal arm broad and extending distally; scar for M. triceps humeralis (just below the pneumatic foramen) pronounced and rounded; humeral head swollen; pectoral crest with a continuous, even curve to the midline of the shaft's dorsal surface; muscle scars for M. pectoralis reduced; shaft expanded around a deep fossa M. brachialis; process flexorius narrow (medially) and twisted inwardly (medially), giving it an acute lateral point (see Fig. 5).

Holotype. Slightly damaged left humerus (P.24240). Collected under the supervision of Dr R. Wells in 1979. Measurements: total length, 73.0 mm; proximal width, 18.5 mm; distal width, 16.0 mm; width of shaft at midline, 7.0 mm; depth of shaft at midline, 6.0 mm.

Etymology. From Latin, *colossus*, of very great size. This fossil species is larger than any of the extant species in the genus *Centropus* and is one of the largest species of cuculid in the world.

Description. Humeral head swollen with small shelf overhanging capital insertion. Ventral tuberculum large; pneumatic foramen small with respect to the rest of the head. Shaft of humerus curved and stout. Dorsal supracondylar process low and rounded. Dorsal condyle proximodistal axis almost parallel with axis of shaft. Large process just medial to the sulcus of M. scapulotricipitalis (refer to diagnosis for all other characters).

Remarks. Many of the characters of the holotype of *Centropus colossus* are considered indicative of some degree of flightlessness (e.g., strongly twisted pectoral crest; reduced muscle scars; stout, curved shaft; etc.) as set out in Rich, McEvey & Baird (1985). Other characteristics of the specimen, such as the very deep M. brachialis fossa and the expanded distal end of the humerus, may be of some use in separating some groups within the Cuculidae. I have refrained from using any single character to determine the relationships of the element and, instead, have used a suite of characters.
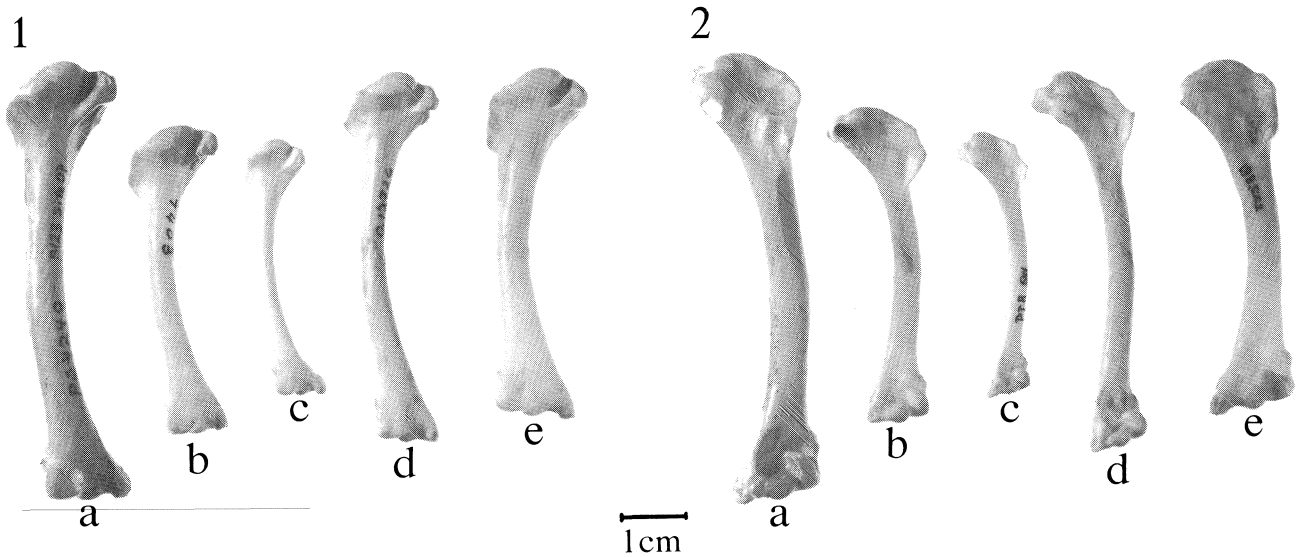
Fig. 6. Humeri of Cuculidae species illustrating differing manifestations of characters which are considered to be correlated with various levels of use of the wings for flight: 1, anconal view; 2, palmar view; a, *Centropus colossus* (P.24240); b, *C. menbeki* (AMNH 7403); c, *Geococcyx californianus* (PTR 574); d, *C. phasianinus* (QM 0.12726); e, *Carpococcyx renauldi* (UNMZ 223881).

Some of these characters are, in fact, common to other flightless species within the family, but in none do they manifest themselves in quite the same way (see Figs 5, 6 and Table 4).

The presence of the genus *Centropus* in this deposit extends its range much further south than is presently recorded. The only extant species of *Centropus* in Australia, *C. phasianinus*, is presently restricted to areas north of Sydney, New South Wales.

CORACIIFORMES

Alcedinidae

Dacelo novaeguineae

Material. Three complete right humeri (P.24437, 24438 & 24439), incomplete left ulna (P.24440), 2 incomplete right ulnae (P.24441 & 24442) and complete right radius (P.24443). The 8 specimens represent a minimum of 3 individuals. Subfamily previously unrecorded in the fossil record.

Remarks. The two Australian species within the genus *Dacelo* have humeri that are at least fifty percent longer than those of all other species in the family Alcedinidae occuring in south-eastern Australia. In the elements discussed, no diagnostic morphologic characters have been found to separate the two Australian species of *Dacelo*. However, the two species can be separated by comparison of the total lengths of these elements (see Table 5). The fossil material falls well within the size range for *D. novaeguineae* (see Table

5) and, therefore, has been assigned to that species. Currently, *D. novaeguineae* can be found along the whole of eastern Australia and the south-western tip of Western Australia, while *D. leachii* is restricted to the northern half of Australia.

PASSERIFORMES

Hirundinidae

Genus and species indeterminate

Material. Complete left humerus (P.24445)

Remarks. Of the four resident species of swallow in Australia (*Hirundo neoxena, Cecropis ariel, C. nigricans* and *Cheramoeca leucosternum*), three can be classed as speleophiles (*Hirundo neoxena, Cecropis ariel* and *C. nigricans*). All three of these cave-nesting species breed in the south-east of Australia, two frequently (*H. neoxena* and *Cecropis ariel*) and one infrequently (*C. nigricans*).

The Australian Hirundinidae, as a group, are osteologically diagnostic in their adaptions to life on the wing. Within the family, however, their uniformity poses many problems since they are so remarkably uniform, with regard to bone morphology and size, that species, and even genera, cannot be differentiated with confidence. Likewise, all three species occur within the south-east and, therefore, even biogeographical probability is ruled out as a method of identification, even though this is an unacceptable criterion. The material must, for the present, be assigned to

Table 4. Morphological character distribution of the humerus in the following specimens (– = character lacking; + = character present). **A**, Area of shaft ventral to the dorsal tubercle swollen as it meets the humeral head therefore not producing a shelf below the humeral head; **B1**, Pneumatic foramen small with the dorsal fossal arm broad and distally extending; **B2**, Muscle scar for M. triceps humeralis just below pneumatic foramina is pronounced (u) and rounded (v); **C**, Humeral head swollen; **D**, Pectoral crest with a smooth even curve to the midline of the shaft's dorsal surface (x), with deep furrow running ventral to the crest (y); **E**, Muscle scars for the attachment of the M. pectoralis are reduced; **F**, Shaft curved and stout; **G**, Fossa for M. brachialis deep and areas of shaft around fossa swollen; **H**, Process flexorious narrow (medially) and twisted inward (medially).

	A	B 1/2	C	D	E	F	G	H
Cuculiformes								
Musophagidae								
Musophaga violacea (MV B12565)	–	–/–	+	–	–	–	–	+
Cuculidae								
Cuculinae								
Clamator coromandus (USNM 343240)	–	+/+	–	–	–	–	–	–
Cuculus sparveroides (USNM 343990)	+	+/u	–	–	–	–	–	–
C. canorus (AMNH 5131)	–	+/+	–	–	–	–	–	–
C. variolosus (MV B77)	+	+/+	+	–	–	–	–	–
C. pyrrhophanus (MV B12657)	–	+/+	+	–	–	–	–	–
Chrysococcyx lucidus (MV B12697)	–	+/+	–	–	–	–	–	–
Scythrops novaehollandiae (CSIRO CUCS18)	+	–/u	–	–	–	–	–	–
Phaenicophaeninae								
Coccyzus erythropthalmus (PTR 454)	–	+/+	–	–	–	–	–	–
Piaya cayana (AMNH 4352)	–	+/+	–	–	–	–	–	–
Rhopodytes tristis (NMNH 344368)	–	+/+	–	–	–	–	–	–
Crotophaginae								
Crotophaga sulcirostris (PTR 675)	+	+/+	–	–	–	–	–	–
Neomorphinae								
Geococcyx californianus (PTR 574)	–	+/+	–	×	+	–	–	–
Carpococcyx renauldi (UMMZ 223881)	–	–/–	–	–	+	+	–	–
Couinae								
Coua caerulea (AMNH 10070)	+	–/–	+	–	+	+	–	–
Centropodinae								
Centropus goliath (USNM 557153)	+	+/+	+	+	+	+	+	+
C. menbeki (AMNH 7403)	+	+/+	+	+	+	+	+	+
C. phasianinus (QM 0.12726)	+	+/+	+	+	+	+	–	+
C. sinensis (USNM 344697)	+	+/+	+	y	+	+	+	+
C. monachus (USNM 322605)	+	+/+	+	y	+	+	+	+
C. colossus (P.24240)	+	+/+	+	+	+	+	+	+

Hirundinidae, indeterminate.

Orthonychidae

Orthonyx hypsilophus n. sp.

Material. Incomplete pelvis (P.24444).

Diagnosis. The fossil pelvis is similar to that of *Orthonyx* and differs from that of all other Australian passeriform genera in having the dorsal iliac crest divisible into two parts, anterior and posterior. The anterior part (median dorsal ridge) is a single crest composed of both the left and right ilia with no influence from the neural crests of the sacral vertebrae. The posterior parts (left and right) divide abruptly from the anterior part, each then running laterally, at right angles to the midline. The dorsolateral iliac crests are less than half as long as the anterior part of the dorsal iliac crest (see Fig. 7).

Compared with the pelvis of *O. temminckii* and *O. spaldingii*, that of the holotype is characterized by having the following: greater overall size (see Table 6);

Table 5. Humeri: total length measurements [GL] of several taxa of Alcedinidae whose present distributions (except *D. leachii*) encompass south-eastern Australia.

	mean	S.D.	min.	max.	N
Ceyx azureus	25.1	0.3	24.7	25.4	4
Dacelo novaeguineae	69.7	1.7	66.5	71.9	10
L-81	68.9	2.6	66.0	70.9	3
D. leachii	64.3	2.6	61.2	67.5	4
Halcyon pyrrhopygia	31.7	0.8	30.8	32.3	3
H. sancta	30.0	0.6	28.5	30.3	10

a dorsally more attenuate, deeper, anterior part of the dorsal iliac crest; very pronounced, fully enclosed pits, medial, and furrows, dorsal, to the acetabula; a concave iliac fossa; and a greater degree of sculpturing on the dorsal surface of the ilia (see Fig. 8)

Holotype. Incomplete pelvis retaining all of the synsacrum, ilia and most of the acetabular portions of the os coxae (P.24444) (see Fig. 7). Collected under the supervision of Dr R. Wells in 1979. Measurements: total length of the synsacrum, 31.5 mm; width between the acetabula, 21.1 mm; depth from dorsalmost edge of the
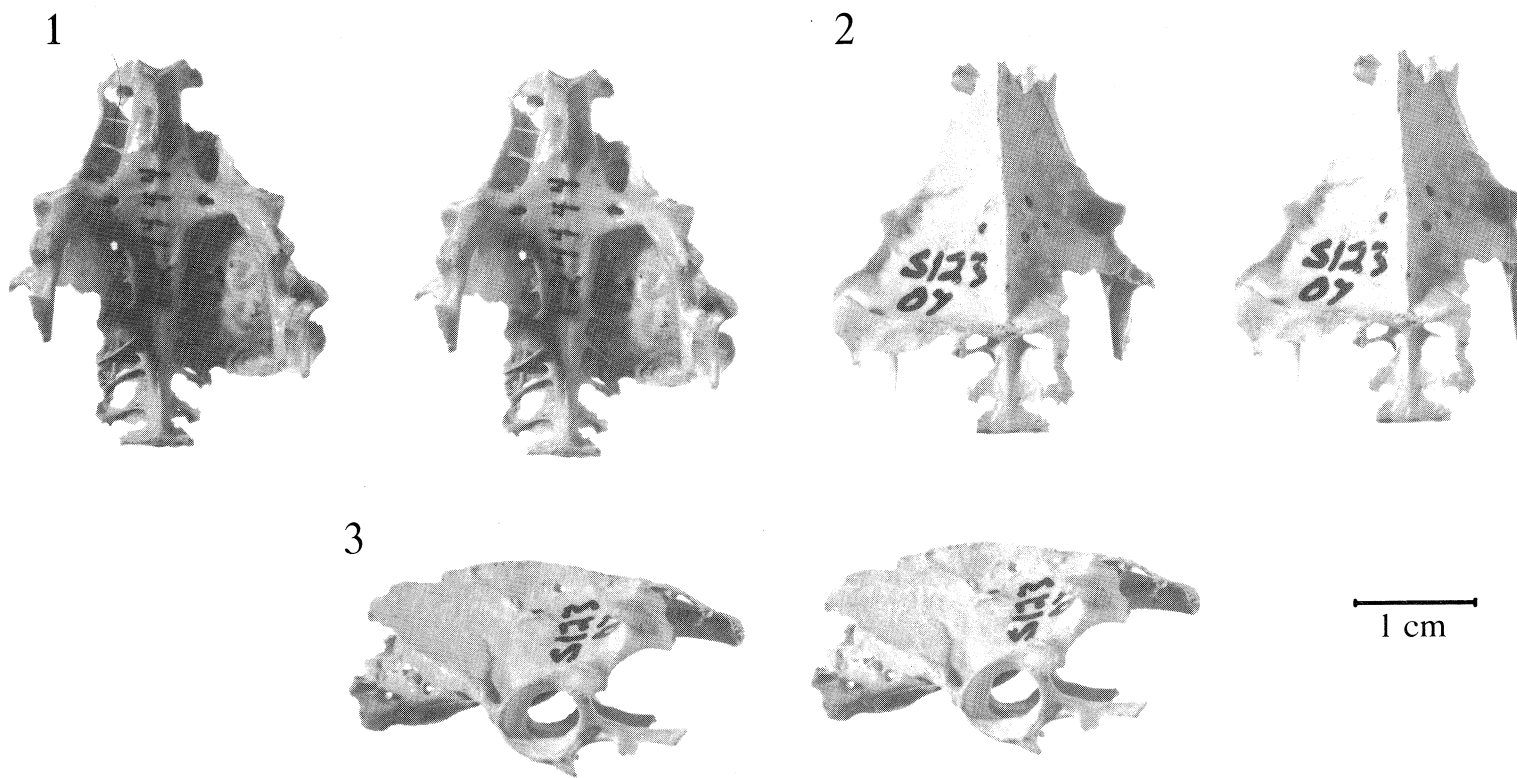
Fig. 7. Stereoviews of the type specimen of *Orthonyx hypsilophus* (P.24444): 1, ventral view; 2, dorsal view; 3, lateral view.
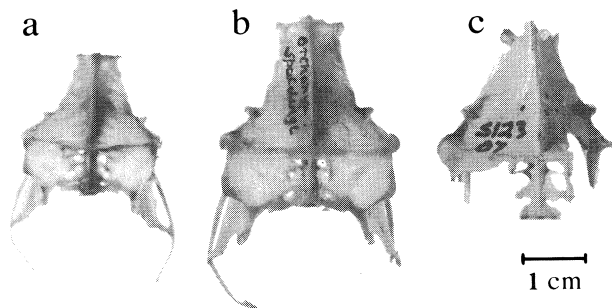

Fig. 8. Dorsal views of *Orthonyx* spp. pelves demonstrating the construction of the dorsal iliac crests and the structural differences amongst the three species: a, *O. temminckii* (AM 0.57019); b, *O. spaldingii* (QM 0.21124); c, *O. hypsilophus* (P.24444).

Table 6. Lengths of synsacra [LV] from *Orthonyx* spp.

	mean	S.D.	min.	max.	N
O. temminckii	20.3	0.8	19.3	21.2	4
O. spaldingii	27.5	0.6	27.1	27.9	2
O. hypsilophus	31.5	–	–	–	1

anterior part of the dorsal iliac crest to ventral synsacrum, 11.8 mm.

Etymology. The specific name *hypsilophus* is derived from the Greek υψι, high, and λοφος, crest or ridge, the combination to be regarded as adjectival in form and declined to agree with the masculine gender of *Orthonyx*. The new species has a comparatively high median dorsal ridge as measured against those in the two extant species of *Orthonyx*.

Description. Both antitrochanters and posterior parts of the dorsal iliac crest maintain strong anteriolaterally projecting shelves. First, fourth, fifth and thirteenth parapophyses enlarged, with the fourth and fifth very swollen. All other parapophyses lamellate but still very much evident. In lateral view, the acetabula lie ventral to the synsacrum and slightly anterior to its median point. Thirteen parapophyses in the synsacrum.

Remarks. The morphological variation that occurs within the genus is probably the result of structural changes associated with increased overall size. Characters that might have otherwise proven useful in determining the phylogeny of *O. hypsilophus* can be demonstrated as being variable within each species, and grading from one species to another. These characters include; the pits and furrows medial to the acetabulae; the concave iliac fossa; the presence of thirteen, instead of twelve, vertebrae in the synsacrum (as determined by counting the numbers of parapophyses); and the first,

fourth, fifth and thirteenth parapophyses enlarged. In the smallest species, *O. temminckii,*the pits exist as very shallow, open-ended indentations with the furrows lacking; the iliac fossa are convex; the synsacrum is made up of either twelve or thirteen fused vertebrae, with additional vertebrae fused to either the anterior or posterior margins; and only the first, fourth and twelfth parapophysed are enlarged. In the medium-sized *O. spaldingii*, the pits are relatively deeper, but still remain open-ended; the iliac fossa are flat; the synsacrum is made up of either twelve or thirteen vertebrae and, depending upon the number of vertebrae, enlarged parapophyses include the first, fourth and twelfth, or first, fourth, fifth and thirteenth (respectively). The additional vertebra is added to the front of the synsacrum and is associated with a swollen fourth parapophysis. *Orthonyx hypsilophus*, the largest of the three species, demonstrated a greater development in all four characters.

Within the genus, the os coxae demonstrates a greatly expanded surface area in the iliac fossa and foreshortened ischia. The development of this unusually shaped pelvis is associated with an equally unusual method of foraging. Zusi (1978), in describing the feeding behaviour of *O. spaldingii*, states that, "when clearing litter the birds pushed leaves to the side with one foot and then the other, each time shifting the weight of their bodies over the supporting foot." This is unusual for, as Zusi mentions, "a single sideways sweep began with the foot forward beneath the bird's throat and extended to the side in an arc of ninety degrees or more". A similar feeding behaviour has been described for *O. temminckii* (Boles & Shields, 1980). The expanded surface area of the iliac fossa accomodates a greatly expanded M. iliotrochantericus caudalis, which originates over the whole of the cranial surface of the iliac fossa. The pits medial to the acetabulae in *O. hypsilophus* are formed by the increased structural support of the origin of M. iliotrochantericus medius. The area of origin of this muscle is barely raised above the dorsal surface of the ilia in *O. temminckii* but is very pronounced, forming a pedestal, in *O. hypsilophus*. Increased surface area of the origins of M. iliotrochantericus cranialis and M. iliotrochantericus caudalis are interpreted from the enlarged muscle scars, for the first, and increased depth of the iliac crest, for the second, in the specimen of *O. hypsilophus*. Differences in the pelvis of *Orthonyx* from that of all other passeriforms are assumed to be adaptions to this unusual method of foraging. Within the genus, the pelvis of *O. hypsilophus* is adapted to greater strength in the clearing of debris during foraging.

The presence of this genus in South Australia during the late Quaternary has interesting biogeographical implications. The two extant species of *Orthonyx* live chiefly in rainforest along the north-eastern seaboard (Blakers *et al.*, 1984), particularly those forests with a deep humus layer (Hindwood, 1934) allowing for adequate forage. *Orthonyx temminckii* does venture out into thickets of *Lantana* and *Rubus* (Lantana and

Blackberry) along roadsides bordering rainforest (Keast, 1944; pers. obs.). What seems to be important is the low intensity of light necessary to cover the birds' movements. Both species seem to survive only in those areas which provide a sufficiently dense canopy, as well as adequate accumulation of litter on the forest floor.

In south-eastern Australia, particularly western Victoria and south-eastern South Australia, mammalian faunas indicating wet forests were last recorded in the Early Pliocene (Turnbull & Lundelius, 1970). By the Late Pliocene the rainforests of much of Australia had been replaced by vegetation dominated by xerophytic genera (e.g., *Eucalyptus* and *Casuarina*) (Galloway & Kemp, 1984). The vegetation of south-eastern Australia, since then, has been mainly a mosaic of wet sclerophyl, dry sclerophyl and savanna woodland. In the 'Green Waterhole Cave' area, as mentioned in the introduction, eucalypt woodland was dominant from beyond radiocarbon dating to 35,000 y.B.P. From 35,000 until 6,000 y.B.P., the more xeric-adapted *Casuarina* dominated woodlands (Dodson, 1975). It is here suggested that *O. hypsilophus* lived in *Melaleuca* thickets that border wet areas, such as lakes, ponds and streams. Throughout southern Victoria and south-eastern South Australia, *Melaleuca ericifolia, M. squarrosa* and *Leptospermum lanigerum* form a very dense, closed scrub, with canopy cover of 70 to 100 percent (Specht *et al.*, 1974). Therefore this habitat would have provided both sufficent canopy and litter. *Melaleuca* is recorded from the area of south-east South Australia throughout the last 50,000 y.B.P. (Dodson, 1975). If this is true, then the genus *Orthonyx* can no longer be considered strictly adapted to rainforest. It is now apparent that the radiation within this genus was ecologically greater than is currently demonstrated. The extinct species was probably adapted to drier habitats, evolving from a rainforest inhabiting ancestor sometime during the Pliocene desiccation.

Acanthizidae

Dasyornis broadbenti

Material. Complete right humerus (P.24446), complete right tibiotarsus (P.24447). The 2 specimens represent a minimum of 1 individual. Family previously unrecorded in the fossil records.

Remarks. Most of the terrestrially adapted birds in Australia have similarly shaped humeri, and this particular shape, presumably, is an adaptation to this mode of life (Rich, McEvey & Baird, 1985). The humeri of *Dasyornis* can be separated from the other similarly adapted birds by possessing a scar for the insertion of the M. scapulohumeralis anterior that is distally extending and acute at its distal end; a flattened humeral head at an angle greater than ninety degrees from the shaft, measured distally; a bulbous internal tuberosity; and a strongly curved pectoral crest. The tibiotarsus of *Dasyornis* differs from that of other similarly adapted birds by its less pronounced tubercle for the attachment

Table 7. Humeri (H) [GL] and tibiotarsi (T) [La]: length measurements of the three species of *Dasyornis* (* = complete skeletal specimens are lacking for both *D. longirostris* and *D. brachypteris*, therefore measurements for these two species were taken from X-rays of skins. These measurements can only be used as rough comparisons as the exact orientation of the element relative to the camera is unknown.)

		mean	S.D.	min.	max.	N
D. longirostris	(H)	19.3	–	–	–	1
	(T)	*33.9	1.3	33.0	34.8	2
D. brachypterus	(H)	*19.5	–	–	–	1
	(T)	*38.3	0.4	38.0	38.5	2
D. broadbenti	(H)	24.5	0.5	24.1	25.0	6
	(T)	46.7	1.8	44.4	48.1	5
L-81	(H)	23.4	–	–	–	1
	(T)	50.1	–	–	–	1

of M. femorotibialis interior, a laterally flattened medial condyle, a swollen lateral condyle, and a high cnemial crest.

Of the three recognised species of *Dasyornis, D. broadbenti* is by far the largest (see Table 7) and the fossil elements are, therefore, attributed to that species. *Dasyornis broadbenti* is the only one of the three species now occuring in the south-east of South Australia, although prehistorically at least two species occurred in that region.

Meliphagidae

Manorina melanocephala

Material. Complete cranium (P.24448). Genus previously unrecorded in the fossil record.

Remarks. This specimen was found on the water surface and, though no fleshy tissue remained, it may be of more recent origin than the rest of the deposit. The skull can be identified as *Manorina* by its short, broad cranium (length, 27.0 mm; width, 20.8 mm) as well as the presence of: a single bar acting as the interorbital partition; a robust process dorsal to the temporal fossa; and a sculptured bone surface, reaching from the temporal fossa to the cerebral prominence. *Manorina melanocephala* may be separated from *M. flavigula* by its larger size and its geographical distribution.

Corvidae

Corvus sp.

Material. Left mandibular ramus (P.24449), anterior sternal fragment (P.24450), complete left ulna (P.24451), complete right radius (P.24381), incomplete left femur (P.24452), and complete right and 2 incomplete left tibiotarsi (P.24453–24455). The 7 specimens represent a minimum of 2 individuals.

Remarks. The Australian representatives of the family Corvidae can be separated allometrically from the Cracticidae by their larger ulnae, sterna and femora. The tibiotarsi have rounded distal trochleae (viewed laterally), as opposed to the semi-circular shape in cracticids. Because of the round trochleae, the

intercondylar fossae of corvids are more proximodistally expanded. Mandibles are identified by their more elongate (not squared) internal articular processes.

If present day distributions are taken into account, then three corvids are possible for the locality, *C. coronoides, C. mellori* and *C. tasmanicus*. With the small number of skeletal specimens available and the dubious identity of many of these (see Rowley, 1970) it is not possible to identify the fossil material to species level. Therefore, the determination will be left at *Corvus* sp.

DISCUSSION

The 'Green Waterhole Cave' deposit is taphonomically unique among cave sites recorded in Australia. Of those fifteen cave deposits whose taphonomic influences are determinable, 73% were carnivore accumulated or show evidence of some form of carnivore activity, 20% are subaerial pitfalls/death traps and 7% were fluvially accumulated (Baird, in press). Each of the above taphonomic groups states the main accumulating force, although the deposits may have been under the influence of several accumulating forces. The L-81 material is, at present, covered by water which was possibly the accumulating force behind the deposit. Although drowned caves are relatively common, water is rarely proposed as an accumulating force.

Cave formation in limestone is often dependent upon the flow of water through the rock. The different water flow types, therefore, present the most satisfactory way of classifying these caves (Sweeting, 1973: 158). The two most common forms of caves are phreatic and vadose. As defined by Sweeting (1973), phreatic caves are those caves formed within the zone of limestone which lies at or just beneath the level of permanently saturated rock, and vadose caves are those caves formed by water circulating under gravity above the level of permanently saturated rock. The bulk of cave genesis typically occurs at or above the saturation level in the karst limestone. During marine transgressions, caves would be formed at greater heights within the carbonate strata than those formed during the previous regressions, assuming equivalent rises in the ground water levels. Those caves topographically lower in the stratigraphy would be drowned by the rising water level. During eustatic lows, the same caves would be left high and dry. A similar effect can occur through minor tectonic uplift. As can be surmised from this sequence of events, at various times any one level of caves may be submerged or exposed depending on fluctuating saturation levels.

Given this brief history of cave formation, it can be seen that, although a cave is drowned, it does not necessarily mean that water was the accumulating force for its deposits. For example, on Oahu in the Hawaiian Island chain, there is a drowned cave (50-0a-B6-139) whose contents include beautifully preserved specimens of a *Corvus* sp. and a *Chaetoptila* sp.. Because of their

high degree of association it was suggested that the animals entered the cave during a dry phase, died and were subsequently covered by water (Olson & James, 1982). The end result is the same as in L-81, except that the degree of association is greater in the Hawaiian cave. The lack of fully articulated skeletons in L-81 suggests that either there has been postdepositional movement in L-81, or a different taphonomic history has been involved. Even though postdepositional movement has occurred, there are other reasons for thinking that the taphonomic processes behind the deposit are unusual. This can be clarified by comparing the L-81 faunal material to other cave faunas from south-eastern Australia

Because carnivores show bias in the types of prey they accumulate, and since 73% of all cave deposits in south-eastern Australia are attributed to carnivores, there tends to be great similarity in faunal lists from one deposit to another (Baird, in press). Large psittaciforms, however, have only been recorded from a few caves and have never formed a large part of any cave fauna. Of the thirty-seven cave deposits mentioned for the south-east of Australia (including N.S.W., Vic. and S.A.; Rich & van Tets, 1982) only two, outside of L-81, contained large psittaciforms. An additional specimen of *Cacatua tenuirostris* (AM # F53469) has recently been recorded from another drowned cave in the south-east of South Australia, The Pines, L-61. I propose that the reasons for the differences in the faunal lists between the 'norm' and L-81 lie in the taphonomy of the deposit. If the faunal list (see Table 8) is divided into five parts (i.e., flocking species, terrestrial species, carrion eaters, speleophiles and indeterminate) it can be seen that at least two groups, the flocking species and the terrestrial species, dominate (83% of all individuals), lending support to the hypothesis that water is the accumulating agent behind this deposit.

Of the sixteen species of birds in the deposit, six species commonly flock (37%) (*Calyptorhynchus magnificus, C. lathami, Callocephalon fimbriatum, Cacatua tenuirostris, Platycercus* sp., *Corvus* sp.. [Cacatuidae undetermined not included]), four species are terrestrial (25%) (*Gallinula mortierii, Centropus colossus, Orthonyx hypsilophus, Dasyornis broadbenti*), three species are possible carrion eaters (19%) (undescribed accipitrid, *Falco* cf. *berigora, Dacelo novaeguineae*), one species is a speleophile (6%) (Hirundinidae indet.), which leaves *Phaps chalcoptera* and the *Manorina melanocephala* undetermined (13%). If we use the same groups but, instead of determining percentage from the total number of species, we use the total number of identifiable individuals (53), the picture becomes clearer. The flocking species now make up (70%) of the total, the terrestrial species (13%), the carrion eaters (9%), the speleophiles (2%), and the undetermined (6%). Given that the flocking species make up such a large part of the total, and that the individual elements lack any diagnostic damage indicative of the action of carnivores, it seems likely that

Table 8. List of the avian specimens known from Green Waterhole Cave, with the scientific and common names, number of specimens (N) and minimum number of individuals (MNI).

	N	MNI
Accipitridae		
n. sp.	7	1
Falconidae		
Falco cf. *berigora*	1	1
(Brown Falcon)		
Rallidae		
Gallinula mortierii	10	4
(Tasmanian Native-Hen)		
Columbidae		
Phaps chalcoptera	1	1
(Common Bronzewing Pigeon)		
Phaps sp.	1	1
Cacatuidae		
Calyptorhynchus magnificus	4	1
(Red-tailed Black Cockatoo)		
C. lathami	1	1
(Glossy Black Cockatoo)		
Callocephalon fimbriatum	1	1
(Gang-gang Cockatoo)		
Cacatua tenuirostris	127	31
(Long-billed Corella)		
indeterminate	18	5
Platycercidae		
Platycercus sp.	1	1
(Rosella sp.)		
Cuculidae		
Centropus colossus n. sp.	1	1
(Giant Coucal)		
Alcedinidae		
Dacelo novaeguineae	7	3
(Kookaburra)		
Hirundinidae		
indeterminate	1	1
Orthonychidae		
Orthonyx hypsilophus n. sp.	1	1
(Extinct Logrunner)		
Acanthizidae		
Dasyornis broadbenti	2	1
(Rufous Bristlebird)		
Meliphagidae		
Manorina melanocephala	1	1
(Noisy Miner)		
Corvidae		
Corvus sp.	7	2
(Raven sp.)		

there was some other process at work in the accumulation of the deposit.

For water to have been the accumulating force, the animals must first have been attracted to the cave, restricted to the area of water and then forced to enter the water. Pledge's (1980) explanation has the animals entering the cave in search of water and, because of a two metre drop, being trapped in the lower reaches of the cave and drowning while attempting to escape. How would this be relevant to the avian content of the deposit?

Attraction to bodies of water similar to the drowned cave is quite frequent in birds. As noted by several authors (Craig & Powers, 1976; Chilgren, 1979), birds in search of water in the western U.S. will arrive at watering tanks and in the frenzy of landing will try to perch on floating debris and each other. A small number

of birds would subsequently be soaked. If there were no access to dry ground, then the birds could eventually drown. There is evidence in the U.S. of Western Meadowlarks (*Sturnella neglecta*), Common Crows (*Corvus brachyrhynchos*) and American Kestrels (*Falco sparverius*) lining the bottoms of stocktanks. Similarly, stock tanks in northern South Australia have been seen, by the author, to be carpeted with the bodies of a *Corvus* sp. and the occasional Little Corella (*Cacatua sanguinea*). Budgerigars (*Melopsittacus undulatus*) have been recorded as drowning when large flocks come down to drink (Forshaw, 1969: 282). Although *Phaps chalcoptera* is a flocking species, its method of approaching a drinking spot is different from most in that it usually lands some distance away and walks to the water (Frith, 1982: 224). The proposed explanation for the accumulation of the avian parts of the L-81 material is similar to that mentioned above. The birds would enter the cave during drought periods, try to land on floating debris not capable of keeping them afloat, wet their feathers, and eventually drown. As compared with Pledge's explanation, the only difference would be the final reason for drowning. The animals collected by this means of accumulating force would, therefore, reflect local population size and flocking habits, and not the bias of predators.

As was found with the mammalian fauna, the avian fauna seems to be made up of both extant and extinct species, which for a 'Late' Pleistocene/Holocene deposit is unusual. Geographical range extensions were recorded for two species, *Gallinula mortierii* and *Calyptorhynchus lathami*, and two genera, *Centropus* and *Orthonyx*. Three species new to science were found: one accipitrid, one cuculid and one passeriform. The accipitrid has yet to be diagnosed, but from all accounts is larger than any extant Australian member of the family (Rich, pers. comm.). The coucal, *Centropus colossus*, is unusual both for its enormous size, being one third larger than its closest Australian relative, and its advanced stage of flightlessness. The passerine, *Orthonyx hypsilophus*, is also unique for its adaptions to terrestriality and its large size. The three new species and the *Cacatua tenuirostris* material seem to be remnants of Pleistocene gigantism, so well known from the other continents (Marshall & Corruccini, 1978). The extinction of large mammals in Australia has been generally thought to have been confined to the period between 26,000 and 15,000 y.B.P. (Horton, 1984) and it is suggested that the large extinct avian species are possibly of similar age.

Relative dating of the site is difficult, for the deposit itself provides no tangible measures of time. Data on sea level transgressions provide a maximum age of opening of 125,000 y.B.P. Dating by faunistic analysis is difficult. The animals are either peculiar to the deposit, which suggests a date greater than 15,000 y.B.P., or ubiquitous to the whole south-eastern corridor, and therefore not suggestive of any date. In any case, because the deposit is slumped and, therefore, of mixed ages, the best one can do using the fauna is try to put a maximum age on the deposit, which at this stage is probably greater than 15,000 y.B.P..

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APPENDIX

Measurements of all the species in the Cacatuidae whose present distribution includes south-eastern Australia (within 137°-152°S and 33°-39°E). Specimens used were from localities within this defined zone and therefore assumed to belong to the local subspecies of each species. Measurements are arranged according to taxonomic order following Condon (1975).

Additional material of *Cacatua sanguinea* were added at the last moment. These data increased the sample population but did not change the statistics for the species appreciably. The corresponding sections in Figure 4 were, therefore, left unchanged.

	mean	S.D.	min	max	N
CRANIUM					
Length [LP]					
Calyptorhynchus magnificus	52.0	4.1	48.5	56.5	3
C. lathami	46.2	1.1	45.0	47.3	4
C. funereus	50.1	1.5	47.8	52.2	7
Callocephalon fimbriatum	39.2	1.1	36.7	39.6	8
Cacatua roseicapilla	37.3	2.0	34.1	40.5	9
C. tenuirostris	43.6	1.6	41.5	44.6	9
C. sanguinea	40.7	1.1	39.0	42.6	11
C. leadbeateri	44.5	1.2	42.4	45.0	4
C. galerita	51.2	3.6	48.0	56.5	10
Width [SBO]					
Calyptorhynchus magnificus	35.8	2.0	33.5	37.0	2
C. lathami	36.9	0.7	36.4	37.9	4
C. funereus	30.6	1.4	29.0	32.5	7
Callocephalon fimbriatum	27.3	1.4	24.9	28.5	8
Cacatua roseicapilla	23.2	1.6	20.4	24.6	10
C. tenuirostris	27.9	1.2	26.5	29.1	9
C. sanguinea	26.5	1.0	25.0	27.8	11
C. leadbeateri	29.5	0.6	29.0	30.0	4
C. galerita	35.2	2.6	31.4	40.3	10
HUMERUS					
Length [GL]					
Calyptorhynchus magnificus	84.3	5.9	75.4	88.5	4
C. lathami	68.5	2.7	66.4	72.2	4
C. funereus	76.2	3.8	67.3	80.2	8
Callocephalon fimbriatum	55.7	1.9	53.5	58.4	8
Cacatua roseicapilla	58.4	2.1	55.5	62.0	11
C. tenuirostris	71.3	1.1	70.0	72.5	7
C. sanguinea	67.4	2.4	63.0	70.5	12
C. leadbeateri	69.5	1.7	68.7	71.5	3
C. galerita	88.0	2.8	85.0	92.0	6
Proximal width [Bp]					
Calyptorhynchus magnificus	21.8	1.1	20.0	23.0	3
C. lathami	17.0	0.7	16.3	17.8	4
C. funereus	19.7	0.8	18.5	20.3	7
Callocephalon fimbriatum	13.3	0.6	12.4	14.2	8
Cacatua roseicapilla	15.0	0.7	14.4	16.0	11
C. tenuirostris	18.2	1.6	17.2	18.5	7
C. sanguinea	16.5	0.7	15.0	17.4	12
C. leadbeateri	15.8	0.8	15.7	17.2	3
C. galerita	21.4	0.4	21.0	22.3	6
ULNA					
Length [GL]					
Calyptorhynchus magnificus	99.5	5.0	91.5	102.5	4
C. lathami	82.1	3.8	79.0	87.2	4
C. funereus	89.9	4.9	79.4	95.3	8
Callocephalon fimbriatum	66.8	2.2	63.9	70.5	8
Cacatua roseicapilla	69.0	2.5	65.3	73.0	11
C. tenuirostris	85.5	1.6	82.9	86.9	7
C. sanguinea	82.2	3.0	76.0	86.0	12
C. leadbeateri	83.0	2.5	80.5	85.7	3
C. galerita	106.7	3.5	102.1	111.5	7

CARPOMETACARPUS	mean	S.D.	min	max	N
Length [GL]					
Calyptorhynchus magnificus	61.1	3.3	56.6	64.0	4
C. lathami	49.6	2.9	47.0	52.9	4
C. funereus	56.8	2.7	50.7	59.2	7
Callocephalon fimbriatum	39.6	2.0	36.7	42.3	7
Cacatua roseicapilla	43.5	1.8	41.8	46.9	11
C. tenuirostris	50.1	1.0	49.0	51.6	7
C. sanguinea	46.2	1.8	43.0	48.2	12
C. leadbeateri	47.3	1.2	46.0	47.8	3
C. galerita	56.4	1.3	55.0	58.5	7
FEMUR					
Length [GL]					
Calyptorhynchus magnificus	55.3	2.7	51.4	58.0	4
C. lathami	44.4	1.8	42.8	46.8	4
C. funereus	54.2	2.3	50.6	57.8	8
Callocephalon fimbriatum	38.3	1.2	36.5	39.9	8
Cacatua roseicapilla	40.9	1.7	38.1	45.0	11
C. tenuirostris	51.9	1.2	50.5	53.5	8
C. sanguinea	47.5	1.2	45.5	49.5	12
C. leadbeateri	45.2	3.3	42.2	48.5	3
C. galerita	59.6	1.7	57.0	61.2	6
TIBIOTARSUS					
Length [La]					
Calyptorhynchus magnificus	77.3	5.0	69.7	81.5	4
C. lathami	61.2	2.2	59.1	64.2	4
C. funereus	76.3	4.2	67.8	81.2	8
Callocephalon fimbriatum	56.1	2.5	52.9	58.8	7
Cacatua roseicapilla	59.5	2.4	54.9	63.3	10
C. tenuirostris	73.6	1.9	71.2	76.0	7
C. sanguinea	67.8	1.9	64.5	71.0	12
C. leadbeateri	64.2	2.9	62.0	67.3	3
C. galerita	84.3	2.9	80.5	87.3	6
TARSOMETATARSUS					
Length [GL]					
Calyptorhynchus magnificus	26.6	2.1	24.2	28.5	4
C. lathami	18.4	0.8	17.5	19.4	4
C. funereus	27.3	1.2	25.1	28.9	7
Callocephalon fimbriatum	17.4	0.8	16.8	18.3	7
Cacatua roseicapilla	21.5	1.1	19.2	23.0	10
C. tenuirostris	24.9	0.6	24.0	25.5	7
C. sanguinea	23.7	0.7	22.6	24.4	11
C. leadbeateri	23.0	0.9	21.9	23.7	3
C. galerita	27.3	0.8	26.5	28.7	6
Distal width [Bd]					
Calyptorhynchus magnificus	14.3	0.9	13.4	15.0	4
C. lathami	11.3	0.5	10.8	11.7	4
C. funereus	12.9	0.3	12.4	13.6	7
Callocephalon fimbriatum	10.3	0.6	9.5	11.3	7
Cacatua roseicapilla	9.7	0.5	9.2	10.0	10
C. tenuirostris	12.1	0.2	12.0	12.2	7
C. sanguinea	11.6	0.6	10.7	12.5	11
C. leadbeateri	12.8	0.8	12.0	13.4	3
C. galerita	16.1	0.8	15.5	16.8	6
CORACOID					
Length [LM]					
Calyptorhynchus magnificus	42.8	2.2	39.8	44.5	4
C. lathami	36.2	1.7	34.2	38.3	4
C. funereus	41.4	2.4	37.6	44.5	8
Callocephalon fimbriatum	30.4	0.9	29.5	31.2	8
Cacatua roseicapilla	35.9	1.5	34.4	39.0	11
C. tenuirostris	42.3	0.9	40.6	43.0	8
C. sanguinea	39.9	1.5	38.0	42.0	12
C. leadbeateri	37.8	0.4	37.5	37.9	2
C. galerita	46.6	1.9	43.5	48.5	6