

Papers in Honour of Ken Aplin

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Late Quaternary Fossil Vertebrates of the Broken River Karst Area, Northern Queensland, Australia

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ABSTRACT. Two new fossil deposits from caves of the Broken River area, northeast Queensland, provide the first regional records of vertebrate species turnover and extinction through the late Quaternary. Fossil assemblages from Big Ho and Beehive Caves are dominated by small-bodied vertebrates, especially mammals. They represent owl roost deposits, although limited presence of larger-bodied taxa such as macropodids may be the result of occasional pitfall trapping. U-series dating demonstrates that Big Ho dates to the penultimate glacial cycle (c. 165 ka) and Beehive to the early Holocene (c. 8.5 ka). A total of 34 mammalian taxa were identified; within the two deposits, seven taxa are unique to Big Ho and another seven are found only in Beehive. The deposits also preserve five extinct fossil taxa (bandicoots and rodents) that add to a growing list of small-bodied species known to have suffered extinction in the late Quaternary. The deposits further yield the remains of four species of bandicoots and rodents (*Chaeropus yirratji*, *Notomys longicaudatus*, *Conilurus albipes*, and *Pseudomys gouldii*) that suffered extinction post-European colonization. These new fossil records represent significant increases in the known geographic and temporal range of several species and begin to fill an important gap in our understanding of the faunal history of tropical northeast Australia.

Introduction

Modern Australian ecosystems emerged during the Quaternary under a backdrop of major fluctuations in atmospheric carbon dioxide concentration, sea levels, and temperature, with a long-term trend towards progressively drier climates (Martin, 2006; Kershaw *et al.*, 2003; Price, 2013). The period was marked not only by significant evolutionary events, but also major extinctions and geographic range shifts of many flora and fauna (e.g., Kershaw, 1994; Jordan *et al.*, 1995; Reed & Bourne, 2000,

2009; Hocknull *et al.*, 2007; Prideaux *et al.*, 2007; Price, 2012; Price *et al.*, 2005; Black *et al.*, 2014). Today, at a time of widespread awareness over detrimental anthropogenic and climatic impacts on Australian ecosystems, it has become critical to understand the history of ecosystem origins and responses to similar past events. The Quaternary fossil record has a significant role to play in yielding that crucial information (Reisinger *et al.*, 2014).

While many vertebrate fossil deposits of Quaternary age have been recognized in Australia, the record is patchy and geographic coverage is strongly biased towards southern

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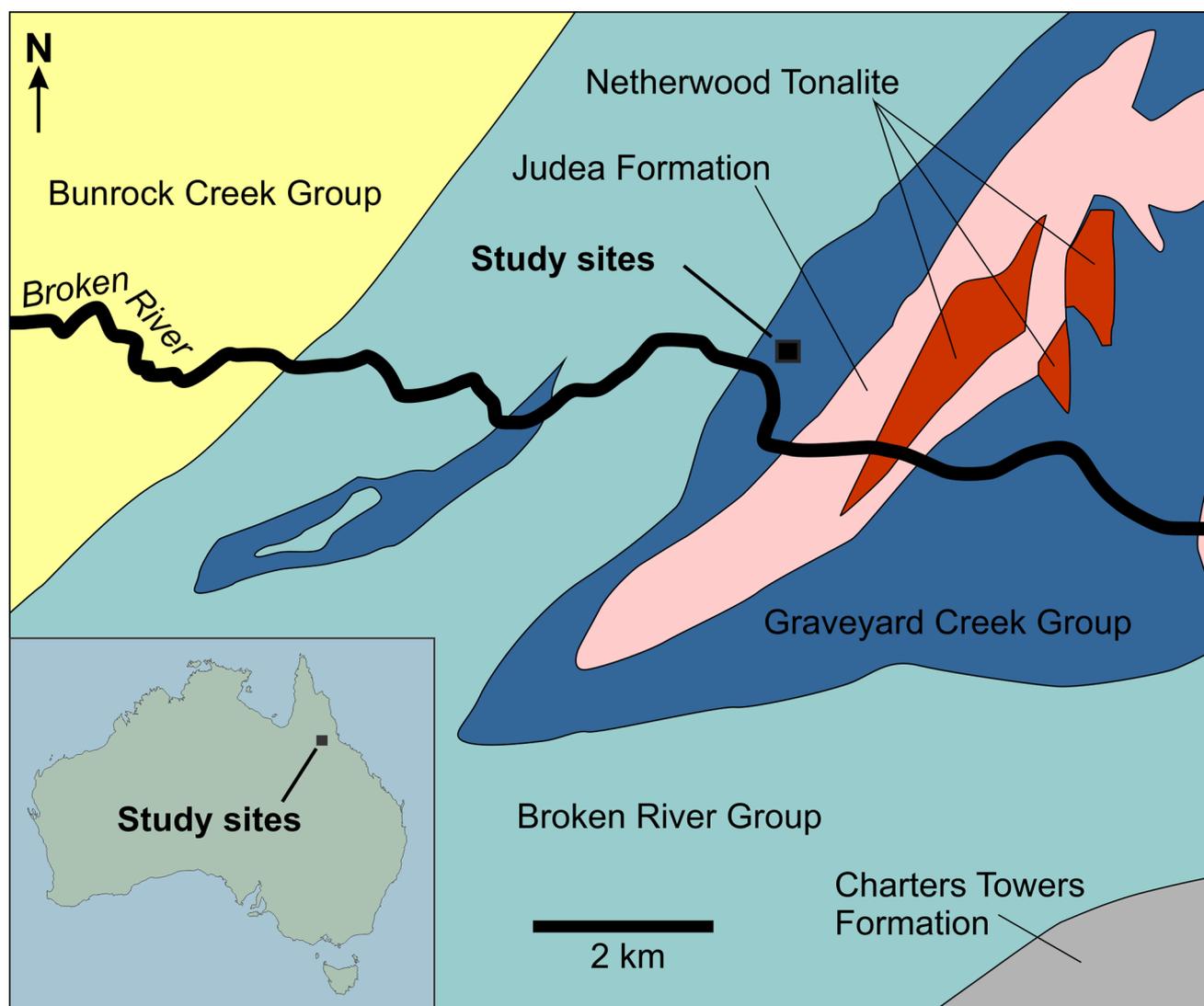


Figure 1. Map showing study sites and regional geological provinces of the Broken River karst area.

Australia. Very little is known about the Quaternary history of ecosystems in northern Australia (Price *et al.*, 2017; Hocknull *et al.*, 2020). This situation is not necessarily due to a paucity of fossil sites in the region, but more likely results from a dearth of field investigations; when these have been conducted, they have yielded records comparable to the south. Areas such as the Darling Downs (southeast Queensland) and Mt Etna (central eastern Queensland), for example, have produced some of the most extensive records of Quaternary vertebrates north of the Queensland–New South Wales border. There, records show waves of extinction of both megafauna and micro-fauna (e.g., rodents, bandicoots) alongside progressive decreases in precipitation and expansion of more open habitats through the late Quaternary (Hocknull, 2005a; Hocknull *et al.*, 2007; Cramb & Hocknull, 2010a; Price & Hocknull, 2011; Price *et al.*, 2009; Price & Sobbe, 2005; Price & Webb, 2006; Price *et al.*, 2015). While some Quaternary vertebrate fossils have been recovered from northern Australia (e.g., Archer *et*

al., 1978; Molnar, 1981; Klinkhammer & Godthelp, 2015; Cramb *et al.*, 2018), the records remain patchy, are mostly undated, and are usually one-off collections or reports of single species.

Here we describe new Quaternary fossil faunas from two limestone caves in the Broken River area, Greenvale, northeast Queensland (Fig. 1). Although Palaeozoic marine fossils have long been known in the area (see Henderson & Withnall, 2013 and references therein), Quaternary vertebrate fossils within the cavernous limestones were only reported in the 1980s and remained unstudied until the 2000s. Since then, individual reports of bilbies, bandicoots, rodents, and megafaunal taxa such as *Diprotodon* and *Thylacoleo* have been produced (Hocknull, 2005b; Cramb & Hocknull, 2010b; Price *et al.*, 2017; Travouillon *et al.*, 2019). Full mammalian palaeocommunities from the region have yet to be documented. The aim of the present paper is to report on the first two (of several) fossil assemblages excavated from caves of the region.



Figure 2. Images of the karst, study caves, and fossils of the Broken River karst area. (A) rillenkarren typical of the Broken River limestone karst; (B) Beehive fossil deposit (arrow indicating fossil-bearing breccia); (C) Big Ho fossil deposit (arrow indicating fossil-bearing breccia exposed as a false floor); (D) partially acid-digested breccia from Beehive showing high concentration of vertebrate fossils.

Geographic and geological settings

The Broken River area has been the subject of explorations by the Chillagoe Caving Club who are working on mapping many of the region's caves. The two deposits reported here are from Big Ho and Beehive, caves that formed in the main outcrop of limestone in the southern part of the Jack Formation, Graveyard Creek Group, part of the larger Broken River Province (Fig. 1). As this part of the outcrop is located on private property, specific locality details remain confidential but are available to *bona fide* researchers upon request to the Chillagoe Caving Club, Chillagoe, Queensland.

The Graveyard Creek Group is 150 m to > 5000 m thick and contains folded Silurian-Mississippian siliciclastic and carbonate sedimentary rocks, with the contained Jack Formation being around 580 m thick (Henderson & Withnall, 2012). The Jack Formation is dominated by limestone and mudstone rich in autochthonous fossils that include corals, molluscs, brachiopods, conodonts, and fish remains, among other taxa (Henderson & Withnall, 2012). The Jack Formation outcrop is heavily karstified and contains extensive and well-developed rillenkarren (Fig. 2A) making access to the caves particularly challenging. The formation is tilted to c. 90° and the caves are largely joint controlled, thus, contain many narrow but tall passages and caverns, including Big Ho and Beehive.

Materials and methods

Collection and curation

Fossil breccias were collected during a short fieldtrip in conjunction with the Chillagoe Caving Club in May 2012. The aim of the trip was to conduct a general survey of selected caves to assess their palaeontological significance. Both of the caves visited contain heavily lithified, fossil-rich breccias. Due to the high degree of lithification, the breccias could only be removed by breaking them into smaller blocks for transport out of the cave; more traditional excavation techniques (e.g., top-down excavations with small hand tools such as trowels) were not possible. The stratigraphic depths of the collected breccias varied from 50–70 mm for both deposits, with the breccia blocks weighing a total of approximately 12 kg. Stratification within both deposits was not evident, thus for the purpose of this study, are considered as two single, discrete accumulation phases. It is likely that the two assemblages are only minimally time-averaged and do not represent a large amount of time in terms of their depositional accumulation, respectively.

Breccia blocks from the two deposits were taken to The University of Queensland for digestion using weak (2–3%) acetic acid. The acid dissolved the carbonate cements and caused the blocks to break down, allowing the vertebrate

fossils to be recovered. Higher concentrations of acid were initially trialled (5–10%) for small, single blocks, but caused too much damage to the contained fossils. Even at the lowest concentrations of acid, gastropods within the breccias were dissolved and thus could not be reported in this study. Following digestion, the loose sediments were wet sieved with 1 mm mesh and fossilized skeletal remains then sorted under microscopes and magnifier lamps. Two c. 500 g breccia blocks, one from each site, remain unprocessed and are retained in the collection as representative material of the original deposits.

Fossils were identified using typical comparative morphological techniques; minor but pertinent remarks concerning the taxonomic identifications are given in the results. We concentrate largely on the identification of mammals due to their abundance, degree of preservation, and ease of identification, although other vertebrates including frogs, squamates, and birds are represented in the deposits. These will be detailed in future reports.

We calculated the number of identified specimens present (NISP) and minimum number of individuals (MNI) for each taxon identified at the lowest taxonomic level possible. The skeletal element used for such calculations varied for each taxon. For frogs, we used pelvis; monitor lizards used osteoderms; snakes used vertebrae; birds used humeri; dragon lizards, skinks, and mammals used teeth/maxillae/mandibular elements).

Fossils figured in this study are accessioned in the collections of the Palaeontology Laboratory at The University of Queensland, Brisbane, Australia (accession abbreviation: UQPL, University of Queensland Palaeontology Laboratory). Additional fossil specimen accession abbreviation: QMF (Queensland Museum Fossil; Queensland Museum, Brisbane, Australia).

Dating

Analytical dating of the fossil-rich breccias is difficult as they are heavily lithified and thus not suited to common Quaternary methods such as luminescence dating. They also lack dateable charcoals that might be amenable for radiocarbon dating. The deposits also lack interbedded and capping flowstones and cannot be dated using U-series stratigraphic bracketing approaches. Thus, the only viable option was direct dating of *in situ* fossils using U-series.

Fresh skeletal tissues typically lack U. However, post-burial diagenesis means that U is commonly taken up from burial sediments by apatite that scavenges U but excludes Thorium. Subsequent radioactive decay of the original U via alpha and beta emissions eventually leads to stable lead isotopes. However, the early part of the decay sequence to form ^{230}Th (i.e., ^{238}U – ^{234}U – ^{230}Th) has a half-life of 500–600 ka, thus, making U-series a viable option for dating late Quaternary vertebrate fossils. The U-series age is calculated by determining the amount of daughter ^{230}Th to parent ^{238}U . In ideal situations, U is taken up rapidly from the sedimentary environment post-burial, and assuming that U has not subsequently leached from the bone, the resulting U–Th age will represent a minimum age for the fossil, but one that is close to the true age. Loss of U from the system post-uptake can lead to age overestimation making the fossil tissues unsuitable for dating. The mode of U uptake and potential of loss from the fossils can easily be determined by constructing ^{230}Th and U-concentration profiles through the dated tissues.

Most of the fossils are from small-bodied vertebrate species (e.g., rodents) that required extraction from the breccias using dilute acetic acid. It was determined that such tissues may not be suitable for dating for two reasons: (a) it is difficult to construct U-profiles and thus test the reliability of the ages using such small specimens; and (b) there is a risk that acetic acid might strip the fossils of U rendering the specimens unsuitable for dating. Consequently, dating focused on broken cross-sections of bones from *in situ* larger-bodied species (macropodids) within the breccias that were not processed in acid baths. Multiple dating samples (powders) were drilled from one bone each in both deposits using a 1 mm diameter bit following procedures described in Price *et al.* (2013). The sampled bones are from approximately the middle of each of the sampled portion of the deposits. These samples were then prepared for U-series dating following techniques described in Zhao *et al.* (2009) and measured using a Nu Plasma multi-collector inductively coupled plasma mass spectrometer at the Radiogenic Isotope Facility, The University of Queensland, following the analytical procedures of Clark *et al.* (2012).

Results and interpretation

Geology

The fossils were preserved in haematite-rich clay matrix-supported breccias. Both Big Ho and Beehive are particularly fossiliferous with clasts dominated by fragmentary small-bodied vertebrate remains. Larger clasts were rarely observed. The breccias are massive with no obvious sedimentary structures, including evidence of stratification, in hand samples collected.

The deposit in Beehive is from a small chamber known to cavers as the “Greenroom”. The deposit is at floor level, adjacent to a limestone wall and lacks associated speleothems (Fig. 2B). It is predominately preserved in phreatic niches along the cave wall. Only the top c. 70 mm of the deposit was collected considering the degree of exposure, lithification, and difficulty in excavating with only hand tools. The outcrop runs around 3 m horizontally and no more than c. 30 cm wide when measured from the wall. The total depth of the deposit is unknown.

The Big Ho breccia is located approximately 4 m above ground level in a large open chamber (Fig. 2C). Enough sunlight enters the chamber to allow an extensive groundcover of maidenhair ferns and mosses to grow. Like Beehive, deposits were concentrated in phreatic niches along the cave wall. Breccia scars at the same level on either side of the chamber indicates that the original deposit was extensive and likely formed the entire floor of the chamber. Remains of the *in situ* breccia now consist only of a false floor that juts out of the limestone wall by no more than 30 cm, and extends horizontally along the wall for approximately 1 m. The most likely mode of deposit formation is as follows: (a) sediment and bone entered the chamber and began to create the deposit; (b) the deposit then lithified into a breccia; and (c) subsequent erosion of the breccia from above and especially underneath created the false floor. The Big Ho breccia was more heavily cemented than the Beehive breccia, less extensively preserved, and topographically higher relative to current floor levels. Thus, on geological evidence and field observations we considered the Big Ho breccia to be substantially older than the Beehive breccia.

Table 1. Taxonomic list for vertebrates of the fossil deposits of the Broken River karst area.

taxon	common name	Beehive		Big Ho	
		NISP	MNI	NISP	MNI
anuran gen. et sp. indet. 1	Frog	3	1	1	1
anuran gen. et sp. indet. 2	Frog	—	—	1	1
scincid gen. et sp. indet.	Skink	5	1	3	1
agamid gen. et sp. indet.	Dragon Lizard	10	1	—	—
<i>Varanus</i> sp. indet.	Monitor Lizard	6	1	2	1
pythonid gen. et sp. indet.	Python	—	—	2	1
elapid gen. et sp. indet.	Venomous snake	3	1	2	1
Aves gen. et sp. indet.	Bird	6	1	—	—
<i>Dasyurus</i> sp.	Quoll	—	—	7	1
<i>Antechinus</i> sp.	Antechinus	6	2	5	1
<i>Phascogale tapoatafa</i>	Brush-tailed Phascogale	5	1	5	1
<i>Planigale</i> sp. cf. <i>ingrami/tenuirostris</i>	Planigale	2	1	5	2
<i>Sminthopsis macroura</i>	Striped-faced Dunnart	11	3	14	5
<i>Sminthopsis</i> sp. cf. <i>murina</i>	Slender-tailed Dunnart	2	1	3	1
<i>Chaeropus yirratji</i>	Northern pig-footed Bandicoot	2	2	1	1
<i>Isoodon peninsulæ</i>	Cape York Brown Bandicoot	1	1	2	2
<i>Isoodon</i> sp. 2	Short-nosed Bandicoot	1	1	2	2
<i>Perameles</i> sp.	Long-nosed Bandicoot	—	—	2	1
<i>Petaurus norfolcensis</i>	Squirrel Glider	5	2	1	1
<i>Trichosurus</i> sp.	Brush-tail Possum	1	1	1	1
?hypsiprymnodontid	Rat Kangaroo	—	—	1	1
macropodid indet.	Macropod	—	—	1	1
macropodid “small”	Macropod	1	1	—	—
<i>Conilurus albipes</i>	White-footed Rabbit Rat	8	1	3	1
<i>Conilurus capricornensis</i>	Capricorn Rabbit Rat	—	—	3	1
<i>Leggadina forresti</i>	Forrest’s Mouse	17	7	38	24
<i>Notomys longicaudatus</i>	Long-tailed Hopping Mouse	34	14	48	26
<i>Notomys</i> sp. 2	Hopping Mouse	9	1	—	—
<i>Pseudomys australis</i>	Plains Mouse	87	47	107	55
<i>Pseudomys</i> sp. cf. <i>P. delicatulus</i>	Delicate Mouse	3	3	7	4
<i>Pseudomys desertor</i>	Desert Mouse	1	1	—	—
<i>Pseudomys gouldii</i>	Gould’s Mouse	13	8	10	7
<i>Pseudomys gracilicaudatus</i>	Eastern Chestnut Mouse	15	10	22	12
<i>Zyzomys</i> sp. 1	Rock Rat	2	1	1	1
<i>Hydromys chrysogaster</i>	Water Rat	—	—	1	1
<i>Melomys cervinipes</i>	Fawn-footed Melomys	2	1	—	—
<i>Rattus</i> spp.	Native Rat	72	36	81	40
<i>Rattus lutreolus</i>	Swamp Rat	1	1	—	—
“Microchiroptera” sp. indet.	Microbat	1	1	1	1
<i>Miniopterus orianae</i>	Bent-wing Bat	—	—	1	1

Taphonomy

Both deposits preserve very similar taphonomic signatures in that the breccias are heavily lithified, lack obvious stratification, and are dominated by the remains of small-bodied vertebrates. Prior to acid digestion (or at least in the early stage of acid digestion), bones within the breccias were mostly complete *in situ* (Fig. 2D). Where fragmentation was observed on skeletal elements, the broken ends lacked evidence of abrasion suggestive of re-working (e.g., Fig. 2D). Subsequent acid processing of the breccias led to higher fragmentation of the bones.

The breccias have a high concentration of skeletal remains (e.g., Fig. 2D). The majority of the fauna are nocturnal, non-cavernous species. The fossils lack tooth markings suggestive of predation from carnivorous mammals. They

bear the appearance of typical owl deposits like those of modern roosts observed elsewhere (e.g., Walton, 1990). Thus, the most parsimonious interpretation is that these assemblages were produced predominantly by owls. Owls typically hunt at night either consuming their prey in the surrounding region or back in the caves. They will tear the prey apart to consume before regurgitating pellets that contain difficult to digest elements such as bones and teeth, fur and feathers. More robust elements (i.e., bone and teeth) are more resilient to post-burial diagenesis and readily make their way into the fossil record (Walton, 1990). Skeletal remains of larger-bodied taxa preserved within the breccias are unlikely to have been brought into the caves by owls, but rather, are likely victims of the caves acting as pitfall traps. Today, it is not unusual to see the remains of modern skeletons of macropodids (especially rock wallabies and

wallaroos) lying on the floors of other caves in the area.

Forty taxa were identified from the two deposits, with 26 identified to species level (Table 1). Mammals (32 taxa) are the most abundant in terms of taxonomically identifiable remains. Most mammalian taxa occur in both deposits, although five are unique to Beehive and another seven are found only in Big Ho. Species richness is similar across deposits: Big Ho contains 27 species of mammal versus 25 for Beehive. To test for potential bias introduced by sampling intensity, we conducted a rarefaction analysis (Fig. 3) using PAST 4.0 (Hammer *et al.*, 2001). For mammals, although Big Ho has more specimens identified to lowest taxonomic level possible than Beehive (372 vs 302), rarefaction diversity curves for both deposits tend towards an asymptote. When compared at a common number of specimens, i.e., 302, both curves predict that 25 species would be present. This further highlights the taphonomic similarities between both deposits. It is likely that more collecting from both sites, especially Beehive, would yield a greater diversity of mammalian species. Pertinent taxonomic remarks for the Broken River taxa are given below.

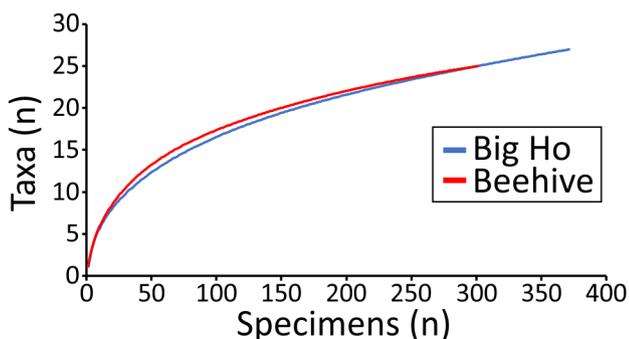


Figure 3. Rarefaction curves comparing Big Ho and Beehive mammalian diversity within respective fossil breccias.

Fauna

Anura

Frogs (Fig. 4A,B) were identified on the basis of postcranial remains. Iliac morphologies indicate that at least two taxa are present.

Sauropsida

Squamates (Fig. 4C–G) were identified to family predominantly on the basis of vertebrae, maxillae, and mandible fragments, revealing the presence of varanid, agamid, and scincid lizards, as well as elapid and pythonid snakes. Osteoderms and jaws were less commonly recovered.

Aves

Birds (Fig. 4H,I) are abundant in both study sites, with a variety of sizes and morphologies hinting at a sizeable diversity of taxa. These specimens await future study.

Mammalia

Marsupialia

Dasyuridae

Dasyurus sp. indet. (Fig. 5A). A medium-sized quoll is represented by isolated molars. Dimensions of the molars indicate that it is within the size range of *D. viverrinus* and *D. geoffroii*, but the available material is insufficient to separate these species.

Antechinus sp. indet. (Fig. 5B). The identification of fossil *Antechinus* is discussed in Cramb & Hocknull (2010a). *Antechinus* is a rare taxon at Broken River, represented by mandibular fragments and isolated teeth. Most species of *Antechinus* have posterior cingula on M^{1-3} , and this is the distinguishing feature of the Broken River specimens. The exact identity of the Broken River specimens cannot be established on the basis of available material.

Phascogale tapoatafa (Fig. 5C). The Brush-tailed Phascogale is a medium-sized dasyurid with a reduced P_3 , posterior cingula on the upper molars, commonly buccal cingula on M^1 , and relatively strong buccal cingulids on the lower molars. It is distinguished from other species (*P. pirata*, *P. calura*, and an undescribed species from Mount Etna) by being larger and having stronger buccal cingula on the upper molars.

Planigale sp. cf. *P. ingrami* / *tenuirostris* (Fig. 5D). Archer's (1976) revision of *Planigale* found that the most reliable dental features separating species were size and presence/absence of a $P^{3/3}$. One specimen from Big Ho has a lower molar row measuring 4.05, within the ranges of *P. ingrami* and *P. tenuirostris*, and equidistant between the means for both species as given by Archer (1976).

Sminthopsis macroura (Fig. 5E). The Stripe-faced Dunnart is medium-size (for a species of *Sminthopsis*), and possesses large entoconids on M_{1-3} that do not contact the hypocristids (Archer, 1981).

Sminthopsis sp. cf. *S. murina* (Fig. 5F). The majority of *Sminthopsis* specimens in the study sites lack entoconids on M_{1-3} . They are assigned to *S. murina* here, although distinguishing that species from other “entoconid-less” species of *Sminthopsis* is difficult (Cramb *et al.*, 2009).

Chaeropodidae

Chaeropus yirratji (Fig. 5G). Three specimens from Big Ho and four from Beehive represent the Northern Pig-footed Bandicoot and were included in the description of the species in Travouillon *et al.* (2019). Characters on the M^1 and M_1 are diagnostic and help separate it from *Chaeropus ecaudatus*. These include the paracone connecting to StB (styler cusp B) only on M^1 (not StA, in unworn teeth); the metaconule on M^{1-3} is well-developed, making molars more rectangular in shape; StD present on M^1 and the paracristid on M_1 does not connect to the protoconid (in unworn teeth).

Peramelidae

Isoodon sp. (Fig. 5H). This taxon is recorded only in Big Ho and is represented only by isolated lower molars (M_1 and M_2). All measurements are within the modern range for *I. macrourus torosus*, but at the smaller end of the range. There are very few diagnostic characters on lower molars of

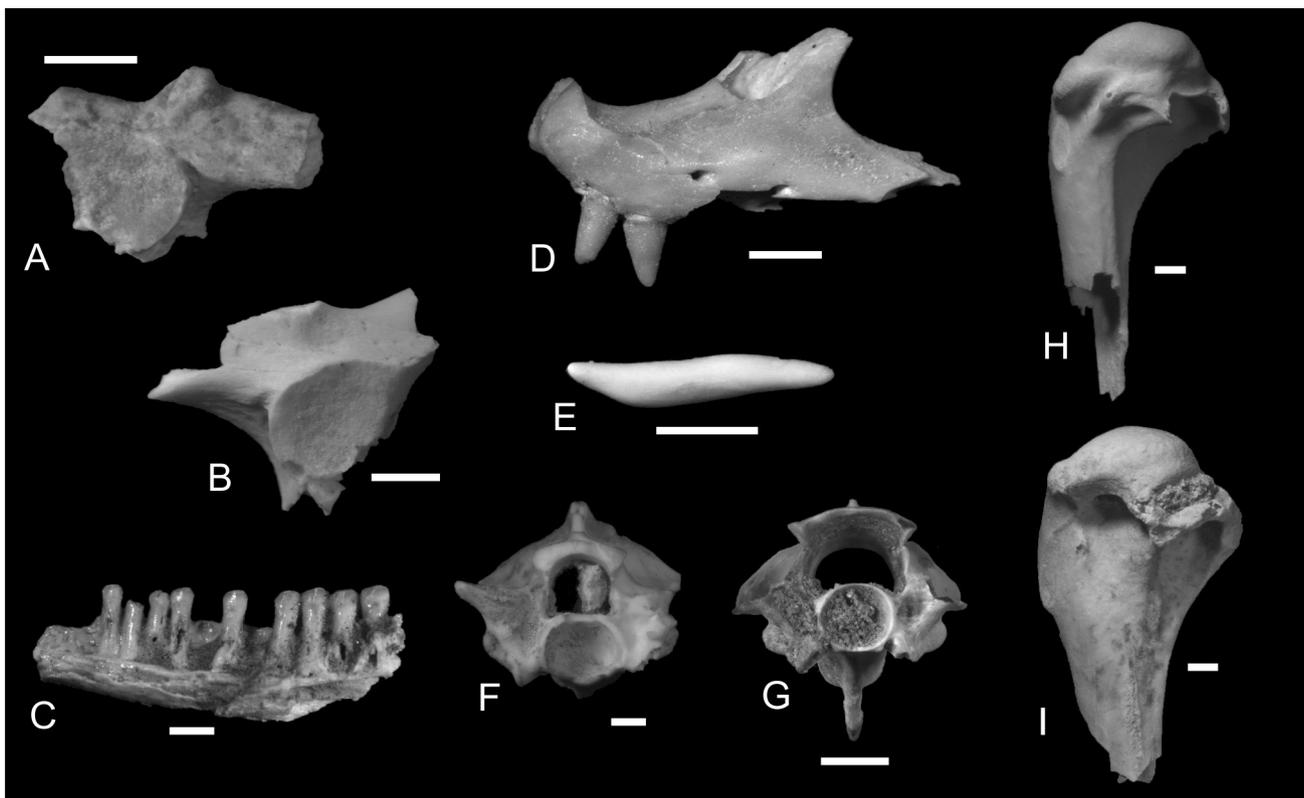


Figure 4. Non-mammal vertebrates of the Broken River karst area. (A–B) anuran pelves (UQPL1–2); (C) scincid dentary (UQPL3); (D) agamid upper jaw (UQPL4); (E) varanid osteoderm (UQPL5); (F) pythonid vertebra (UQL6); (G) elapid vertebra (UQPL7); (H–I) avian humeri (UQPL8–9). Scale bars = 1 mm.

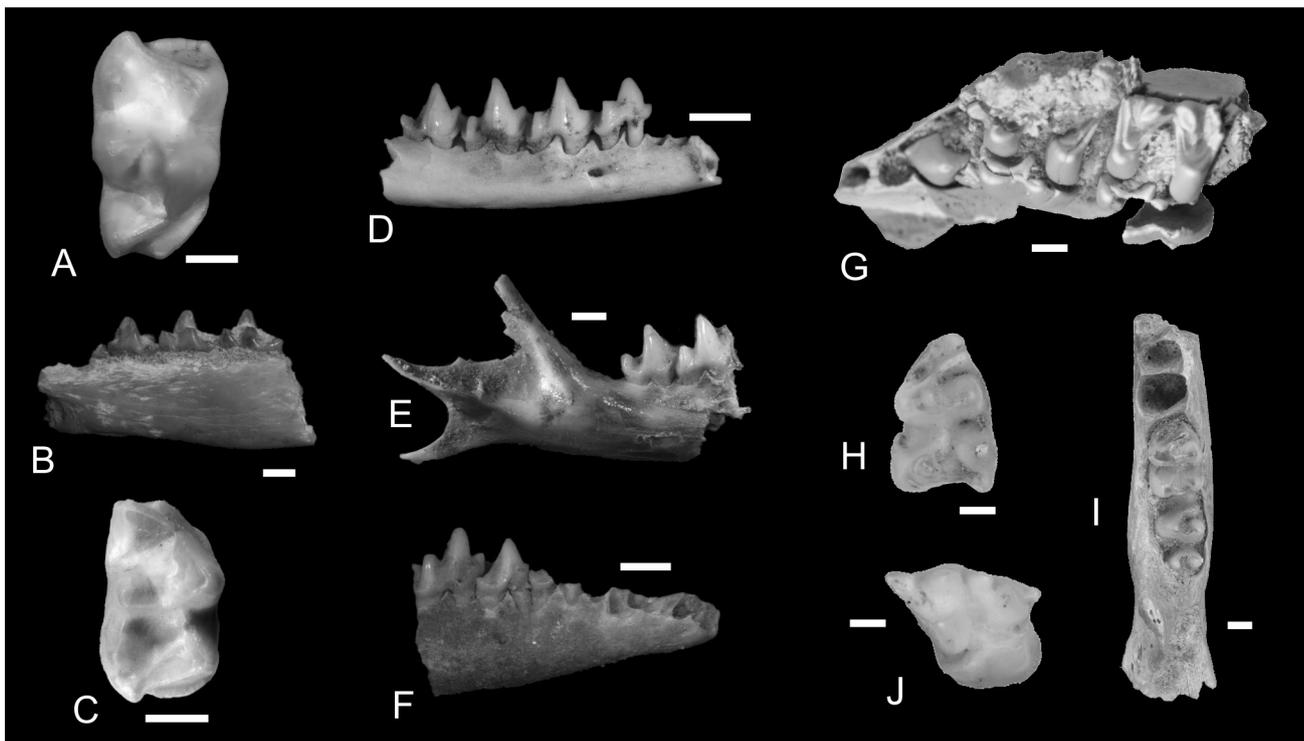


Figure 5. Dasyurids and bandicoots of the Broken River karst area. (A) *Dasyurus* lower molar (UQPL10); (B) *Antechinus* sp. dentary (UQPL11); (C) *Phascogale tapoatafa* lower molar (UQPL12); (D) *Planigale* sp. cf. *P. ingrami/tenuirostris* dentary (UQPL13); (E) *Sminthopsis macroura* dentary (UQPL14); (F) *Sminthopsis* sp. cf. *S. murina* dentary (UQPL15); (G) *Chaeropus yirratji* maxilla (QMF58987); (H) *Isoodon* sp. lower molar (UQPL17); (I) *Isoodon peninsulae* mandible (UQPL16); (J) *Perameles* sp. upper molar (UQPL18). Scale bars = 1 mm.

Isoodon. Despite being clearly a specimen of *Isoodon*, and being too large to be any other species than *I. macrourus*, there are a number of differences compared to the modern taxon. The paraconid on M_1 is large and in line with the metaconid (the paraconid is commonly reduced and more buccally positioned in all described species of *Isoodon*). The posthypocristid is not perpendicular to the toothrow on either the M_1 or M_2 , which is a feature typically seen in *Isoodon auratus*, *I. fusciventer*, and *I. peninsulae* but not in *I. macrourus*. It is an undescribed species of *Isoodon*. We do not erect a new species here, but rather wait on the discovery of additional, more comprehensively diagnosable material.

Isoodon peninsulae (Fig. 5I). The Cape York Brown Bandicoot is the most common species of bandicoot present in both Big Ho and Beehive. The dental measurements are slightly larger than the modern range for this taxon, but still below that of *I. macrourus*. The overall morphology matches that of *I. peninsulae*. It differs from *I. auratus*, *I. fusciventer*, and *I. macrourus* in having a preparacrista of M^1 buccally orientated then posterobuccally orientated. It differs from *I. fusciventer* and *I. macrourus* in having a styler crest present on M^1 and no StC/D on M^4 . It differs from *I. fusciventer*, *I. macrourus*, and *I. obesulus* in having a small anterior cingulum on M^1 not connected to the talon, and a large anterior cingulum of M^2 not connected to talon. It differs from *I. macrourus* and *I. obesulus* in having the posthypocristid of M_1 and M_2 oblique to the tooth row.

Perameles sp. (Fig. 5J). This taxon is only represented by two isolated molars, a left M^1 and a left M_2 , both from Big Ho. The M^1 length is within the range of modern *Perameles pallescens*, but the tooth is wider than in the modern species. The M_2 width is also within the modern range, but the length is longer. The M_2 typically has no reliable characters to identify specimens to known species (see Travouillon, 2016). The M^1 has several characters which are diagnostic: it differs from *Perameles bougainville*, *P. fasciata*, *P. myosuroides*, *P. notina*, and *P. gunnii* in having a short styler crest not connected to StD. It differs from *Perameles eremiana*, *P. fasciata*, *P. myosuroides*, *P. notina*, and *P. papillon* in that the preparacrista not reconnecting to the postparacrista posteriorly. It differs from *Perameles bougainville*, *P. eremiana*, *P. fasciata*, *P. myosuroides*, and *P. papillon* in having StB and StC distinguishable with StC larger than StB. It differs from all *Perameles* except *P. eremiana* and *P. nasuta* in having a very small StA. It differs from *P. nasuta* and *P. pallescens* in having a postprotocrista that ends posteriorly to metacone. It differs from *P. fasciata* in having no anterior cingulum. While there are enough characters to separate it from all modern taxa, it is not described as a separate species here, as it cannot be compared to the extinct fossil species *Perameles sobbei*, from which no M^1 has been recovered to date. The M_2 matches the morphology of *P. sobbei* (e.g., Price, 2002), but it also matches that of other *Perameles*, such as *P. pallescens*. As a result, we consider this taxon as *Perameles* sp. until further material is recovered, but it is undoubtedly an extinct species.

Petauridae

Petaurus norfolcensis (Fig. 6A). The Squirrel glider is a medium-sized *Petaurus* distinguished by having molar rows longer than those of *P. breviceps* and *P. biacensis* but shorter than *P. australis*, *P. gracilis*, and *P. abidi*.

Phalangeridae

Trichosurus sp. indet. (Fig. 6B). Phalangerids are easily distinguished from similarly-sized pseudocheirids by their bunodont molars.

Few morphological characters separate the species of *Trichosurus*, but *T. vulpecula* is extant in the Broken River area and is thus considered to be the most likely identity of the fossil specimens. One specimen from Big Ho is an unerupted molar, indicating that the individual was a juvenile.

Hypsiprymnodontidae

cf. *Hypsiprymnodontidae* gen. et sp. indet. (Fig. 6C). An isolated premolar fragment has the distinctive “buzz-saw” shape and ridges seen in hypsiprymnodontids, some burramyids, and propleopines. The size of the specimen is similar to *Hypsiprymnodon*, but its generic and specific identity is unknown.

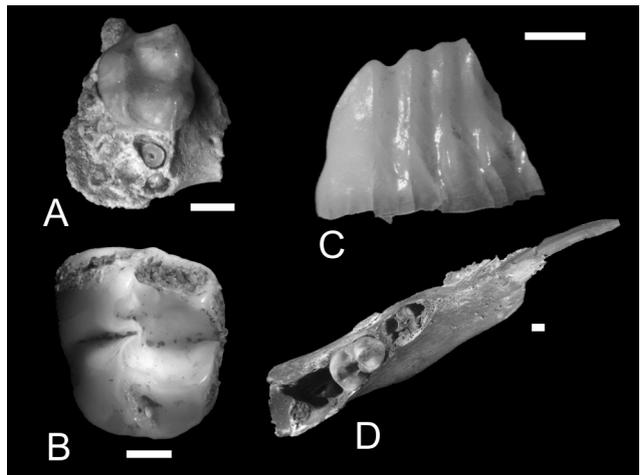


Figure 6. Diprotodonts from the Broken River karst area. (A) *Petaurus norfolcensis* upper molar (UQPL19); (B) *Trichosurus* sp. upper molar (UQPL20); (C) ?hypsiprymnodontid premolar (UQPL21); (D) juvenile macropodid mandible (UQPL22). Scale bars = 1 mm.

Macropodidae

Macropodidae indet. (Fig. 6D). Macropodid remains are uncommon, fragmentary, and appear to be from immature individuals. A partial mandible from Beehive represents a very young individual, most likely from a rock wallaby (*Petrogale* sp.) although additional material is required to confirm the identification.

Placentalia

Muridae

Rats and mice are most readily identified to species by their upper molars and maxillae, which form the majority of referred specimens here.

Conilurus albipes (Fig. 7A). Distinguishing features of the species are listed by Cramb & Hocknull (2010b). The Broken River sites are the northern-most records of this species.

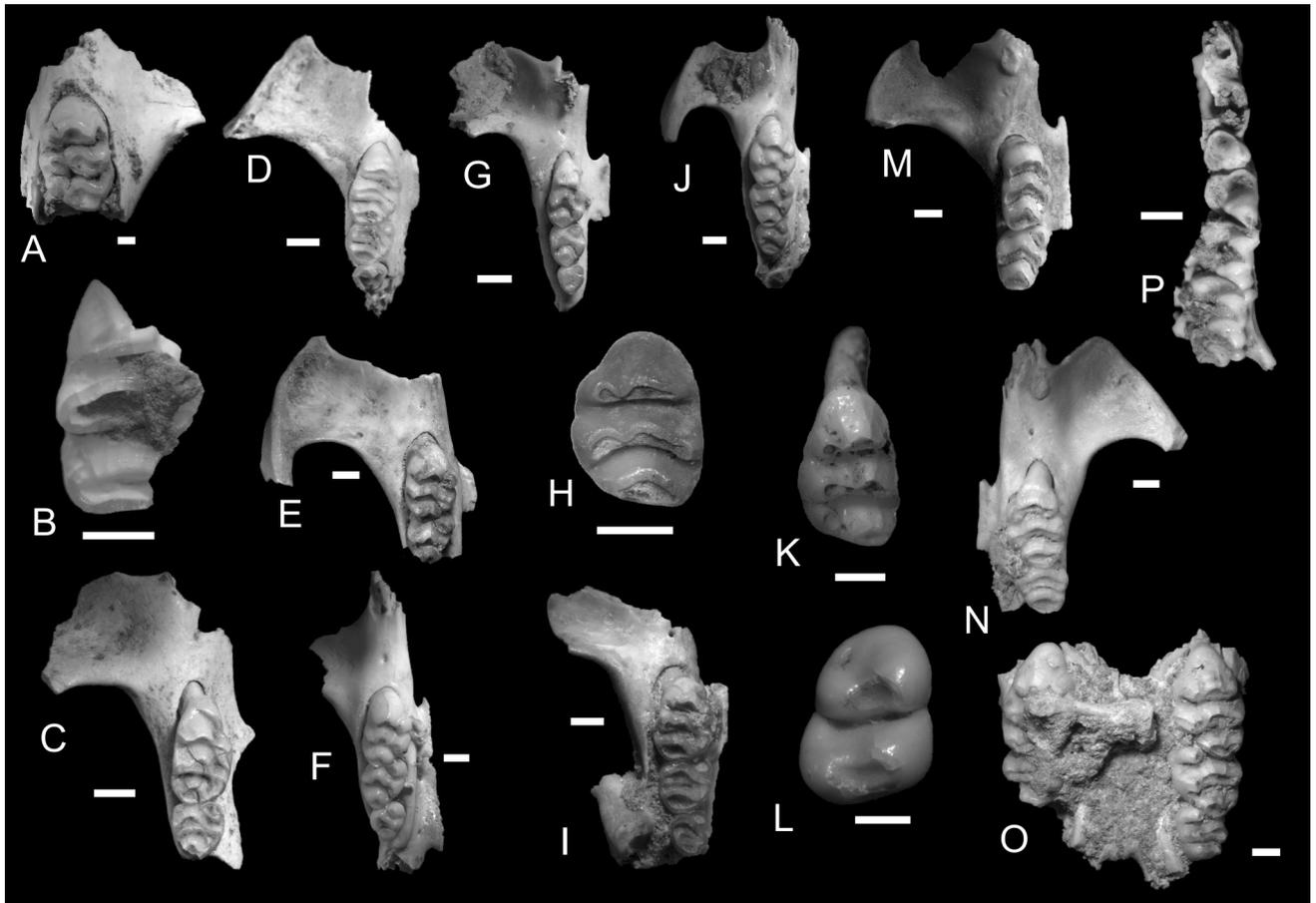


Figure 7. Placentals from the Broken River karst area. (A) *Conilurus albipes* maxilla (UQPL23); (B) *Conilurus capricornensis* molar fragment (UQPL24); (C) *Leggadina forresti* maxilla (UQPL25); (D) *Notomys longicaudatus* maxilla (UQPL26); (E) *Notomys* sp. 2 maxilla (UQPL27); (F) *Pseudomys australis* maxilla (UQPL28); (G) *Pseudomys* sp. cf. *P. delicatulus* maxilla (UQPL29); (H) *Pseudomys desertor* molar (UQPL30); (I) *Pseudomys gouldii* maxilla (UQPL31); (J) *Pseudomys gracilicaudatus* maxilla (UQPL32); (K) *Zyzomys* sp. molar (UQPL33); (L) *Hydromys chrysogaster* molar (UQPL34); (M) *Melomys cervinipes* maxilla (UQPL35); (N) *Rattus* sp. maxilla (UQPL36); (O) *Rattus lutreolus* maxilla (UQPL37); (P) *Miniopterus orianae* maxilla (UQPL38). Scale bars = 1 mm.

Conilurus capricornensis (Fig. 7B). Isolated molar fragments from Big Ho are referred to a large species of *Conilurus* that has proportionally shorter, broader cusps than *C. albipes*. Of the three species, *C. capricornensis* is the best fit for these specimens. The type locality for the species is also in the Broken River area (Cramb & Hocknull, 2010b).

Leggadina forresti (Fig. 7C). Distinguishing features for species of *Leggadina* are listed by Cramb *et al.* (2017).

Field guides (e.g., Menkhorst & Knight, 2010; Van Dyck *et al.*, 2013) show the distributions of *L. forresti* and *L. lakedownensis* as non-overlapping, with the latter present in northeast Queensland. However, *L. forresti* is recorded as extant in the area so its palaeo-occurrence in the study sites is perhaps not surprising.

Notomys longicaudatus (Fig. 7D). The Long-tailed Hopping-mouse is identified by its large, *Pseudomys*-like molars; broad T8–9 complex on M¹; proportionally short molar row; concave anterior margin of zygomatic plate with associated spine; and deep zygomatic bar.

Notomys sp. 2 (Fig. 7E). This species was originally identified by Ken Aplin based on specimens from Christmas Creek (an unpublished collection from west of the study

sites). It has since been found in other deposits in the Broken River area. It is a moderately large species that cannot be placed in any described species with confidence (Ken Aplin pers. comm., November 2009).

Pseudomys australis (Fig. 7F). The Plains Mouse is distinguished by having molars that are proportionally narrow, each tapering posteriorly; cusps taller than those of *P. gracilicaudatus*, but not as tall as *P. oralis*; a T3 on M¹ that is heavily reduced or absent; accessory cusp absent; and a proportionally long M³. The anterior palatal foramen is posteriorly narrow. Specimens from the study sites are among the northern-most records of this species.

Pseudomys sp. cf. *P. delicatulus* (Fig. 7G). Small species of *Pseudomys* are difficult to distinguish. Two species are known to occur in eastern tropical Queensland today: *P. delicatulus* and *P. patrius*. A maxilla from Big Ho preserves the posterior end of the anterior palatal foramen, which extends past the anterior margin of M¹. This suggests that it is probably *P. delicatulus*, although the presence of *P. patrius*, or other small species of *Pseudomys*, cannot be excluded.

Pseudomys desertor (Fig. 7H). An isolated M¹ is assigned to *P. desertor* due to its broad T4 and T8–9 complex, and straight posterior margin on the anterior loph.

Pseudomys gouldii (Fig. 7I). Gould's Mouse is a medium-sized *Pseudomys* characterized by the following features of M^1 : crown not as broad as *P. gracilicaudatus*, variably developed accessory cusp, commonly with a link between the bases of T1 and T2; reduced or absent T3; cusps of middle loph all well-defined; T4 noticeably larger than T1; and T8–9 tapering posteriorly. Several of these features are diagnostic of *P. australis*, but the fossils appear to be closer to *P. gouldii* in that they commonly have an accessory cusp; a less elongate M^3 ; and a posteriorly broader anterior palatal foramen.

Pseudomys gracilicaudatus (Fig. 7J). The Eastern Chestnut Mouse is a medium-sized mouse that has broad molars and commonly has a well-developed accessory cusp on M^1 . It is very similar to *P. nanus*, leading Watts & Aslin (1981) to suggest that these two species are best separated by geographic distribution (a dubious proposition when applied to fossils). Known distributions of *P. gracilicaudatus* and *P. nanus* suggest that *P. gracilicaudatus* is the most likely species in the study sites.

Zyzomys sp. (Fig. 7K). A large species of rock rat is found in several cave sites in eastern Queensland. Godthelp (1997) stated that both *Z. argurus* and *Z. woodwardi* were present in the Chillagoe area until recently. However, examination of more complete specimens from Mount Etna has indicated that the larger species of *Zyzomys* found in eastern tropical Queensland sites is an undescribed species. It is identified in the study sites by the dimensions of M^1 , which is larger than that of *Z. argurus*.

Hydromys chrysogaster (Fig. 7L). A single right M_2 is the only evidence of this species in the study sites. Isolated molars are easily recognized by their bulbous molar lophs with indistinguishable cusps. The single specimen here is unworn, indicating that it was a young individual.

Melomys cervinipes (Fig. 7M). *Melomys* and *Uromys* molars are distinguished by having well-developed lingual cusps on M^{1-2} but lacking a T7; having more than three roots on M^1 ; molar cusps that seem to wear rapidly, so that most specimens exhibit joining of the cusps to form flat-topped lophs; and fine ornament on the molar enamel. *Melomys cervinipes* is distinguished from *M. burtoni* by being larger and having four roots on M^1 . *Melomys capensis* also has four roots on M^1 , and it is probably not possible to distinguish *M. capensis* and *M. cervinipes* on the basis of isolated molars. The specimens in Beehive are close to the mean M^1 width of *M. cervinipes*, and are also considered more likely to be this species on the basis of extant distributions.

Rattus sordidus/tunneyi/villosissimus/colletti group (Fig. 7N). Four of the seven indigenous species of *Rattus* form an obvious group based on morphology and molecular phylogenetics: *R. sordidus*, *R. tunneyi*, *R. villosissimus*, and *R. colletti* (Aplin, 2006). Molar measurements of species within this complex are similar, making identification of fossil specimens difficult.

Rattus lutreolus (Fig. 7O). Isolated molars of the Swamp Rat can be distinguished from other Australian species of *Rattus* by their larger size. One specimen from Beehive is a partial palate, with associated maxillae and palatines.

Miniopteridae

Miniopterus orianae (Fig. 7P). Diagnostic craniodental characters for Australian microbats are given by Martinez (2010). Multiple species of microbats are present in the study sites based on different sized limb elements, but only *M. orianae* is represented by generic and specific diagnostic craniodental material: a left maxilla with P^{1-2} and M^{1-3} . *Miniopterus orianae* (*M. schreibersii* in Martinez, 2010) is distinguished from *M. australis* by the larger dimensions of the M^1 , particularly width.

Geochronology

We produced 10 U-Th dates (Table 2) for two fossil bones (Fig. 8), one each from Big Ho (broken cross-section of a femur) and Beehive (broken cross-section of a tibia). Uranium concentration is relatively consistent in both specimens (c. 7 ppm for Big Ho and 3.5 ppm for Beehive) regardless of proximity to the outer natural surface of the bones. Similarly, ^{230}Th ages are relatively consistent through both respective cross-sections. This suggests that both bones rapidly took up U following burial and both have acted as closed systems after recrystallization of the calcium phosphate; there is no evidence of U leaching. Thus, the dates for Big Ho (c. 165 ka) and Beehive (c. 8.5 ka) are reliable minimum ages and are most likely close to the burial ages of the collected portions of the respective deposits. Considering the shallow stratigraphic depth of the sampled portion of both deposits (i.e., 50–70 mm depth), lack of stratification, and no geological evidence of sedimentological hiatuses, it is unlikely that the breccias accumulated over long periods of time. Thus, we consider the ages as reliable approximations for the contained fossil assemblages from both respective breccias.

The hypothesized relative ages of the breccias as estimated by geological inferences is supported by direct U-series dating (i.e., that Big Ho is older). Both deposits are clearly late Quaternary, with Big Ho dating to the penultimate glacial cycle between Marine Isotope Stage (MIS) 7A and 6, while Beehive dates to the early Holocene (MIS 1).

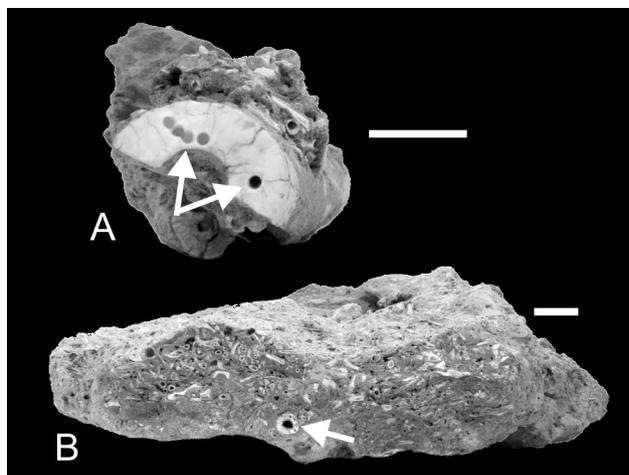


Figure 8. U-series dated fossil samples from the Broken River karst area. (A) breccia karst from Beehive; (B) breccia clast from Big Ho. Arrows indicate dated specimens. Scale bars = 10 mm.

Table 2. U-series isotopic data for the two dated bones from Big Ho (BH) and Beehive (BeH) caves of the Broken River karst area.

sample name	U (ppm)	²³² Th (ppb)	²³⁰ Th/ ²³² Th	²³⁰ Th/ ²³⁸ U	²³⁴ U/ ²³⁸ U	uncorr. age (ka)	corrected age (ka)	corrected initial ²³⁴ U/ ²³⁸ U
BeH-1A	3.031 ± 0.002	124.19 ± 0.21	8.9 ± 0.1	0.120 ± 0.001	1.411 ± 0.002	9.6 ± 0.1	8.8 ± 0.4	1.426 ± 0.003
BeH-1B	3.996 ± 0.003	4.43 ± 0.01	288.9 ± 1.8	0.106 ± 0.001	1.402 ± 0.001	8.5 ± 0.1	8.5 ± 0.1	1.412 ± 0.001
BeH-1C	4.268 ± 0.002	9.68 ± 0.01	145.9 ± 0.8	0.109 ± 0.001	1.395 ± 0.001	8.9 ± 0.1	8.8 ± 0.1	1.406 ± 0.001
BeH-1D	3.452 ± 0.002	7.96 ± 0.02	136.1 ± 1.2	0.103 ± 0.001	1.401 ± 0.001	8.3 ± 0.1	8.3 ± 0.1	1.410 ± 0.001
BeH-1E	3.491 ± 0.002	5.49 ± 0.01	185.2 ± 1.7	0.096 ± 0.001	1.405 ± 0.001	7.7 ± 0.1	7.7 ± 0.1	1.414 ± 0.001
BH-A	6.492 ± 0.005	95.82 ± 0.24	176.6 ± 0.9	0.859 ± 0.004	1.094 ± 0.003	161.6 ± 1.9	161.2 ± 1.9	1.148 ± 0.004
BH-B	8.113 ± 0.006	5.96 ± 0.04	3622.5 ± 28.6	0.876 ± 0.003	1.095 ± 0.002	168.7 ± 1.7	168.7 ± 1.7	1.152 ± 0.003
BH-C	7.041 ± 0.006	13.35 ± 0.06	1398.8 ± 8.1	0.874 ± 0.003	1.093 ± 0.003	168.2 ± 2.0	168.1 ± 2.0	1.150 ± 0.004
BH-D	5.465 ± 0.006	48.94 ± 0.20	292.4 ± 1.8	0.863 ± 0.004	1.091 ± 0.003	164.2 ± 2.2	164.0 ± 2.2	1.145 ± 0.005
BH-E	7.035 ± 0.007	31.22 ± 0.10	597.7 ± 3.3	0.874 ± 0.004	1.096 ± 0.002	167.2 ± 2.0	167.1 ± 2.0	1.154 ± 0.003

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios, but normalized to measured values of secular-equilibrium HU-1 (Pike *et al.*, 2002). All errors are given at the 2σ level. ²³⁰Th ages are calculated using Isoplot EX 3.0 (Ludwig, 2003) with decay constants $\lambda_{238} = 1.551 \times 10^{-10} \text{ yr}^{-1}$ (for ²³⁸U), $\lambda_{234} = 2.826 \times 10^{-6} \text{ yr}^{-1}$ (for ²³⁴U) and $\lambda_{230} = 9.158 \times 10^{-6} \text{ yr}^{-1}$ (for ²³⁰Th), respectively (Cheng *et al.* 2000). 2σ errors in the uncorrected (uncorr.) ages were propagated directly from the uncertainties in the (²³⁰Th/²³⁸U) and (²³⁴U/²³⁸U). The corrected (corr.) ²³⁰Th age was calculated using the assumed bulk earth or upper crust value equivalent to the detrital ²³⁰Th/²³²Th activity ratio of 0.83.

Discussion

Palaeoenvironment

The palaeohabitat signatures from the two deposits are very similar to each other. Both contain several taxa that indicate a mosaic of open grassland (e.g., *Pseudomys* spp., *Leggadina forresti*, *Sminthopsis* spp.) and woodland habitats (e.g., *Phascogale tapoatafa*, *Antechinus* sp., *Trichosurus* sp.). Local permanent waterbodies are inferred by the presence of *Hydromys chrysogaster* (Big Ho) and *Rattus lutreolus* (Beehive).

Open-habitat adapted taxa such as *Chaeropus yirratji*, *Pseudomys australis*, *Leggadina forresti*, and *Notomys longicaudatus* are by far the most abundant species in both deposits. However, it is uncertain if open habitats were more common around the caves than wooded areas, or if their abundance simply reflects a feeding bias whereas the owls preferred to hunt, or were more successful hunters, in open environments rather than woodlands. In any case, most owl species hunt within a 3 km radius of their roost sites (Walton, 1990), indicating that the inferred palaeohabitats existed proximal to the caves.

Several arid-adapted species are present in the fossil assemblages that are now locally extinct, such as *Pseudomys australis* and *P. gouldii*. Their presence at Broken River during both the penultimate glacial cycle and early Holocene hints at an expanded arid zone during those times. Indeed, similar expansions of the arid zone towards the coastline have been inferred based on vertebrate-rich deposits from elsewhere such as Mt Etna (Hocknull *et al.*, 2007), although the climate event recorded in those deposits occurred before 170 ka.

Diversity

The Broken River fossil record preserves a record of both continuity and change in terms of species persistence through time. Numerous species have been recorded in both deposits in relatively similar proportions (e.g., species of *Pseudomys*,

Notomys longicaudatus, *Leggadina forresti*). For taxa that appear in only one of the deposits, they are typically uncommon and generally represented by relatively low numbers of specimens (e.g., ?hypsiprymnodontid, *Dasyurus* sp., *Rattus lutreolus*, *Pseudomys desertor*), hence we err on the side of caution in reading too much into those scant records. Strikingly, however, five species (16%) of mammals in the Broken River deposits reported here represent globally extinct taxa. Of those five, only one, *Conilurus capricornensis*, has been formally described (Cramb & Hocknull, 2010b). The Big Ho specimens represent the oldest record of that species. The timing of its extinction is unclear but is probably late Holocene.

The other extinct but hitherto undescribed fossil taxa include one species in each of *Zyromys*, *Notomys*, *Isoodon*, and *Perameles*. The species of *Perameles* is so far known only from Big Ho and the *Notomys* species only from Beehive. Species of *Isoodon* and *Zyromys* probably have a long history in the region as they are recorded from both deposits. Overall, these taxa add to the growing bestiary of Australian small-bodied species that went globally extinct during the Late Pleistocene (e.g., Cramb *et al.*, 2018; Klinkhammer & Godthelp, 2015), highlighting that vertebrate extinctions during this period did not just occur among large-bodied “megafauna” (cf. Flannery, 1990).

Several species are recorded in the Broken River records that suffered extinction since European colonization of the continent. These include *Chaeropus yirratji*, *Notomys longicaudatus*, *Conilurus albipes*, and *Pseudomys gouldii*. In each case, the fossil records are far outside of the known historic geographic range of each species. It is unknown if those species occurred locally at Broken River at the time of European colonization or were extirpated from the region prior to their arrival. It is possible that they were present but were decimated rapidly and never recorded in modern ecological surveys of the area. Similar extirpation records for small-bodied mammal species have been noted elsewhere in Australia (e.g., Fusco *et al.*, 2016; Price *et al.*, 2019).

Meaningful comparisons of the Broken River fossil species with modern regional records is hampered by a paucity of geographic distributional data, especially for non-volant mammals. We obtained a species list for the area based on records within the Queensland Government's Wildnet database (accessed 26 January 2020). For the area within a 5 km radius of Broken River (thus encompassing a typical owl's hunting range), only four non-volant native mammal species are recorded: three species of macropodoid (*Aepyprymnus rufescens*, *Osphranter robustus* and *Petrogale assimilis*) and the brushtail possum, *Trichosurus vulpecula*. Extending the search area to a 50 km radius recovered 27 non-volant mammals. Of these, nine are historically introduced species (e.g., pigs, cattle), ten are relatively large-bodied native species (mostly macropodoid), and the remainder are in a similar weight range to those of the Broken River fossil assemblages. For rodents, modern surveys record only four native species, compared to 13 species in our early Holocene record (i.e., the Beehive assemblage). This could indicate a major decline in diversity of rodents between the early Holocene and today, or simply a lack of modern ecological surveys for small-bodied mammals. We strongly suspect a combination of both. This hypothesis is testable if younger pre-European colonization fossils deposits can be found, in combination with a dedicated small-mammal trapping survey of the region.

Final remarks

Big Ho and Beehive represent the first report of complete fossil mammal assemblages from the Quaternary of northern Australia. While preliminary, they are part of a larger project to record the palaeontological history of the Broken River region. As part of this effort, many other caves have been explored and fossil deposits excavated, with laboratory processing of breccias (e.g., acid digestion, sorting of bones, taxonomic identification) and dating (mostly U-series) ongoing. Most caves we visited yielded fossil deposits, but like Big Ho and Beehive, the deposits are heavily lithified and difficult to extract. Speleothems are rarely associated with the breccias, making dating with methods such as U-series and optically stimulated luminescence challenging. Considering the paucity of information about Australia's Quaternary history of the region, and the promising results generated in this study, future research will no doubt provide further evidence of biotic change in tropical northeast Australia. Such records are critical for testing the timing and potential causes of the extinctions documented. We note also that these investigations would not be possible without the support of private landowners and "citizen scientists" within the speleological community who have been willing to introduce us to the caves of the area. At a time of limited funding for research in general, and a time of great concern over the future of Australian ecosystems, such partnerships are becoming increasingly vital and will likely lead to new insights and discoveries about our unique continent, the results of which will benefit us all.

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