# Palaeontological investigation of a Pleistocene vertebrate assemblage from Specimen Cave, Naracoorte, South Australia

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Nerita Turner November 2018



# PALAEONTOLOGICAL INVESTIGATION OF A PLEISTOCENE VERTEBRATE ASSEMBLAGE FROM SPECIMEN CAVE, NARACOORTE, SOUTH AUSTRALIA

# PALAEONTOLOGICAL INVESTIGATION OF SPECIMEN CAVE

# ABSTRACT

The Naracoorte Caves World Heritage Area (NCWHA) in southern Australia preserves an almost continuous fossil record of the last 500,000 years but contains a noticeable temporal gap between ~100 ka and ~200 ka. This study presents the first comprehensive assessment of a fossil assemblage from the Naracoorte region from this "gap". Fossils analysed in this study were excavated from Specimen Cave by the author, in the first documented palaeontological excavation of this cave. Preliminary dating from previous studies gives Specimen Cave an age of ~130 ka, placing it within the missing gap. The Specimen Cave fossil assemblage preserves a rich and diverse fauna which, shares many similarities with other NCWHA deposits. The deposit is dominated by small mammals, which constitute >90% of the fauna. The most abundant family in the deposit was Muridae (rodents), which also has the greatest species richness and density of all families. The large mammal fauna, which constitutes a very minor (<10%) component of the assemblage, is dominated by Macropodidae (kangaroos). The overall fauna is indicative of a woodland or open forest habitat, and this is the most likely vegetation to have existed in the proximal palaeoenvironment of the cave. The most likely mode of accumulation of the deposit is a pitfall trap, indicated by the presence of large mammals and the dominance of saltatory species in the large mammal fauna. The presence of megafauna such as Procoptodon sp. cf. P. goliah, provide the first robust evidence that some species of this large mammal group did not experience localised extinctions during this period. Comparisons to other mid Pleistocene NCWHA deposits reveal Specimen Cave has lower species richness than deposits older than 200 ka and younger than 100 ka. This apparent loss of richness is primarily attributed to the study's limited sample size.

# **KEYWORDS**

Paleontological, Pleistocene, mammal, Naracoorte Caves, fossil record, taxonomy, pitfall, palaeocommunity

# **TABLE OF CONTENTS**

| Abstract                                 | i |
|--|---|
| Keywords                                 | i |
| List of Figures and Tables               |   |
| 1. INTRODUCTION                          | 6 |
| 2. Geological Setting and Background     |   |
| 2.1. Geology of the Naracoorte region    |   |
| 2.2. Chronology of the Naracoorte caves  | 9 |
| 2.3. Specimen Cave                       |   |
| 3. METHODS                               |   |
| 3.1. Excavation                          |   |
| 3.2. Sorting and acid preparation        |   |
| 3.3. Specimen Cave fauna                 |   |
| 3.3.1. Identification                    |   |
| 3.3.2. Existing species list             |   |
| 3.3.3. Richness                          |   |
| 3.3.4. relative abundance                |   |
| 3.3.5. Body Mass and specimen Density    |   |
| 3.3.6. Habitat and diet                  |   |
| 3.4. Comparisons to other NCWHA deposits |   |
| 4. RESULTS                               |   |
| 4.1. Excavation passage morphology       |   |
| 4.2. In situ observations                |   |
| 4.2.1. articulation and associations     |   |
| 4.2.2. Sediments                         |   |
| 4.3. Specimen Cave fauna                 |   |
| 4.3.1. Richness                          |   |
| 4.3.2. Relative abundances               |   |
| 4.3.3. Body mass and specimen density    |   |
| 4.3.4. Habitat and diet                  |   |
| 4.4. Comparisons to other NCWHA deposits |   |
| 4.4.1. Species assemblages               |   |
| 4.4.2. Richness trends                   |   |
| 4.4.3. Relative abundances               |   |

| 5. D   | ISCUSSION  |
|--------|--|
| 5.1.   | Sediments  |
| 5.2.   | Faunal relative abundances   |
| 5.2.1. | Small mammals67  |
| 5.2.2. | Large mammals  |
| 5.3.   | Mode of accumulation   |
| 5.4.   | Habitat and diet71   |
| 5.5.   | Climate72  |
| 5.6.   | Megafauna extinction   |
| 5.7.   | Comparisons to other Naracoorte deposits                           |
| 5.7.1. | Species assemblages74  |
| 5.7.2. | Richness74   |
| 5.7.3. | Relative abundances76  |
| 5.8.   | Limitations and future directions77                                |
| 6. C   | ONCLUSIONS   |
| ACKN   | NOWLEDGMENTS   |
| REFE   | RENCES   |
| Appen  | dix 1. Chronology of the Naracoorte Caves                          |
| Appen  | dix 2: Comparison of the fauna of mid Pleistocene Naracoorte Caves |

# LIST OF FIGURES AND TABLES

Figure 1. Age span of the dated Naracoorte fossil deposits, showing the position of Specimen Cave within the missing age bracket between ~206 and ~93 ka. References: Ayliffe et al., 1998; Moriarty et al., 2000; Reed & Bourne, 2000, 2009; Pate et al., 2002, 2006; Forbes et al., 2007; Prideaux et al., 2007; Darrénougué et al., 2009; Macken et al., 2011; St Pierre et al., 2012; Macken & Reed, 2013 ; Mahlknecht, 2018 ; R. Weij, University of Melbourne Figure 2. Map of a portion of the Naracoorte Caves World Heritage Area, showing the location of Specimen Cave (Adapted from Moriarty et al., 2000). Inset: Map of South Australia showing the location of Naracoorte (Adapted from Macken et al., 2013)......11 Figure 3. The modern entrance to Specimen Cave. ..... 12 Figure 4. The human-made hole used to access Pit 1. The hole passes through the U-series dated flowstone layer. The hole is approximately 1 metre wide and the depth from the hole to Figure 5. Map of Specimen Cave (5U35), highlighting the key features, including the location of excavation Pit 1, the present day entrance and a possible Pleistocene pitfall trap entrance. Modified from CEGSA Map number 5U35.CEG1119.....14 Figure 6. The grid square reference numbers of Pit 1. The pit and the grid squares were Figure 8. Species richness (total number of species) of small mammal families represented in the Specimen Cave species lists. The species richness value of the 'existing list' in this graph includes species in the existing list that were not identified in this study. The value for 'both studies' includes species identified in this study and in the existing species list (Reed & Bourne, 2000). 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness. 'Pseudomys apodemoides/novaehollandiae' (Muridae) and 'Sminthopsis crassicaudata/murina' (Dasyuridae) are each counted as single species...25 Figure 9. Species richness (total number of species) of large mammal families in represented in the Specimen Cave species lists. The species richness value of the 'existing list' in this graph includes species in the existing list that were not identified in this study. The value for 'both studies' includes species identified in this study and in the existing species list (Reed & Bourne, 2000). 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness. 'Macropus fuliginosus/giganteus' counted as one Figure 10. The number of identifiable specimens (NISP) and the minimum number of individuals (MNI) of small taxa, showing the strong linear correlation between the two Figure 11. Relative abundance (RA%) of mammal groups in Pit 1 of Specimen Cave. RA% is Figure 12. A: Relative abundances (RA%) of small placental and marsupial mammals from Pit 1 and Pit 2 (calculated as a percentage of the NISP of all small mammals). B: Relative abundances (RA) of small marsupial families from Pit 1 and Pit 2 (calculated as a percentage of the NISP of small marsupials). Specimens from the overburden layer of Pit 1, not included. Figure 13. Small mammal species richness (total number of species) from Grant Hall, Main Fossil Chamber (VFC), Cathedral Cave and Specimen Cave. Caves are arranged on the xaxis from oldest to youngest (left to right). Specimen Cave species richness includes species identified in this study and by Reed and Bourne (2000). VFC = Victoria Fossil Cave. 'Sp.

indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the

| Table 1. Translations and meanings of taxonomic nomenclature abbreviations  |    |
|---|----|
| Table 2. Updated Specimen Cave mammal list                                  |    |
| Table 3. The NISP, MNI and RA% of small mammals in Pit 1                    |    |
| Table 4. The NISP, MNI and RA% of small mammals in Pit 2                    | 57 |
| Table 5. NISP and RA% of large mammals from Specimen Cave                   |    |
| Table 6. RA% and density of small mammals                                   | 59 |
| Table 7. Diet and preferred habitat of large mammal taxa from Specimen Cave | 60 |
| Table 8. Preferred habitats of small mammal taxa from Specimen Cave         | 61 |

## **1. INTRODUCTION**

The fauna of late Quaternary Australia provides key insight into the modern fauna of the continent. This period was characterised by climatic fluctuations, ecological change and faunal extinctions, the most dramatic of which saw the extinction of the continent's megafauna; a group of large mammals (>45 kg) that went extinct around 46,000 years (ka) ago (Moriarty et al., 2012; Prideaux et al., 2007; Roberts et al., 2001). One of Australia's most important Late Quaternary fossil localities is the Naracoorte Caves World Heritage Area (NCWHA), in south-east South Australia. Over 100 vertebrate fossil deposits have been identified here, spread throughout 26 of the region's limestone caves (Macken & Reed, 2013; Reed & Bourne, 2000). These deposits span ~520,000 ka to the present, making the NCWHA one of the only localities in the world to preserve a near complete record of fauna spanning the last half a million years (Moriarty et al., 2000; Prideaux et al., 2007). Extensive palaeontological research into several NCWHA fossil deposits (e.g. Victoria Fossil Cave) has yielded valuable information on many aspects of the Pleistocene palaeocommunities of southern Australia, including their species richness and diversity and how they changed through time (Macken et al., 2012; Prideaux et al., 2007).

Several key sites within the NCWHA have undergone geochronological study, allowing the temporal span of the Naracoorte deposits to be assessed (Ayliffe et al., 1998; Darrénougué et al., 2009; Macken, Staff & Reed, 2013; Moriarty et al., 2000; Prideaux et al., 2007; St Pierre et al., 2012). This research reveals that the Naracoorte record spans much of the past 500,000 years but highlights a temporal gap in the faunal record between ~100 ka and ~200 ka (E. Reed, personal communication, 2018). This is important as it means there is a major gap in the current understanding of the region's faunal history. To fill this gap, more studies must be undertaken on fossils sites dated between 100 ka and 200 ka.

The current study centres on a fossil-bearing sediment section in Specimen Cave, which potentially spans this time frame. Uranium-series (U-series) dating of flowstone overlying the fossil deposit has yielded a minimum age of approximately 139 ka (R. Weij, University of Melbourne, unpublished data with permission), placing the underlying sediments within the 'faunal gap'. The presence of Pleistocene fossil material in Specimen Cave has been known since 1908, following the discovery of *Thylacoleo carnifex* bones (Naracoorte Herald, 1908; The Register, 1908; Reed & Bourne, 2000). Despite this discovery, no formal geological studies or palaeontological excavations have since been undertaken (Reed & Bourne, 2000). The overarching objective of this study is to undertake the first paleontological excavation of Specimen Cave to provide the first comprehensive assessment of a faunal assemblage and palaeocommunity in the Naracoorte region between 100 ka and 200 ka. This will be achieved by addressing the following specific aims:

- Undertake the first palaeontological excavation in Specimen Cave. This excavation is an essential component of this study for two reasons:
  - it will expand the existing faunal list for Specimen Cave and the Naracoorte region during this period of the Pleistocene
  - it will allow the Specimen Cave fauna to be constrained within an age bracket for the first time. The constraints of this age bracket were obtained from two independent studies (Mahlknecht, 2018; R. Weij, University of Melbourne, unpublished data with permission)
- 2) Characterise the faunal assemblage using a range of parameters including species assemblages, species richness and the relative abundances of species. It is hypothesised that:
  - the faunal list will contain species that appear in other Naracoorte cave lists and be characterised by similar patterns of diversity.

- the small mammal fauna will be dominated by rodents, while the large fauna is expected to be dominated by macropods
- Determine the nature of the proximal palaeoenvironment by investigating the habitat preferences and diets of the animals identified in the fossil assemblage.
  - This information can be used to infer the climatic conditions prevailing at the time of deposition.
- Determine a mode of accumulation of the deposit using a range of parameters associated with the fauna, including their lifestyle and locomotion.
  - It is hypothesised that the fossils were accumulated by an owl or via a pitfall trap, as these are the two most common modes of accumulation observed in the Naracoorte caves fossil record.
- 5) Investigate how fauna and environment changed through time by comparing the results of this study with similar information from older and younger Naracoorte cave deposits, with particular focus on the Cathedral Cave and Grant Hall, Victoria Fossil Cave (VFC).

# 2. GEOLOGICAL SETTING AND BACKGROUND

## 2.1. Geology of the Naracoorte region

The Naracoorte Caves complex is situated in an uplifted portion of a large, shallow-marine unit known as the Gambier Limestone. The caves formed during the early Pleistocene between 1.1 and 0.8 Ma (White & Webb, 2015). High water table levels at this time triggered reactions between meteoric water and ground water, which caused dissolution within the Gambier Limestone. A marine regression during the Pleistocene lowered the regional water table, allowing the caves to drain. Sediment then accumulated in the caves via surface runoff (Moriarty et al., 2000).

# 2.2. Chronology of the Naracoorte caves

The oldest known Naracoorte Caves fossil deposits lie within the Fossil Chamber of Cathedral Cave and the Main Fossil Chamber of VFC. OSL dating has been used to determine the ages of both deposits. The Cathedral Cave deposit accumulated between  $528 \pm 41$  ka and  $206 \pm 16$  ka (Prideaux et al., 2007) and the Main Fossil Chamber (VFC) deposit accumulated between ~213 ka and  $478 \pm 22$  ka (Ayliffe et al., 1998; Moriarty et al., 2000; Reed & Bourne, 2000). The next oldest known deposit lies within Grant Hall (VFC) and accumulated between  $93 \pm 8$  ka and  $70 \pm 5$  ka (Macken et al., 2011). The Cathedral Cave and Grant Hall deposits are separated temporally by a bracket of ~113 kya between ~206 ka and ~93 ka. No other dated Naracoorte cave deposit, except Specimen Cave, falls within this age bracket (Figure 1).



Figure 1. Age span of the dated Naracoorte fossil deposits, showing the position of Specimen Cave within the missing age bracket between ~206 and ~93 ka. References: Ayliffe et al., 1998; Moriarty et al., 2000; Reed & Bourne, 2000, 2009; Pate et al., 2002, 2006; Forbes et al., 2007; Prideaux et al., 2007; Darrénougué et al., 2009; Macken et al., 2011; St Pierre et al., 2012; Macken & Reed, 2013 ; Mahlknecht, 2018 ; R. Weij, Univeristy of Melbourne (unpublished data with permission) Data from two independent studies were used to constrain the age of the Specimen Cave deposit. The first study used U-series techniques to date a layer of flowstone situated above the deposit. The results of this study returned a minimum age of the flowstone of  $136.2 \pm 15.7$  ka (R. Weij, University of Melbourne, unpublished data with permission). The second study was completed by Mahlknecht (2018) as a complementary study to this palaeontological investigation. Ages of the fossil-bearing sediments were obtained using OSL dating and constrain the age of the deposit between  $151 \pm 9$  ka and  $156 \pm 13$  ka. When combined, the results of these studies bracket the age of the Specimen Cave deposit between  $156 \pm 13$  ka and  $136.2 \pm 15.7$  ka.

# 2.3. Specimen Cave

The study site for this project is Specimen Cave (Australian Speleological Reference number 5U35), which is located on private property adjacent to the NCWHA. The modern-day entrance to the cave is a <1 m diameter by 2 m long solution pipe, located in a slight surface depression (Figure 3). This entrance is located within 500 m of the entrances to Wet Cave, Cathedral Cave and Alexandra Cave, which are within the main Naracoorte Caves visitor precinct (Figure 2).



Figure 2. Map of a portion of the Naracoorte Caves World Heritage Area, showing the location of Specimen Cave (Adapted from Moriarty et al., 2000). Inset: Map of South Australia showing the location of Naracoorte (Adapted from Macken et al., 2013)



Figure 3. The modern entrance to Specimen Cave.

Fossil material was first discovered in Specimen Cave in July 1908 by the caretaker of the Naracoorte Caves, Mr William Reddan who sent a small collection to the South Australian Museum (SAM). The first written record of fossil material from Specimen Cave appeared in *The Naracoorte Herald* newspaper in December 1908, which reported that the Director of the SAM, Dr E. C. Stirling, and Mr F. Zietz, discovered cranial elements of the "marsupial lion" *Thylacoleo carnifex*. Stirling reported these finds to the Museum Board in 1908 (Reed & Bourne, 2000). During their exploration, Sterling and Zietz collected bones from the surface of the cave floor, which were taken back to Adelaide for further examination (Naracoorte Herald, 1908; The Register, 1908; Reed & Bourne, 2000). The next recorded investigation of Specimen Cave was undertaken by Maddock in 1971. Bones were collected from the cave floor during this investigation but no identifications were included in the associated report (Maddock, 1971). Specimen Cave is only referenced in two other publications, both of which provide species lists of the cave (Reed & Bourne, 2000; Williams, 1970). These lists were

created using the material previously collected from the cave floor and now registered in the SAM palaeontology collection (vertebrate fossils). The most up-to-date species list contains 15 mammal species, and one reptile species (Reed & Bourne, 2000).

# 3. METHODS

# 3.1. Excavation

The main excavation pit (Pit 1) was established in a small passage beneath the main cave chamber, referred to as the excavation passage. Access was through an existing human-made hole in the cave floor, located ~30 metres northeast of the cave entrance (Figures 4 & 5).



Figure 4. The human-made hole used to access Pit 1. The hole passes through the U-series dated flowstone layer. The hole is approximately 1 metre wide and the depth from the hole to the pit surface is approximately 85 cm.



Figure 5. Map of Specimen Cave (5U35), highlighting the key features, including the location of excavation Pit 1, the present day entrance and a possible Pleistocene pitfall trap entrance. Modified from CEGSA Map number 5U35.CEG1119.

The pit location was selected based on its accessibility, the undisturbed quality of the sediment and its proximity to the flowstone dated by R. Weij from the University of Melbourne (unpublished data with permission) (E. Reed, personal communication, 2018) and the sediment dated by Mahlknecht (2018). Previously, a tunnel was dug by cavers extending from the excavation passage and this was explored during fieldwork. Before digging commenced, a  $\sim$ 30 cm layer of disturbed overburden was removed to expose the underlying undisturbed sediment. A sample of this material was analysed in the study (the "Overburden" layer). Pit 1 consisted of a 1 m<sup>2</sup> pit, divided into four, 50 cm x 50 cm grid squares (Figure 6).



Figure 6. The grid square reference numbers of Pit 1. The pit and the grid squares were marked out with tent pegs and bricklayers' line.

Due to the passage morphology, the pit could only be excavated from one side and often only by one person at a time. This slowed excavation and limited the depth to which the pit could be dug. Pit 2 was established in another, isolated recess off the main chamber, after large fossils were discovered there on the first day of excavation. This pit was constrained to one, 50 cm x 50 cm square due to the size of the recess. Both pits were excavated using dental picks, brushes and trowels. Large bones were examined *in situ* to identify any articulation or association with other bones, then removed and packed separately. All other excavated material was bagged and wet-screened to isolate small animal elements. This involved transferring the material to sieves and running water over it until all fine sediment was removed (Figure 7).



Figure 7. The sieve and hose used to wet-screen the excavated material

Three layers were excavated in Pit 1. Layer 1 (0-5 cm) and Layer 2 (5-8.5 cm) were excavated across all grids. Layer 3 (8.5-12 cm) was excavated in grid 2. The OSL samples used to constrain the minimum and maximum ages of the deposit were taken from depths of ~0 cm and ~26 cm below the dig surface (Mahlknecht, 2018). Two layers were excavated from Pit 2. Layer 1 extended from the pit surface to a flowstone layer approximately 4 cm

below the surface. Layer 2 extended approximately 4 cm below this flowstone. Observations of the general properties of the sediment, including colour, mineral composition and texture, were made during the excavation. The presence of large rocks and pieces of flowstone was also noted.

## 3.2. Sorting and acid preparation

Diagnostic elements were first isolated from the wet-screened material. These diagnostic elements included all cranial-dental bones (maxillae, dentaries and crania), reptile vertebrae, and teeth and post-cranial material of large mammals. Identifications were based on diagnostic features of these elements. Calcite-encrusted bones underwent acid preparation to remove calcite that was obscuring diagnostic features. Acid preparation took place in a lab at SAM. Experimental method loosely followed descriptions by Whitelaw and Kool (1991). Bones were submerged in a solution of sulfamic acid (1% w/v in H<sub>2</sub>O) until diagnostic features became visible or until the acid risked damaging the bone. Sulfamic acid was selected over more commonly used acids, such as acetic and formic acid, as it presents fewer hazards and can be used for longer periods of time without losing activity (Padilla et al., 2010).

# 3.3. Specimen Cave fauna

#### 3.3.1. IDENTIFICATION

Where possible, specimens were identified to species based on diagnostic features, descriptions of which were obtained from the literature and through assistance from Mr G. Medlin of SAM and Ms Jessie Treloar and Ms Elizabeth Reed of University of Adelaide (Appendix A). Skulls from the SAM mammal collection, and photographs of the Victorian

Museum mammal collection, were used for reference. Specimens that could not be identified

to species, due to a lack of visible species-specific diagnostic features, were identified to

family or genus and named accordingly (Table 1).

Abbreviation Translation Meaning Species Species sp. sp. indet "species indeterminata" Specimens could be identified to family or genus but their species could not be determined, primarily due to the lack of visible diagnostic features Specimens possess most of the diagnostic features of a "compares with" sp. cf known species but some characters are unclear or different

Table 1. Translations and meanings of taxonomic nomenclature abbreviations used in this study (Sigovini et al. 2016).

# 3.3.2. EXISTING SPECIES LIST

The specimens used to produce the previously published species list (Reed & Bourne, 2000) are believed to have been collected from the surface of the excavation passage (E. Reed, personal communication, 2018), below the dated flowstone. The overburden of Pit 1 also came from below the flowstone. It is therefore assumed that the specimens identified in the overburden and the existing species list, accumulated before the flowstone formed and are older than 139 ka (R. Weij, University of Melbourne, unpublished data with permission). Pit 2 appears to belong to the same approximate stratigraphic layer as Pit 1. As all the Specimen Cave material appears to be of a very similar age, the existing species list was combined with this study's species list to produce an updated Specimen Cave species list.

## 3.3.3. RICHNESS

Family richness was calculated by counting the number of identified families. Species richness was calculated for each family by counting the number of identified species. The number of identifiable specimens (NISP) was calculated by counting all identified elements of a given taxon. The minimum number of individuals (MNI) of small mammals was calculated by first separating identified diagnostic elements into the following types: left maxillae, right maxillae, left dentaries, right dentaries and crania. The most abundant element type was then counted (White, 1953).

## 3.3.4. RELATIVE ABUNDANCE

Small animal relative abundance (RA%) was calculated using the following equation:

Relative abundance<sub>(*a,b*)</sub> = NISP<sub>(*a,b*)</sub>/NISP<sub>total(*b*)</sub> × 100% where a = taxon and b = layer (Macken et al., 2012)

# 3.3.5. BODY MASS AND SPECIMEN DENSITY

The relative abundances and densities of very small mammals (maximum body weight <100 g) in Specimen Cave, Blanche Cave, Wet Cave and Cathedral Cave, were calculated to provide information regarding the mode of accumulation of the Specimen Cave deposit. Body masses were sourced from Van Dyck and Strahan (2008). Density was calculated by dividing the NISP in each unit by the approximate volume of that unit. Volumes were estimated by multiplying the area of the pit by the unit depth. Density was calculated for Layers 1-2 of Pit 1 of Specimen Cave, as the volume of the overburden was unknown. Layer 3 was also omitted because it was only excavated in grid 2.

## 3.3.6. HABITAT AND DIET

Habitat preferences and diets of identified species were researched to provide information regarding the proximal environment. Information for extant species was sourced from Van Dyck and Strahan (2008) and supplemented by additional references where indicated. Using modern-day data of extant species requires the assumption to be made that the environmental tolerances and preferences of these species were not significantly different during the Pleistocene (Hadly as cited in Macken *et al.*, 2012, p. 421). Information for extinct species was collected from several sources (Brown & Wells, 2000; Macken et al., 2012; Prideaux et al., 2007; Prideaux, 2004).

## 3.4. Comparisons to other NCWHA deposits

The data collected during this study were compared to similar data from two older deposits -Fossil Chamber (Cathedral Cave) and Main Fossil Chamber (VFC) – and one younger deposit - Grant Hall (VFC). These deposits were selected for comparison as they are the closest in age to Specimen Cave. Data used in comparisons included species lists, species richness values and relative abundance values. Data for Cathedral Cave were sourced from Brown and Wells (2000) and Prideaux et al. (2007). Data for Grant Hall were sourced from Fraser and Wells (2006) and Macken et al. (2012). Species lists for Main Fossil Chamber (VFC) were sourced from Reed and Bourne (2000, 2009).

## 4. RESULTS

## 4.1. Excavation passage morphology

The excavation passage extends upwards away from Pit 1 for ten metres in a north-easterly direction before constrictions are met. Stale air at the end of the passage suggests it does not

connect with the surface or another large chamber. No holes or surface depressions were observed that indicate a connection to the surface.

## 4.2. In situ observations

## 4.2.1. ARTICULATION AND ASSOCIATIONS

Vertebrate bone material was recovered from all layers of all grid squares. No *in situ* articulation or association between elements was observed.

## 4.2.2. SEDIMENTS

Both pits consisted primarily of sandy sediments, interbedded with clay and carbonaceous sediments. These clays and carbonates formed distinct patches but did not appear to form distinct layers. Layer 1 consisted of dark, fine-grained sediment and contained flowstone fragments. Sediment below this flowstone was lighter in colour and had a sandier texture. A similar flowstone layer was encountered in Pit 2. Sediment in Layer 2 of Pit 1 was darker and contained a greater proportion of clay. Layer 3 was defined by another switch to light-coloured, sandy sediment. This sandy sediment was observed across most of the pit, except grid 1 and 2, which contained more clay. The surfaces of many of the bones were completely or partially covered by a calcite crust. Encrusted specimens were randomly distributed across the grid squares and no spatial pattern was observed.

# 4.3. Specimen Cave fauna

## 4.3.1. RICHNESS

Table 2. Updated Specimen Cave mammal list, with common species names and taxonomic authority of species. \*Identified in this study. ^Identified in the existing faunal list (Reed & Bourne, 2000). <sup>(P)</sup> Extinct during the Pleistocene. <sup>(H)</sup> Historically extinct. <sup>(N)</sup> No longer found in the Naracoorte region. Common names as per Van Dyck & Strahan, 2008. N/A = no common name assigned to species

| Family          | Subfamily       | Species                                  | Taxonomic           |                  |  |
|-----------------|-----------------|--|---------------------|------------------|--|
|                 | (if applicable) | Scientific name                          | Common name         | authority        |  |
| Vombatidae      |                 | Vombatus ursinus ^                       | Common wombat       | Geoffroy, 1803   |  |
| (wombats)       |                 |  |                     |                  |  |
| Thylacinidae    |                 | Thylacinus cynocephalus^ (H)             | Thylacine;          | Harris, 1808     |  |
|                 |                 |  | Tasmanian tiger     |                  |  |
| Dasyuridae      |                 | Dasyuridae sp. indet *                   |                     |                  |  |
| (carnivorous    |                 | Sarcophilus sp. cf. S. laniarus ^ (P)    | N/A                 | Owen, 1838       |  |
| marsupials)     |                 | Dasyurus viverrinus * <sup>(N)</sup>     | Eastern quoll       | Shaw, 1800       |  |
|                 |                 | Sminthopsis sp. indet *^                 |                     |                  |  |
|                 |                 | Sminthopsis crassicaudata/murina         | Fat-tailed/slender- | Gould, 1844/     |  |
|                 |                 | *^                                       | tailed dunnart      | Waterhouse, 1838 |  |
|                 |                 | Antechinus sp. indet *                   |                     |                  |  |
|                 |                 | Antechinus flavipes *                    | Yellow-footed       | Waterhouse, 1837 |  |
|                 |                 |  | antechinus          |                  |  |
|                 |                 | Phascogale tapoatafa * <sup>(N)</sup>    | Brush-tailed        | Meyer, 1793      |  |
|                 |                 |  | phascogale          |                  |  |
| Peramelidae     |                 | Peramelidae sp. indet *                  |                     |                  |  |
| (bandicoots)    |                 | Perameles sp. indet *^ (N)               | Bandicoot sp. indet |                  |  |
|                 |                 | Perameles bougainville *^ (N)            | Western barred      | Quoy & Gaimard,  |  |
|                 |                 |  | bandicoot           | 1824             |  |
|                 |                 | Isoodon obesulus * ^                     | Southern brown      | Shaw, 1797       |  |
|                 |                 |  | bandicoot           |                  |  |
| Phalangeridae   |                 | Trichosurus vulpecula *                  | Common brush-       | Keer, 1792       |  |
| (possums)       |                 |  | tailed possum       |                  |  |
| Thylacoleonidae |                 | <i>Thylacoleo carnifex</i> $* \land (P)$ | Marsupial lion      | Owen, 1858       |  |
| Potoroidae      |                 | Potoroidae sp. indet *                   |                     |                  |  |
| (potoroos, rat- |                 | Potorous platyops * ^ (H)                | Broad-faced         | Gould, 1844      |  |
| kangaroos,      |                 |  | potoroo             |                  |  |
| bettongs)       |                 | Potorous tridactylus * <sup>(N)</sup>    | Long-nosed          | Kerr, 1792       |  |
|                 |                 |  | potoroo             |                  |  |
|                 |                 | Bettongia lesueur * <sup>(N)</sup>       | Boodie; burrowing   | Quoy & Gaimard,  |  |
|                 |                 |  | bettong             | 1824             |  |
|                 |                 | Bettongia penicillata *^ (N)             | Woylie; brush-      | Gray, 1837       |  |
|                 |                 |  | tailed bettong      |                  |  |
|                 |                 | Bettongia gaimardi * <sup>(N)</sup>      | Eastern bettong     | Desmarest, 1822  |  |
| Pseudocheridae  |                 | Pseudocheirus peregrinus*                | Common ringtail     | Boddaert, 1795   |  |
| (possums)       |                 |  | possum              |                  |  |
|                 |                 | Ceracartetus sp. indet *                 |                     |                  |  |

| Burramvidae     |              | Cercartetus nanus *   | Eastern pygmy                          | Desmarest, 1818  |
|-----------------|--------------|---|--|------------------|
| (pygmy          |              |   | possum                                 | ,,               |
| possums)        |              |   | Possan                                 |                  |
| Petauridae      |              | Petaurus brevicens *  | Sugar glider                           | Waterhouse 1839  |
| (gliders)       |              | Petaurus sp. cf. P. norfolcensis *                                | Sagur glider                           | Kerr 1792        |
| (gliders)       |              | (N)   | Squirrer grider                        | Keii, 1792       |
| Macropodidae    |              | Macropodidae sp. indet *  |  |                  |
| (kangaroos,     | Macropodinae | Macropus giganteus ^  | Eastern grey                           | Shaw, 1790       |
| wallabies &     |              |   | kangaroo                               |                  |
| relatives)      |              | Macropus fuliginosus/ giganteus *                                 | Western/eastern                        | Desmarest, 1817/ |
|                 |              |   | grey kangaroo                          | Shaw, 1790       |
|                 |              | Macropus rufogriseus * ^  | Red-necked                             | Desmarest, 1817  |
|                 |              |   | wallaby                                |                  |
|                 |              | Macropus sp. cf. M. titan^  | N/A                                    | Macropus titan   |
|                 |              | Protemnodon sp. indet <sup>(P)</sup>                              | N/A                                    |                  |
|                 |              | Protemnodon roechus ^ (P)   | N/A                                    | Owen, 1874       |
|                 |              | <i>Protemnodon</i> sp. cf. <i>P. anak</i> $\wedge$ <sup>(P)</sup> | N/A                                    | Owen, 1874       |
|                 |              | <i>Thylogale</i> sp. indet $^{(N)}$                               | Pademelon sp. indet                    |                  |
|                 |              | cf. Thylogale * <sup>(N)</sup>                                    | Cf. Pademelon                          |                  |
|                 |              | Wallabia bicolor *  | Swamp wallaby                          | Desmarest, 1804  |
|                 | Sthenurinae  | Sthenurinae sp. indet * <sup>(P)</sup>                            | ~ ···································· | ,                |
|                 | (short-faced | <i>Procoptodon</i> sp. cf. <i>P. goliah</i> $*^{(P)}$             | N/A                                    | Owem, 1846       |
|                 | kangaroos)   | Simosthenurus occidentalis *^ (P)                                 | N/A                                    | Glauert, 1910    |
| Muridae (rodent |              | Muridae sp. indet *   |  |                  |
| family)         |              | Notomys mitchelli *   | Mitchell's hopping                     | Ogilby 1813      |
|                 |              | ivolomys michell  | mouse                                  | Ogiloy, 1015     |
|                 |              | Conilurus albipes * <sup>(H)</sup>                                | White-footed                           | Lichtenstein,    |
|                 |              |   | rabbit-rat                             | 1829             |
|                 |              | Mastacomys chrysogaster * <sup>(N)</sup>                          | Broad-toothed rat                      | Thomas, 1882     |
|                 |              | Pseudomys sp. indet *   |  |                  |
|                 |              | Pseudomys auritus * (H)   | Long-eared mouse                       | Thomas, 1910     |
|                 |              | Pseudomys australis * <sup>(N)</sup>                              | Plains mouse                           | Gray, 1832       |
|                 |              | Pseudomys fumeus * <sup>(N)</sup>                                 | Smoky mouse                            | Brazenor, 1934   |
|                 |              | Pseudomys gouldii * <sup>(N)</sup>                                | Gould's mouse                          | Waterhouse, 1839 |
|                 |              | Pseudomys   | Silky mouse/ New                       | Finlayson 1932/  |
|                 |              | apodemoides/novaehollandiae *                                     | Holland's mouse                        | Waterhouse, 1843 |
|                 |              | Pseudomys shortridgei *   | Heath mouse                            | Thomas, 1907     |
|                 |              | Rattus fuscines *   | Bush rat                               | Waterhouse 1839  |
|                 |              | Rattus lutroolus *  | Australian swamp                       | Grav 1841        |
|                 |              | Ranas tarreotas   | rat                                    | Glay, 1041       |
|                 |              | Rattus tunneyi * <sup>(N)</sup>                                   | Pale field rat                         | Thomas, 1904     |
| Agamidae        |              | Agamidae sp. indet  |  |                  |
| (iguanian       |              |   |  |                  |
| lizards)        |              |   |  |                  |
| Scincidae       |              | Scincidae sp. indet   |  |                  |
| (skinks)        |              | _   |  |                  |
| Class Aves      |              | Aves sp. indet  |  |                  |
|                 |              |   |  |                  |

Seven small mammal families were identified in this study, four of which – Muridae, Burramyidae, Petauridae and Phalangeridae - are new additions to Specimen Cave. These additions expand the small mammal list from three to eight families. 27 small mammal species were identified in this study, 23 of which are new additions. These additions expand the small mammal species richness from five to 27 (Figure 8). Other new vertebrate additions include Aves (bird) and Agamidae (reptile) (Table 2). The only large mammal families identified in this study were Macropodidae and Thylacoleonidae. Species from two Macropodidae subfamilies, Macropodinae and Sthenurinae, were identified (Table 2). Five Macropodidae species were identified, two of which - *Wallabia bicolor* and *Procoptodon* sp. cf. *P. goliah* - are new additions to the Specimen Cave list. These additions expand the overall large mammal richness from ten to 13 species (Figure 9).

## 4.3.2. RELATIVE ABUNDANCES

The NISP and MNI of small mammals were strongly linearly correlated ( $R^2 = 0.9938$ ) (Figure 10). Based on this correlation, it can be expected that the proportional relationships between small mammals, expressed by their relative abundances, will remain the same regardless of whether NISP or MNI values are used to calculate relative abundance (Macken et al., 2012).





Figure 8. Species richness (total number of species) of small mammal families represented in the Specimen Cave species lists. The species richness value of the 'existing list' in this graph includes species in the existing list that were not identified in this study. The value for 'both studies' includes species identified in this study and in the existing species list (Reed & Bourne, 2000). 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness. '*Pseudomys apodemoides/novaehollandiae*' (Muridae) and '*Sminthopsis crassicaudata/murina*' (Dasyuridae) are each counted as single species.



■ This study ■ Existing list ■ Both studies

Figure 9. Species richness (total number of species) of large mammal families in represented in the Specimen Cave species lists. The species richness value of the 'existing list' in this graph includes species in the existing list that were not identified in this study. The value for 'both studies' includes species identified in this study and in the existing species list (Reed & Bourne, 2000). 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness. 'Macropus fuliginosus/giganteus' counted as one species.



Figure 10. The number of identifiable specimens (NISP) and the minimum number of individuals (MNI) of small taxa, showing the strong linear correlation between the two values.

The NISP of all mammals from Pit 1 was 575. The NISP of small mammals was 551 and the relative abundance was 95.8%. The NISP of large mammals was 24 and the relative abundance was 4.4%. Placental mammals were represented only by Muridae, which was the most abundant family overall. In Pit 1, the NISP of Muridae was 494 and the relative abundance was 85% of all mammals. The NISP of small marsupials was 65 and the RA% was 11% (Figure 11, Table 3)



Figure 11. Relative abundance (RA%) of mammal groups in Pit 1 of Specimen Cave. RA% is calculated from the NISP values of each group and the total NISP of all mammals.

Macropodidae was the only large family identified in Pit 1 and had a relative abundance of 100%. The NISP of all mammals from Pit 2 was 60. The NISP of small mammals was 55 and the relative abundance was 91.7%. The NISP of large mammals was five and the relative abundance was 8.3%. The NISP of Muridae was 49 and the relative abundance was 89.1% of small mammal families. The NISP of small marsupials was six, giving them a relative abundance of 10.9%. The second most abundant small mammal family, and the most abundant marsupial family, in both pits was Dasyuridae, which had a NISP of 19 and a relative abundance of 3.5% of small mammals in Pit 1 and a relative abundance of 9.1% in Pit 2 (Table 4). The NISP of the two large mammal families, Macropodidae and Thylacoleonidae, were near equal (three and two, respectively) (Table 5)





Figure 12. A: Relative abundances (RA%) of small placental and marsupial mammals from Pit 1 and Pit 2 (calculated as a percentage of the NISP of all small mammals). B: Relative abundances (RA) of small marsupial families from Pit 1 and Pit 2 (calculated as a percentage of the NISP of small marsupials). Specimens from the overburden layer of Pit 1, not included.

The most abundant species in Pit 1 was *Pseudomys apodemoides/novaehollandiae*, which had a relative abundance of 17.4%. The next most abundant species was *Pseudomys auritus*, which had a relative abundance of 8.3% (Table 3).

| Table 3. The number of identifiable specimens (NISP), minimum number of individuals (MNI) and       | relative abundance (RA%) of small mammals in Pit 1.    |
|---|--|
| Relative abundance is calculated as the percentage of the total small mammals for each pit section. | ^ Species could not be distinguished from osteological |
| remains   |  |

|                        |      | Layer 1 | L    |      | Layer 2 | 2    |      | Layer 3 |      | 0    | verburd | len  |      | Total |      |
|------------------------|------|---------|------|------|---------|------|------|---------|------|------|---------|------|------|-------|------|
| Species                | NISP | MNI     | RA%  | NISP | MNI   | RA%  |
| Muridae sp. indet.     | 92   | 41      | 47.9 | 95   | 39      | 45.2 | 23   | 10      | 37.7 | 43   | 20      | 48.9 | 253  | 104   | 45.9 |
| Mastacomys fuscus      | 8    | 3       | 4.2  | 11   | 5       | 5.2  | 7    | 4       | 11.5 | 1    | 1       | 1.1  | 27   | 9     | 4.9  |
| Pseudomys sp. indet.   | 7    | 3       | 3.6  | 9    | 4       | 4.3  | 0    | 0       | 0.0  | 4    | 2       | 4.5  | 20   | 8     | 3.6  |
| Pseudomys auritus      | 18   | 10      | 9.4  | 19   | 9       | 9.0  | 4    | 2       | 6.6  | 5    | 4       | 5.7  | 46   | 24    | 8.3  |
| Pseudomys australis    | 0    | 0       | 0    | 2    | 2       | 1.0  | 0    | 0       | 0    | 1    | 1       | 1.1  | 3    | 3     | 0.5  |
| Pseudomys fumeus       | 1    | 1       | 0.5  | 1    | 1       | 0.5  | 1    | 1       | 1.6  | 1    | 1       | 1.1  | 4    | 2     | 0.7  |
| Pseudomys gouldii      | 2    | 1       | 1.0  | 4    | 2       | 1.9  | 0    | 0       | 0.0  | 2    | 2       | 2.3  | 8    | 4     | 1.5  |
| Pseudomys              |      |         |      |      |         |      |      |         |      |      |         |      |      |       |      |
| novaehollandiae/       |      |         |      |      |         |      |      |         |      |      |         |      |      | 1     |      |
| apodemoides ^          | 25   | 12      | 13.0 | 34   | 14      | 16.2 | 21   | 7       | 34.4 | 16   | 8       | 18.2 | 96   | 41    | 17.4 |
| Pseudomys shortridgei  | 11   | 8       | 5.7  | 15   | 11      | 7.1  | 1    | 1       | 1.6  | 5    | 4       | 5.7  | 32   | 20    | 5.8  |
| Rattus sp. indet.      | 1    | 1       | 0.5  | 0    | 0       | 0.0  | 0    | 0       | 0    | 1    | 1       | 1.1  | 2    | 1     | 0.4  |
| Rattus lutreolus       | 0    | 0       | 0    | 0    | 0       | 0.0  | 0    | 0       | 0    | 2    | 1       | 2.3  | 2    | 1     | 0.4  |
| Rattus tunneyi         | 0    | 0       | 0    | 1    | 1       | 0.5  | 0    | 0       | 0    | 0    | 0       | 0    | 1    | 1     | 0.2  |
| Total Muridae          | 165  | 55      | 85.9 | 191  | 59      | 91.0 | 57   | 22      | 93.4 | 81   | 25      | 92.0 | 494  | 159   | 89.7 |
| Dasyuridae sp. indet.  | 2    | 1       | 1.0  | 1    | 1       | 0.5  | 1    | 1       | 1.6  | 1    | 1       | 1.1  | 5    | 3     | 0.9  |
| Antechinus sp. indet.  | 4    | 2       | 2.1  | 2    | 2       | 1.0  | 0    | 0       | 0    | 1    | 1       | 1.1  | 7    | 4     | 1.3  |
| Antechinus flavipes    | 1    | 1       | 0.5  | 0    | 0       | 0    | 0    | 0       | 0    | 0    | 0       | 0    | 1    | 1     | 0.2  |
| Dasyurus viverrinus    | 1    | 1       | 0.5  | 0    | 0       | 0    | 0    | 0       | 0    | 0    | 0       | 0    | 1    | 1     | 0.2  |
| Phascogale tapoatafa   | 1    | 1       | 0.5  | 0    | 0       | 0    | 0    | 0       | 0    | 0    | 0       | 0    | 1    | 1     | 0.2  |
| Sminthopsis            |      |         |      |      |         |      |      |         |      |      |         |      |      |       |      |
| crassicaudata/murina   | 3    | 1       | 1.6  | 2    | 2       | 1.0  | 0    | 0       | 0    | 0    | 0       | 0    | 5    | 2     | 0.9  |
| Total Dasyuridae       | 12   | 6       | 6.3  | 5    | 2       | 2.4  | 1    | 1       | 1.6  | 2    | 1       | 2.3  | 20   | 7     | 3.6  |
| Peramelidae sp. indet. | 1    | 1       | 0.5  | 4    | 2       | 1.9  | 2    | 1       | 3.3  | 1    | 1       | 1.1  | 8    | 3     | 1.5  |
| Perameles sp. indet.   | 2    | 1       | 1.0  | 0    | 0       | 0    | 0    | 0       | 0    | 2    | 1       | 2.3  | 4    | 1     | 0.7  |
| Perameles bougainville | 0    | 0       | 0    | 2    | 2       | 1.0  | 0    | 0       | 0    | 0    | 0       | 0    | 2    | 2     | 0.4  |
| Isoodon obesulus       | 0    | 0       | 0.0  | 1    | 1       | 0.5  | 1    | 1       | 1.6  | 2    | 1       | 2.3  | 4    | 1     | 0.7  |
| Total Peramelidae      | 3    | 1       | 1.6  | 7    | 4       | 3.3  | 3    | 1       | 4.9  | 3    | 2       | 3.4  | 16   | 6     | 2.9  |
| Potoroidae sp. indet.  | 2    | 1       | 1.0  | 2    | 1       | 1.0  | 0    | 0       | 0    | 0    | 0       | 0    | 4    | 2     | 0.7  |

| Bettongia lusueur      | 1   | 1 | 0.5   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 1   | 1 | 0.2   |
|------------------------|-----|---|-------|-----|---|-------|----|---|-------|----|---|-------|-----|---|-------|
| Bettongia penicillata  | 0   | 0 | 0.0   | 1   | 1 | 0.5   | 0  | 0 | 0     | 0  | 0 | 0     | 1   | 1 | 0.2   |
| Potorous platyops      | 1   | 1 | 0.5   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 1   | 1 | 0.2   |
| Potorous tridactylus   | 2   | 1 | 1.0   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 2   | 1 | 0.4   |
| Total Potoroidae       | 6   | 2 | 3.1   | 3   | 2 | 1.4   | 0  | 0 | 0     | 0  | 0 | 0     | 9   | 3 | 1.6   |
| Cercartetus sp. indet. | 1   | 1 | 0.5   | 3   | 2 | 1.4   | 0  | 0 | 0     | 0  | 0 | 0     | 4   | 2 | 0.7   |
| Cercartetus nanus      | 3   | 2 | 1.6   | 1   | 1 | 0.5   | 0  | 0 | 0     | 2  | 1 | 2.3   | 6   | 3 | 1.1   |
| Total Burramyidae      | 4   | 3 | 2.1   | 4   | 3 | 1.9   | 0  | 0 | 0     | 2  | 1 | 2.3   | 10  | 5 | 1.8   |
| Petaurus breviceps     | 1   | 1 | 0.5   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 1   | 1 | 0.2   |
| Petaurus sp. cf. P.    |     |   |       |     |   |       |    |   |       |    |   |       |     |   |       |
| norfolcensis           | 1   | 1 | 0.5   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 1   | 1 | 0.2   |
| Total Petauridae       | 2   | 1 | 1.0   | 0   | 0 | 0     | 0  | 0 | 0     | 0  | 0 | 0     | 2   | 1 | 0.4   |
| Pseudocheirus          |     |   |       |     |   |       |    |   |       |    |   |       |     |   |       |
| peregrinus             |     |   | 0     |     |   | 0     |    |   | 0     | 1  |   | 1.1   | 1   | 1 | 0.2   |
| TOTAL                  |     |   |       |     |   |       |    |   |       |    |   |       |     |   |       |
| MARSUPIALS             | 27  |   | 14.1  | 19  |   | 9.0   | 4  |   | 6.6   | 7  |   | 8.0   | 57  |   | 10.3  |
| TOTAL SMALL            |     |   |       |     |   |       |    |   |       |    |   |       |     |   |       |
| MAMMALS                | 192 | - | 100.0 | 210 | - | 100.0 | 61 | - | 100.0 | 88 | - | 100.0 | 551 | - | 100.0 |

| Table 4. The number of identifiable specimens (NISP), minimum number of individuals (MNI) and    |
|--|
| relative abundance (RA%) of small mammals in Pit 2. Relative abundance is calculated as the      |
| percentage of the total small mammals for each pit section. ^ Species could not be distinguished |
| from osteological remains.   |

|   | Lay  | er 1 |      | Layer 2 |     |      | TOTAL |     |      |
|---|------|------|------|---------|-----|------|-------|-----|------|
| Species                                     | NISP | MNI  | RA%  | NISP    | MNI | RA%  | NISP  | MNI | RA%  |
| Muridae sp. indet.                          | 16   | 8    | 38.1 | 5       | 4   | 38.5 | 21    | 12  | 38.2 |
| Conilurus albipes                           | 2    | 1    | 4.8  | 0       | 0   | 0.0  | 2     | 1   | 3.6  |
| Mastacomys fuscus                           | 3    | 1    | 7.1  | 0       | 0   | 0.0  | 3     | 1   | 5.5  |
| Notomys mitchelli                           | 1    | 1    | 2.4  | 0       | 0   | 0.0  | 1     | 1   | 1.8  |
| Pseudomys sp. indet.                        | 6    | 3    | 14.3 | 0       | 0   | 0.0  | 6     | 3   | 10.9 |
| Pseudomys auritus                           | 5    | 4    | 11.9 | 2       | 1   | 15.4 | 7     | 5   | 12.7 |
| Pseudomys fumeus                            | 2    | 2    | 4.8  | 0       | 0   | 0.0  | 2     | 2   | 3.6  |
| Pseudomys novaehollandiae/<br>apodemoides ^ | 4    | 4    | 9.5  | 1       | 1   | 7.7  | 5     | 4   | 9.1  |
| Pseudomys shortridgei                       | 2    | 2    | 4.8  | 2       | 1   | 15.4 | 4     | 3   | 7.3  |
| Rattus sp. indet.                           | 1    | 1    | 2.4  | 0       | 0   | 0.0  | 1     | 1   | 1.8  |
| Rattus fuscipes                             | 1    | 1    | 2.4  | 0       | 0   | 0.0  | 1     | 1   | 1.8  |
| Total Muridae                               | 39   | 12   | 92.9 | 10      | 4   | 76.9 | 49    | 16  | 89.1 |
| Dasyurus viverrinus                         | 1    | 1    | 2.4  | 0       | 0   | 0.0  | 1     | 1   | 1.8  |
| Sminthopsis<br>crassicaudata/murina ^       | 0    | 0    | 0.0  | 1       | 1   | 7.7  | 1     | 1   | 1.8  |
| Total Dasyuridae                            | 2    | 1    | 4.8  | 3       | 2   | 23.1 | 5     | 3   | 9.1  |
| Perameles sp. indet.                        | 1    | 1    | 2.4  | 0       | 0   | 0.0  | 1     | 1   | 1.8  |
| TOTAL MARSUPIALS                            | 3    |      | 7.1  | 3       |     | 23.1 | 6     |     | 10.9 |
| TOTAL SMALL<br>MAMMALS                      | 42   | -    |      | 13      | -   |      | 55    | -   |      |

The two Macropodidae families identified, Macropodinae and Sthenurinae, have equal

relative abundances. The most abundant large mammal species was Macropus

fuliginosus/giganteus (grey kangaroos) (Table 5).

|                               |      |        | Pit 2 |            |      |      |            |      |  |
|-------------------------------|------|--------|-------|------------|------|------|------------|------|--|
|                               | Laye | rs 1-3 | Overb | Overburden |      | otal | Layers 1-2 |      |  |
| Species                       | NISP | RA%    | NISP  | RA%        | NISP | RA%  | NISP       | RA%  |  |
| Macropodidae sp. indet.       | 9    | 37.5   | 1     | 25         | 10   | 51.6 | 3          | 50.0 |  |
| Procoptodon sp. cf. P. goliah | 1    | 4.2    | 0     | 0          | 1    | 4.2  | 0          | 0    |  |
| Simosthenurus occidentalis    | 1    | 4.2    | 0     | 0          | 1    | 4.2  | 0          | 0    |  |
| Sthenurinae sp. indet.        | 3    | 12.5   | 2     | 8.3        | 5    | 20.8 | 0          | 0    |  |
| Total Sthenurinae             | 5    | 25     | 2     | 50         | 7    | 29.2 | 0          | 0    |  |
| Wallabia bicolor              | 1    | 4.2    | 0     | 0          | 1    | 4.2  | 0          | 0    |  |
| Protemnodon sp. indet         | 0    | 0      | 0     | 0          | 0    | 0    | 1          | 16.7 |  |
| cf. Thylogale                 | 1    | 4.2    | 0     | 0          | 1    | 4.2  | 0          | 0    |  |
| Macropus rufogriseus          | 1    | 4.2    | 0     | 0          | 1    | 4.2  | 0          | 0    |  |
| M. fuliginosus/giganteus^     | 3    | 12.5   | 1     | 4.2        | 4    | 16.7 | 0          | 0    |  |
| Total Macropodinae            | 6    | 30     | 1     | 25         | 7    | 29.2 | 1          | 16.7 |  |
| Thylacoleo carnifex           | 0    | 0      | 0     | 0          | 0    | 0    | 2          | 33.3 |  |
| Total                         | 20   | 83.3   | 4     | 16.7       | 24   | -    | 6          | -    |  |

Table 5. Number of identifiable specimens (NISP) and relative abundance (RA%) of large mammals from Specimen Cave. Layers 1-3 were combined, as the NISP was so low. ^ The grey kangaroos, *M. fuliginous* and *M. giganteus*, could not be distinguished from osteological remains

# 4.3.3. BODY MASS AND SPECIMEN DENSITY

Very small mammals (< 100 g) had a relative abundance of 81.6% and a density of 4.1 NISP/L in Layers 1-2. This density compares to some units in Wet Cave, Blanche Cave and Cathedral Cave, but does not approach the density seen in Unit A of Blanche Cave (43.9 NISP/L) (Table 6).

Table 6. Relative abundance (RA%) and density of small mammals (NISP/litre of sediment) in Specimen Cave and in sections of known owl deposits in the NCWHA. Relative abundance calculated as a percentage of the total NISP of all animals in the given unit. Original obtained from Macken et al., 2012 (supplementary material) for Cathedral Cave; Macken & Reed, 2014 (supplementary material) and Macken et al., 2013 for Wet Cave and Blanche Cave

| Cave                          | Unit       | RA%  | Density<br>(NISP/L) |
|-------------------------------|------------|------|---------------------|
| Blanche Cave (3 <sup>rd</sup> | Unit C     | 87.2 | 2.7                 |
| chamber)                      | Unit B     | 89.1 | 5.9                 |
|                               | Unit A     | 89.4 | 43.9                |
| Wet Cave                      | Unit E     | 93.8 | 5.2                 |
| Cathedral Cave                | Unit E     | 70.7 | 2.8                 |
|                               | Unit D     | 67.2 | 6.7                 |
|                               | Unit C     | 63.5 | 5.1                 |
|                               | Unit B     | 47.4 | 1.6                 |
| Specimen Cave - Pit 1         | All layers | 81.6 |                     |
|                               | Layers 1-2 | 82.6 | 4.1                 |

# 4.3.4. HABITAT AND DIET

The large mammal fauna is dominated by herbivores, with near equal proportions of grazers, browsers and mixed-feeders (Table 7) and saltatory (jumping) macropodids (Reed, 2006). The Specimen Cave fauna inhabited a range of habitats, with most species showing preference for forests or woodlands (Tables 7 & 8). The assemblage contains both arboreal (tree-dwelling) and terrestrial taxa (Table 8).

Table 7. Diet and preferred habitat of large mammal taxa from Specimen Cave. Data for extinct data are inferred. O.F = Open Forest, W.S = Wet Sclerophyll, S = Scrub/shrubland, H = Heathland, G = Grassland, W = Woodland, M = Mallee, R = Rainforest. \*Extinct during Pleistocene. \*\*Extinct since European settlement. 'No longer occurs in the Naracoorte region. (*i*) insectivore. References: (Sanson, 1978; Van Dyck & Strahan, 2008; Brown & Wells, 2000)

|                 |  | Diet/grade             |                       |           |        | Habitat |   |   |   |   |   |
|-----------------|--|------------------------|-----------------------|-----------|--------|---------|---|---|---|---|---|
| Family          | Species  | Herbivore<br>(browser) | Herbivore<br>(grazer) | Carnivore | O<br>F | W<br>S  | S | H | W | M | R |
| Tachyglossidae  | Tachyglossus<br>aculeatus                                    |                        |                       | X (i)     | Х      |         | X | X | Х | X |   |
| Thylacinidae    | Thylacinus<br>cynocephalus                                   |                        |                       | Х         | X      |         |   |   | X |   |   |
| Vombatidae      | Vombatus<br>ursinus  |                        | X                     |           |        |         |   | X | X |   |   |
| Thylacoleonidae | Thylacoleo<br>carnifex                                       |                        |                       | Х         | Х      |         |   |   | Х |   |   |
| Macropodidae    | <i>Macropus</i> sp. cf. <i>M. titan</i>                      |                        | Х                     |           |        |         |   |   |   |   |   |
|                 | M. fuliginosus/<br>giganteus                                 |                        | X                     |           | X      |         | X | X | X | X |   |
|                 | M. rufogriseus   | Х                      | Х                     |           | Х      |         |   | Х |   |   |   |
|                 | M. giganteus   |                        | Х                     |           | Х      |         | Х | Х | Х | Х |   |
|                 | Protemnodon<br>sp. cf. P. anak                               | Х                      |                       |           |        |         |   |   |   |   |   |
|                 | Protemnodon<br>roechus                                       | Х                      |                       |           |        |         |   |   |   |   |   |
|                 | 'Procoptodon.'<br>browneorum                                 |                        | Х                     |           | Х      |         |   |   |   |   |   |
|                 | <i>'Procoptodon'</i><br>sp. cf. <i>P</i> .<br><i>goliah*</i> |                        | X                     |           |        |         |   |   |   |   |   |
|                 | 'P.' gilli*  |                        | Х                     |           | Х      |         |   |   |   |   |   |
|                 | Simosthenurus<br>baileyi*                                    | Х                      |                       |           |        |         |   |   |   |   |   |
|                 | S. maddocki  | X                      |                       |           |        |         |   |   |   |   |   |
|                 | S. occidentalis  | X                      |                       |           | Х      |         |   |   |   |   |   |
|                 | Wallabia<br>bicolor  | X                      | X                     |           | Х      |         |   | X | X |   |   |

Table 8. Preferred habitats of small mammal taxa from Specimen Cave. Habitats of extinct species are inferred. F = Forest, S = Scrub/shrubland, H = Heathland, G = Grassland, W = Woodland, M = Mallee, R = Rainforest, A.P. = Arid plains. (*b*) Burrowing. Data for *Sminthopsis* includes the habitat preferences of both *S. murina* and *S. crassicaudata*. References: Van Dyck & Strahan, 2008; Fraser & Wells, 2006; Reed & Bourne, 2000)

|                |                     |          |         |                            |   |   |          |   |   | Under- |   |        |
|----------------|---------------------|----------|---------|----------------------------|---|---|----------|---|---|--------|---|--------|
|                |                     | Lifestyl | e       | Inferred/preferred habitat |   |   |          |   |   | growth |   |        |
|                |                     | Arbor-   | Terres- |                            |   |   |          |   |   |        | А | Thick/ |
| Family         | Species             | eal      | trial   | F                          | S | Н | G        | W | Μ | R      | Р | dense  |
| Muridae        | Conilurus albipes   |          | Х       | Х                          |   |   |          |   |   |        |   |        |
|                | Mastacomys fuscus   |          | Х       | Х                          |   | Х |          |   |   |        |   | X      |
|                | Notomys mitchelli   |          | Х       |                            |   |   |          | Х | Х |        |   | X      |
|                | Pseudomys auritus   |          | Х       | Х                          | Х | Х | Х        | Х |   |        |   | X      |
|                | Pseudomys           |          | Х       |                            |   |   |          |   |   |        |   |        |
|                | australis           |          |         |                            |   |   |          |   |   |        | Х |        |
|                | Pseudomys fumeus    |          | Х       |                            |   |   |          |   |   |        |   |        |
|                | Pseudomys gouldii   |          | Х       |                            |   |   |          |   |   |        | Х |        |
|                | Pseudomys           |          | Х       |                            |   |   |          |   |   |        |   |        |
|                | shortridgei         |          |         | Х                          | Х | Х |          |   | Х |        |   |        |
|                | Pseudomys           |          |         |                            |   |   |          |   |   |        |   |        |
|                | apodemoides         |          |         |                            |   |   |          |   |   |        |   |        |
|                | Rattus lutreolus    |          | Х       | Х                          |   | Х | Χ        |   |   |        |   |        |
|                | Rattus fuscipes     |          | Х       | Χ                          | Χ |   |          | Х |   | Χ      |   |        |
|                | Rattus tunneyi      |          | Х       | Χ                          |   |   | Χ        | Х |   |        |   |        |
| Dasyuridae     | Antechinus flavipes |          | Х       |                            | Х |   |          |   |   |        |   |        |
|                | Dasyurus            |          |         |                            |   |   |          |   |   |        |   |        |
|                | viverrinus          |          | Х       | Х                          |   | Х | Χ        | Х |   |        |   |        |
|                | Phascogale          |          |         |                            |   |   |          |   |   |        |   |        |
|                | tapoatafa           | Х        |         | Х                          |   |   |          | Х | Х | Х      |   | X      |
|                | Sminthopsis         |          | Х       |                            |   |   |          | Х |   |        |   |        |
| Peramelidae    | Perameles           |          |         |                            |   |   |          |   |   |        |   |        |
|                | bougainville        |          | Х       |                            |   | Х | Х        |   |   |        |   | Х      |
|                | Isoodon obesulus    |          | Х       | Х                          | Х | Х |          | Х |   |        |   | Х      |
| Potoroidae     | Bettongia lesueur   |          | X(b)    |                            | Х | Х | Х        | Х | Х |        | Х |        |
|                | Bettongia           |          |         |                            |   |   |          |   |   |        |   |        |
|                | penicillata         |          | Х       |                            |   |   |          |   |   |        | Х | -      |
|                | Potorous platyops   |          | Х       | Х                          |   |   |          |   |   |        |   |        |
|                | Potorous            |          |         |                            |   |   |          |   |   |        |   |        |
|                | tridactylus         |          | Х       | Х                          |   | Х |          | Х |   |        |   | Х      |
| Burramyidae    | Cercartetus nanus   | Х        |         | Х                          |   | Х |          | Х |   | Х      |   | Х      |
| Petauridae     | Petaurus breviceps  | Х        |         |                            |   |   |          | Х |   | Х      |   | Х      |
|                | Pseudocheirus       |          |         |                            |   |   |          |   |   |        |   |        |
| Pseudocheridae | peregrinus          | Х        |         | Х                          | Х | Х | <u> </u> | Х |   | Х      |   | Х      |
|                | Trichosurus         |          |         |                            |   |   |          |   |   |        |   |        |
| Phalangeridae  | vulnecula           | x        |         | x                          |   |   |          | x |   |        |   |        |
| i narangenuae  | vaipecaia           | Δ        | 1       | Λ                          | 1 | 1 | 1        | Δ | 1 | 1      | 1 | 1      |

## 4.4. Comparisons to other NCWHA deposits

## 4.4.1. SPECIES ASSEMBLAGES

The only small mammal identified in Specimen Cave that is missing from the older deposits and from Grant Hall is *Petaurus* sp. cf. *P. norfolcensis*. The only other Naracoorte cave deposits that contain this species are Blanche Cave and Wet Cave. Several small mammal species that appear in the other deposits were not identified in Specimen Cave, most of which appear in consistently low relative abundances throughout the Cathedral Cave and Grant Hall deposits (Appendix #). All macropodid species from Specimen Cave appear in one or both of the older deposits, except *Macropus* sp. cf. *M. titan* and *Protemnodon* sp. cf. *P. anak*. Several more Macropod species identified in Specimen Cave are absent from Grant Hall (Appendix #).

#### 4.4.2. RICHNESS TRENDS

Small mammal family richness is very similar across the deposits. All families present in the other deposits, except Phalangeridae and Miniopteridae, were identified in this study. The overall small mammal species richness of Specimen Cave (26 species) is lower than Cathedral Cave, Main Fossil Chamber (VFC) and Grant Hall, which possess 36, 37 and 34 species respectively (Fraser & Wells, 2006; Macken et al., 2012; Prideaux et al., 2007; Reed & Bourne, 2000, 2009).

Six trends were identified in the species richness values between the deposits. Trends A-C describe the relationship between the older deposits (Main Fossil Chamber (VFC) and Cathedral Cave) and Specimen Cave. Trend A involves a decrease in species richness between the older deposits and Specimen Cave; trend B involves no change; and trend C involves an increase. Trends D-F describe the relationship between the Specimen Cave and Grant Hall deposits. Trend D involves a decrease in species richness between Specimen Cave and Grant Hall; trend E involves no change; and trend F involves an increase. Families exhibiting trend A are Dasyuridae, Burramyidae, Peramelidae and Miniopteridae. This trend is most marked in Dasyuridae, which decreases in apparent richness from 11 species in both older deposits to four species in Specimen Cave (Prideaux et al., 2007; Reed & Bourne, 2000, 2009). Families exhibiting trend B are Phalangeridae and Pseudocheridae. Potoroidae exhibits trend A in Main Fossil Chamber (VFC) and trend B in Cathedral Cave, while Muridae exhibits trend B in Fossil Chamber (VFC) and trend A in Cathedral Cave. Trend C is exhibited by Petauridae. Families exhibiting trend D are Petauridae, Phalangeridae and Potoroidae. Trend E is exhibited by Pseudocheridae. All other families exhibit trend F, which is most marked in Dasyuridae (Figure 13).

Large mammal family richness differs across the deposits. The richest large mammal fauna is in Main Fossil Chamber (VFC), which contains ten families (Reed & Bourne, 2000, 2009). Specimen Cave has the lowest family richness (five). The overall large mammal species richness of Specimen Cave (17 species) is lower than Main Fossil Chamber (VFC) (30 species) and Cathedral Cave (26 species) (Prideaux et al., 2012; Reed & Bourne, 2000, 2009) but equal to Grant Hall (Fraser & Wells, 2006; Macken et al., 2012). The richest family in all deposits is Macropodidae.

All large mammal families exhibit trend A, except Dasyuridae, Thylacindidae and Thylacoleonidae, which exhibit trend C. Trend A is most marked in Macropodidae, which decreases in richness from 18 species in Main Fossil Chamber (VFC) to 13 species in Specimen Cave (Reed & Bourne, 2000, 2009). Trend D is exhibited by

Dasyuridae and Macropodidae. Trend F is exhibited by Diprotodontidae,

Phascolarctidae and Tachyglossidae. All other families exhibit trend E (Figure 14).



Figure 13. Small mammal species richness (total number of species) from Grant Hall, Main Fossil Chamber (VFC), Cathedral Cave and Specimen Cave. Caves are arranged on the x-axis from oldest to youngest (left to right). Specimen Cave species richness includes species identified in this study and by Reed and Bourne (2000). VFC = Victoria Fossil Cave. 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness. *Pseudomys apodemoides/novaehollandiae* and *Sminthopsis murina/crassicaudata* are counted as single species. References: Cathedral Cave: Reed & Bourne, 2000; Reed & Bourne, 2009, Prideaux et al., 2007. Grant Hall: Reed & Bourne, 2000; Fraser & Wells, 2006; Macken et al., 2012



Figure 14. Species richness of large mammal families from Main Fossil Chamber (VFC), Cathedral Cave, Specimen Cave and Grant Hall. Caves are arranged on the x-axis from oldest to youngest (left to right) (Main Fossil Chamber (VFC) and Cathedral Cave are roughly the same age. Specimen Cave species richness includes species identified in this study and in Reed & Bourne (2000). VFC = Victoria Fossil Cave. 'Sp. indet.' taxa are not included in the species richness counts. 'Sp. cf.' taxa are included in the species richness

# 4.4.3. RELATIVE ABUNDANCES

The small mammal component of Specimen Cave shares many similarities with the other deposits. The dominant family in all deposits is Muridae; however, the relative abundance differs. In Grant Hall, relative abundances in range from 45% (Fraser & Wells, 2006) to 86% (Macken et al., 2012). In Cathedral Cave, they range from 23% to 55% (Prideaux et al., 2007). The relative abundance of Muridae in Specimen Cave (88%) is most comparable to Grant Hall. The dominant Muridae species differs across the deposits. *Pseudomys fumeus, Pseudomys australis, Pseudomys auritus* and *Mastacomys fuscus* have high relative abundances throughout Cathedral Cave (Prideaux et al., 2007). *P. fumeus* also appears in high abundances throughout Grant Hall (up to

40%) (Fraser & Wells, 2006; Macken et al., 2012). These species abundances differ from Specimen Cave. The most abundant murids in Specimen Cave are *Pseudomys apodemoides/novaehollandiae* and *P. auritus*. Low relative abundances of *P. fumeus* are unusual in the context of the other deposits.

The abundance of large mammals in Specimen Cave, relative to small mammals, is similar to some units within Grant Hall, but significantly lower than other units (Macken et al., 2012). Fraser and Well's (2006) excavation yielded much greater relative abundances of large mammals (48 – 85%). All large mammal species identified in the Specimen Cave deposit are represented by too few specimens to make meaningful interpretations of their relative abundances.

# 5. DISCUSSION

# 5.1. Sediments

The flowstone in the deposit is likely to be have formed due to higher levels of effective moisture in the subsurface environment (Macken et al., 2013). High levels of effective moisture can result from higher amounts of precipitation or decreased evaporation rates associated with lower temperatures (Ayliffe et al., 1998). Calcite encrustation and cementation is a common surface feature of fossils (Bao et al., 1998). In karst environments, these crusts form on bones and fossils that are exposed to carbonate-rich waters (Fernandez-Jalvo and Andrews 2016). This suggests the Specimen Cave bones were exposed to a carbonate-rich water source after their deposition. The variation in the extent of encrustation across the pit and throughout the layers suggests spatially isolated water sources such as drips. Currently, there are no active water drips above either dig pit; however, there are several in the main chamber. Similar water drips could

have existed above the fossil bed at the time of its accumulation, suggesting there was a higher level of effective moisture in the sub-surface environment than today. This is corroborated by the NCWHA speleothem record, which shows an increase in speleothem formation at this time, related to increases in effective moisture (Ayliffe et al., 1998).

## 5.2. Faunal relative abundances

## 5.2.1. SMALL MAMMALS

There are several explanations for the low relative abundance of large mammals in Specimen Cave. The low numbers could primarily reflect the small sample size. They could be related to the fragmentary condition of the bones, many of which possessed no diagnostic features and could not be identified to family. This reduced the overall large mammal NISP. It is also possible that the low numbers are a result of body mass filtering, an effect frequently observed in pitfall deposits. This effect occurs when animals above a certain size fail to fall through the small pitfall trap entrances, resulting in their absence from the associated deposit (Reed, 2008).

One of the most notable features of the small mammal fauna of Specimen Cave is the very high relative abundance of Muridae. Similarly high relative abundances are recorded in several other NCWHA deposits (e.g. Brown & Wells, 2000; Macken et al., 2012; McDowell, 2001; Prideaux et al., 2007). Today, Muridae is the largest single mammal family in the world (Van Dyck & Strahan, 2008) and murid species are often the most numerous mammals across their range (Watts & Kemper, 1989). Based on their modern abundances, and high relative abundances in other NCWHA deposits, it is concluded that the high relative abundance of Muridae in Specimen Cave is an accurate

reflection of their abundance in the palaeocommunity. The high relative abundances of Pseudomys apodemoides/novaehollandiae and P. auritus could be a result of identification, as both of these taxa are easily distinguishable from other Muridae species. P. apodemoides is very common throughout the NCWHA fossil deposits and has been observed in high abundances (Fraser & Wells, 2006). If the specimens identified as P. apodemoides/novaehollandiae actually belong to P. apodemoides, high relative abundances could be a reflection of the proximal palaeoenvironment. It has been suggested that a moderate relative abundance of this species could indicate the presence of nearby heathland and grassland habitats (Prideaux et al., 2007). The high relative abundances of *P. auritus* could also be a reflection of a grassy proximal environment (Prideaux et al., 2007). The high numbers of 'Muridae sp. indet.' specimens, relative to other Muridae taxa are undoubtedly a result of identification bias. Many of the specimens from this deposit lacked the minimum number of diagnostic features required to confidently assign them to a genus or species. Specimens that did not possess enough observable diagnostic features could only be identified to Muridae sp. indet. The high relative abundance of 'Pseudomys sp. indet' can be similarly explained.

## 5.2.2. LARGE MAMMALS

Several factors could be responsible for the extremely low abundances of nonmacropodid animals in Specimen Cave. The apparent absences of Vombatidae, Thylacinidae and *Sarcophilus laniurus* (Dasyuridae) from the excavated deposit are very likely to be "false absences", as these animals appear in the existing species list. "False absences" occur when a species is present in a deposit but has not yet been detected (Macken & Reed, 2013). The absence of very large families, namely Diprotodontidae, could be attributed to body mass filtering. The high relative abundance of Macropodidae in Specimen Cave could also be a result of the saltatory locomotion of these animals. This locomotion makes them more susceptible to falling into pitfall traps than cursorial (walking) animals. Macropods also have great difficulty climbing out of traps, owing to their weak forelimbs and inability to move their hind limbs separately (Fraser & Wells, 2006). The high relative abundance of Macropodidae could be a result of some, or all, of these pitfall trap sampling effects; however, it could also reflect the dominance of this family in the palaeocommunity, as seen in other NCWHA deposits (Fraser & Wells, 2006; Reed, 2006). The most abundant macropodids in Specimen Cave appear to be grey kangaroos. These kangaroos occur in high relative abundances throughout the NCWHA and are suggested to have had similarly high relative abundances in the palaeocommunity (Fraser & Wells, 2006; Macken et al., 2012; Prideaux et al., 2007). Although it is plausible that they were also dominant in the palaeocommunity of Specimen Cave, such a conclusion cannot be confidently made, owing to the low NISP of these animals.

# 5.3. Mode of accumulation

The two most common types of cave deposit in the Naracoorte region are owl deposits and pitfall deposits (Prideaux et al., 2007). Owl deposits form in caves below owl roosts and consist primarily of undigested prey material, which owls regurgitate as "pellets". These pellets are highly concentrated and, as a result, owl deposits are characterised by very high densities of small animals (Macken & Reed, 2013; Reed, 2012). Owl deposits are known from several Naracoorte caves, including Blanche Cave, Wet Cave and

Robertson Cave (Macken & Reed, 2013, 2014). Pitfall deposits accumulate in caves that are connected to the surface via small openings or holes. Bones accumulate when animals fall through these holes and die. Pitfall deposits are known from several Naracoorte caves, including VFC (Fraser & Wells, 2006; Reed, 2006, 2008; Wells et al., 1984) and Cathedral Cave (Brown & Wells, 2000; Prideaux et al., 2007). The presence of large animals in Specimen Cave strongly suggests a pitfall trap acted as the primary mode of accumulation. The dominance of saltatory species amongst the large mammals provides additional evidence for a pitfall deposit, as these animals are particularly susceptible to pitfall entrapment (Fraser & Wells, 2006; Reed, 2006). The deposit appears to have been subject to body mass filtering, indicated by the absence of very large mammals such as Diprotodon optatum and Zygomaturus trilobus (Reed, 2008). This suggests the pitfall trap entrance was relatively small. The small mammal component of the assemblage is likely to have accumulated via the same pitfall trap. Although the relative abundance of very small mammals is high, the overall density is much lower than in other owl deposits. This provides sufficient evidence against an owl acting as the sole mode of accumulation of the small fauna (Macken & Reed, 2013). An owl is also unlikely to have roosted in Specimen Cave, as they appear to prefer caves with much wider entrances (Reed, 2012). The presence of arid-adapted species in Specimen Cave is unusual, as the majority of the fauna inhabit open forests or woodlands. This is also observed in the Grant Hall deposit and it has been suggested that the arid species were collected by owls from nearby arid microhabitats, then deposited below their roosts (Fraser & Wells, 2006). An owl also could have collected the arboreal species identified in Specimen Cave. As these animals live in trees, they rarely encounter pitfall trap entrances and are often poorly represented in pitfall deposits

(Brown & Wells, 2000). More robust evidence for an owl deposit could be provided by future taphonomic studies (Reed, 2012).

The complex morphology of Specimen Cave makes determining the location of the pitfall trap entrance difficult. One possible location is within the extension of the excavation passage. The upward sloping nature of this extension suggests it could form part of a large sediment cone (Figure 3, Geology and Background). Sediment cones form in caves below surface entrances and are common features of pitfall traps (Kos 2001, Reed 2008). Another possible entrance could be the modern entrance. Although the deposit is currently isolated from this entrance by the flowstone layer, it may have been connected in the past, as the flowstone formed after the bones accumulated.

## 5.4. Habitat and diet

The preferred and inferred habitats and diets of the Specimen Cave fauna suggest the proximal palaeoenvironment consisted of an open forest or woodland. The second most abundant species, *Pseudomys auritus*, became extinct following European settlement (Van Dyck & Strahan, 2008) and its habitat preferences are poorly understood. Prideaux et al. (2007) suggest that the presence of *P. auritus* in an assemblage could indicate grassland and open woodland was present in the proximal environment. This is based on the discovery of *P. auritus* with other grassland and woodland species in Mid Pleistocene deposits (Prideaux et al., 2007). The high abundance of *Pseudomys apodemoides/novaehollandiae* could also indicate the presence of woodland or grassland, as *P. apodemoides* typically inhabits grassland and *P. novaehollandiae* typically inhabits woodland (Prideaux et al., 2007; Van Dyck & Strahan, 2008). Most of the remaining species presently occupy forest/woodland or grassland habitat, providing evidence for this vegetation in the proximal environment. The presence of large tree is

suggested by the presence of arboreal species (Brown & Wells, 2000). The presence of ground-dwelling species that require groundcover for refuge, such as *Isoodon obesulus* and *Perameles bougainville*, suggests the environment must have been relatively open, with a thick understory of low-lying scrub (Brown & Wells, 2000; Fraser & Wells, 2006). *Pseudomys australis* and *Pseudomys shortridgei*, currently inhabit, or are believed to have inhabited, arid plains. These arid habitats are mutually exclusive to the forest/woodland habitat preferences of the other species. A possible explanation for this is the aforementioned owl accumulation (Fraser & Wells, 2006).

The large mammal component of the fauna consists of relatively equal proportions of browsing, grazing and mixed-feeding herbivores. This coexistence of browsers and grazers suggests both grasses and shrubs/trees were present in the proximal environment. An open forest or woodland would have supported this vegetation assemblage (Brown & Wells, 2000).

## 5.5. Climate

According to Mahlknecht's (2018) study, the Specimen Cave faunal assemblage was deposited around the time of the penultimate glacial maximum (~150 ka). Immediately prior to this glacial maximum, there was a period of high effective precipitation, lasting from 220 ka to 155 ka. Evidence for this wetter period is indicated by increased formation of speleothems in the region (Ayliffe et al., 1998). Owing to the errors on the OSL dates (Mahlknecht, 2018), it is difficult to determine if the deposit accumulated towards the end of the wetter period or during the drier glacial maximum. The fauna is more reflective of a forest or woodland environment and therefore a wetter climate (Prideaux et al., 2007). The presence of flowstone and calcite could reflect either

climatic scenario, as these minerals can form in response to increased precipitation or decreased evaporation driven by low temperatures (Ayliffe et al., 1998).

## 5.6. Megafauna extinction

The Middle Pleistocene has been identified as an extremely important period for investigating faunal responses to climate fluctuations prior to human arrival into Australia. The period is characterised by large-scale climate fluctuation and the penultimate glacial maximum (ca. ~150 ka). Information on fauna from this period, coupled with climate records, could help to elucidate the driver of the late Pleistocene megafauna extinction around 46 ka (Moriarty et al, 2000). Of particular importance is the drier period between 155 ka and 115 ka. Although no other studies have identified megafauna from this period, they clearly did not experience large-scale extinctions as they are present in younger, Late Pleistocene NCWHA deposits (Ayliffe et al., 1998; Fraser & Wells, 2006; Macken et al., 2012; Prideaux et al., 2007). The megafauna identified in Specimen Cave represent the first record of these animals in the Naracoorte region between ~206 ka and ~90 ka and in the drier period between 155 ka and 115 ka. This indicates that many megafauna species persisted in the Naracoorte region into the beginning of this dry period and did not experiencing major range contractions. This provides preliminary support for Prideaux et al's (2007) theory that megafauna were relatively resilient to precipitation-driven climate change and did not experience longterm, climate-mediated species extinctions in the Naracoorte region during the Pleistocene. It also supports the theory that climate change was not the sole or primary driver of their late Pleistocene extinction (Prideaux et al., 2007). Further support for this theory could be provided through additional studies of Specimen Cave that focus on

collecting information regarding the responses of megafauna to Mid-Pleistocene climate fluctuations, particularly those leading up to the penultimate glacial maximum.

## 5.7. Comparisons to other Naracoorte deposits

## 5.7.1. SPECIES ASSEMBLAGES

If the identification of *Petaurus* sp. cf. *P. norfolcensis* is correct, it would represent the oldest known occurrence of this species in the region. The only other records come from Late Pleistocene-Holocene deposits in Robertson Cave, Blanche Cave and Wet Cave. The presence of *P. norfolcensis* in these younger deposits suggests the species only experienced a range expansion into the Naracoorte region during the Late Pleistocene (<50 ka), as it is missing from the Mid-Late Pleistocene deposits of Cathedral Cave and Grant Hall (Macken et al., 2012). The presence of *P. norfolcensis* in Specimen Cave would provide evidence for a much earlier range expansion in the Mid-Late Pleistocene.

## 5.7.2. RICHNESS

The major faunal differences between the investigated deposits lie in the overall lower species richness of Specimen Cave. This low apparent species richness most likely reflects differences in sample size between the deposits. It could also be the result of false absences or a reflection of difficulties with identification, caused by the lack of visible diagnostic features.

Several factors could be responsible for the apparent loss of species richness within Dasyuridae between the accumulation of the older deposits and Specimen Cave. Three of the dasyruid species not identified in Specimen Cave, *Antechinus minimus*, *Antechinus swainsonii* and *Antechinus agilis*, all occur intermittently throughout the

investigated deposits, indicating they experienced recurring range contractions during this period (Macken et al., 2012). It is plausible that these species experienced similar patterns of range contraction around the time of the Specimen Cave accumulation, explaining their absence from the deposit. The apparent absences of these species could also represent false absences, as they appear in low relative abundances throughout the NCWHA fossil record (Macken et al., 2012). The absence of another Dasyurid species, Phascogale calura, could also be false, as it too occurs in low abundances throughout the NCWHA. The same conclusions can be made regarding the apparent increase of Dasyruidae species richness between the accumulations of the Specimen Cave and Grant Hall deposits. The small loss of species richness within Muridae is likely to be caused by a false absence of Hydromys chrysogaster, as this species generally appears in low abundances throughout the NCWHA fossil record. Similar false abundances of Cercartetus lepidus and Bettongia gaimardi could explain the apparent losses of species richness in Burramyidae and Potoroidae (Fraser & Wells, 2006; Macken et al., 2012). The apparent decline of species richness in Peramelidae (trend A) is indicated by the absence of Perameles gunnii from Specimen Cave. This species occurs throughout the NCWHA, and often in high abundances (Brown & Wells, 2000; Fraser & Wells, 2006; Macken et al., 2012), indicating that its absence from Specimen Cave is unlikely to be "false".

The same factors used to explain the low abundance of large mammals (sample size, body mass filtering) can be used to explain the apparent decline in species richness of this group.

## 5.7.3. RELATIVE ABUNDANCES

The lower relative abundance of *Pseudomys fumeus* in Specimen Cave could be a result of false absences, caused by difficulties in distinguishing Muridae species. It is also possible that the low relative abundance is a true reflection of the community. Although this species generally occurs in high relative abundances in other NCWHA deposits, its abundance has been shown to fluctuate through time. For example, in Cathedral Cave, its relative abundance decreases dramatically across a glacial maximum (Prideaux et al., 2007), potentially signalling a response to climate. *P. fumeus* is also known to have specific dietary requirements, which strongly influence habitat selection. Habitats with access to nitrogen-rich food sources, such as seeds, appear to be particularly favourable (Van Dyck & Strahan, 2008). A lack of suitable vegetation and food in the proximal environment could cause the relative abundance of *P. fumeus* to decrease.

The low relative abundance of *Rattus fuscipes* in Specimen Cave could reflect a low relative abundance or absence in the palaeocommunity. Although recorded in Cathedral Cave, *R. fuscipes* is represented by very low numbers throughout the assemblage (Prideaux et al., 2007). It is possible that its relative abundance in the palaeocommunity remained low throughout the Mid Pleistocene, explaining its absence from Specimen Cave. *R. fuscipes* has a much higher relative abundance in Grant Hall, suggesting it experienced a significant population boom after the Specimen Cave assemblage was deposited. Today, *R. fuscipes* inhabits a wide range of habitats and, unlike *Pseudomys fumeus*, does not appear to have any strict habitat or dietary requirements (Van Dyck & Strahan, 2008). Future studies of older layers within Specimen Cave could provide information on abundance trends of *R. fuscipes* and identify potential drivers of population booms.

## 5.8. Limitations and future directions

The main limitation of this study was the small sample size, which was most noticeable when comparing Specimen Cave to the other cave deposits. This limitation could be resolved in future studies by deepening the dig pit. Another limitation was the condition of the fossils. Many fossils were fragmentary and lacked visible diagnostic features, making species identification difficult. Refining the acid preparation could partially resolve this issue if more calcite could be removed. Additional taphonomic studies of the small mammal material would help to elucidate whether or not an avian predator was responsible for accumulating some of the bones.

# 6. CONCLUSIONS

This study provides the first age-constrained record of fauna in the Naracoorte region in the period between ~206 ka and ~93 ka (Mahlknecht, 2018; R. Weij, University of Melbourne, unpublished data with permission). The following conclusions can be drawn from these results:

- The deposit contains a similar faunal assemblage to other caves in the Naracoorte region, with all identified species present in at least one other Naracoorte assemblage (e.g. Macken et al., 2012; Reed & Bourne, 2000, 2009).
- 2) The assemblage is dominated by small mammals (<5 kg), which make up 95% of the identified fauna. Like most other Naracoorte deposits, the small mammal fauna is dominated by Muridae (Reed & Bourne, 2000, 2009), which has the greatest relative abundance, the greatest species richness and the highest density of all families. This is expected to be an accurate reflection of their abundance in the palaeocommunity.</p>

- 3) Large mammals are poorly represented in the assemblage, making up 4% of the fauna. Like most other Naracoorte deposits (Reed & Bourne, 2000, 2009) the large mammal fauna is dominated by Macropodidae (kangaroos). The high abundance of Macropodidae could reflect their abundance in the palaeocommunity. It could also be a result of their frequent entrapment in pitfall caves (Reed, 2006)
- 4) The habitat preferences of the identified fauna suggest the proximal palaeoenvironment of Specimen Cave was dominated by an open forest or woodland, with a grassy understory. This environment would have allowed browsing and grazing herbivores to coexist and aligns with the habitat preferences of most of the identified species
- 5) The presence of large mammals in the deposit indicates that a pitfall trap acted as the primary mode of accumulation of the deposit. Relatively low densities of small mammals provides sufficient evidence against an owl deposit; however, it is possible that an owl was responsible for depositing arid and arboreal species
- 6) The Specimen Cave deposit has lower family and species richness than older and younger NCWHA deposits. This apparent decline in richness can be attributed to the limited sample size and may not necessarily reflect significant faunal change in the time leading up to, and proceeding, the deposit's accumulation
- 7) The presence of megafauna in Specimen Cave provide the first robust evidence that many species of this group did not experience regional extinctions or range contractions in the dry period between ~155ka and ~115 ka.

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# **APPENDIX 1. CHRONOLOGY OF THE NARACOORTE CAVES**

| Cave/chamber                  | Age range                    | Method             | Reference(s)             |
|-------------------------------|------------------------------|--------------------|--------------------------|
| Cathedral Cave,               | $206 \pm 16$ ka to $528 \pm$ | Optical dating     | Prideaux et al., 2007    |
| Fossil Chamber                | 41 ka                        |                    |                          |
| Victoria Fossil Cave,         | ~213 ka to $478 \pm 22$      | OSL dating         | Ayliffe et al., 1998;    |
| Fossil Chamber                | ka                           |                    | Moriarty et al., 2000;   |
|                               |                              |                    | Reed & Bourne, 2000      |
| Specimen Cave                 | $119\pm13$ ka to $156\pm$    | OSL dating         | Mahlknecht, 2018         |
|                               | 13 ka                        |                    |                          |
| Victoria Fossil Cave,         | $70 \pm 5$ ka to $93 \pm 8$  | OSL dating,        | Macken et al., 2011      |
| Grant Hall                    | ka                           | supported by U/Th  |                          |
|                               |                              | dating of teeth    |                          |
| Wet Cave                      | $740 \pm 40$ yr BP to        | AMS radiocarbon    | Pate et al., 2002, 2006  |
|                               | >45 ka                       | dating             |                          |
| Robertson Cave,               | $8080 \pm 100$ yr BP to      | Radiocarbon dating | Forbes et al., 2007      |
| Inner Chamber                 | $31.45 \pm 0.25$ ka          | _                  |                          |
| Robertson Cave,               | 24.3 ka – 935 yr BP          | Radiocarbon dating | Fallon et al., 2010      |
| Entrance Chamber              |                              |                    |                          |
| Blanche Cave, 3 <sup>rd</sup> | $12.47 \pm 0.06$ ka to       | U/Th series dating | St Pierre et al., 2012;  |
| Chamber                       | $43.26 \pm 1.84$ ka          |                    | Darrenougue et al., 2009 |

Table A1. Age ranges of the key dated Naracoorte Caves and the methods used to attain these ages

Table A2. OSL ages of Specimen Cave from Mahlknecht's (2018) study

| Sample<br>number | Approximate age<br>(ka) | Standard error<br>/- (ka) | In cave depth (m<br>from cave datum) |
|------------------|-------------------------|---------------------------|--------------------------------------|
| 1                | 124                     | 12                        | 7.31                                 |
| 5                | 119                     | 13                        | 7.45                                 |
| 4                | 125                     | 12                        | 7.7                                  |
| 2                | 151                     | 9                         | 7.79                                 |
| 3                | 156                     | 13                        | 8.05                                 |

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# **APPENDIX 2: COMPARISON OF THE FAUNA OF MID PLEISTOCENE NARACOORTE CAVES**

Table 1. Mammal taxa from Victoria Fossil Cave, Cathedral Cave and Specimen Cave. New record for Specimen Cave. 'Sp. indet.' taxa are not included in species richness. 'Sp. cf.' taxa are included. *P. novaehollandiae /apodemoides* is counted as a single species. Original data: Reed & Bourne, 2000, 2009 (all deposits); Fraser & Wells, 2006; Macken *et al.*, 2012 (Grant Hall). Brown & Wells, 2000; Prideaux *et al.*, 2007 (Cathedral Cave)

|             |                                 | Specimen Cave           |            | Cathedral Cave | Victoria Fossil Cave |                        |
|-------------|---------------------------------|-------------------------|------------|----------------|----------------------|------------------------|
| Family      | Species                         | Reed &<br>Bourne (2000) | This study | Fossil Chamber | Grant Hall           | Main Fossil<br>Chamber |
| Dasyuridae  | Dasyuridae sp. indet            |                         | X*         |                |                      |                        |
|             | Sarcophilus sp. cf. S. laniurus | Х                       |            |                |                      | Х                      |
|             | S. laniurius                    | Х                       |            | Х              |                      |                        |
|             | Dasyurus maculatus              |                         |            | X              |                      | Х                      |
|             | D. viverrinus                   |                         | X*         | Х              | Х                    | Х                      |
|             | Sminthopsis sp. indet.          | Х                       | X*         |                | Х                    |                        |
|             | S. crassicaudata                |                         |            | Х              | Х                    | Х                      |
|             | S. murina                       |                         |            | Х              | Х                    | Х                      |
|             | S. crassicaudata/murina         |                         | X*         |                |                      |                        |
|             | Ningaui sp. cf. N. yvonnae      |                         |            |                |                      | Х                      |
|             | Ningaui yvonnae                 |                         |            | Х              |                      |                        |
|             | Antechinus sp. cf. A. flavipes  |                         |            |                | Х                    |                        |
|             | Antechinus sp. indet.           |                         | X*         | Х              | Х                    |                        |
|             | A. agilis                       |                         |            | Х              |                      |                        |
|             | A. flavipes                     |                         | X*         | Х              | Х                    | Х                      |
|             | A. stuartii                     |                         |            |                |                      | Х                      |
|             | A. swainsonii                   |                         |            | Х              | Х                    | Х                      |
|             | A. minimus                      |                         |            | Х              | Х                    |                        |
|             | Phascogale calura               |                         |            | Х              | Х                    | Х                      |
|             | P. tapoatafa                    |                         | X*         | Х              | Х                    | Х                      |
|             | Species richness                |                         | 5          | 12             | 9                    | 11                     |
| Peramelidae | Peramelidae sp. indet.          |                         | X*         |                |                      |                        |
|             | Perameles sp. cf. P. gunnii     |                         |            |                | Х                    |                        |

|                | Perameles sp. indet              | Х | X* |   |   |   |
|----------------|----------------------------------|---|----|---|---|---|
|                | P. gunnii                        |   | X* | Х | X | X |
|                | P. bougainville                  | Х | X* | Х | X | X |
|                | Isoodon obesulus                 | Х | X* | Х | X | X |
|                | Species richness                 | 2 | 3  | 3 | 4 | 3 |
| Phalangeridae  | Trichosurus vulpecula            | Х |    | Х |   | X |
| Potoroidae     | Potoroidae sp. indet.            |   | X* |   |   |   |
|                | Aepyprymnus rufescens            |   |    |   |   | X |
|                | Potorous sp. indet.              |   |    |   | X |   |
|                | P. platyops                      | Х | X* | Х | X | X |
|                | P. tridactylus                   |   | X* | Х | X | X |
|                | Bettongia sp. indet.             |   |    | Х |   |   |
|                | B. gaimardi                      |   |    | Х |   | X |
|                | B. penicillata                   | X | X* | Х | X | X |
|                | Bettongia sp. cf. B. lesueur     |   |    |   |   | X |
|                | B. lesueur                       |   | X* |   |   |   |
|                | Species richness                 |   | 5  | 4 | 3 | 6 |
| Pseudocheridae | Pseudocheirus peregrinus         |   | Х  | Х | X |   |
| Burramyidae    | Cercartetus sp. indet.           |   | X* |   |   |   |
| •              | C. lepidus                       |   |    | Х | X | X |
|                | C. nanus                         |   | X* | Х | X | X |
|                | Species richness                 |   | 1  | 2 | 2 | 2 |
| Petauridae     | Petaurus breviceps               |   | X* | Х | X | X |
|                | Petaurus sp. cf. P. norfolcensis |   | X* |   |   |   |
|                | Species richness                 |   | 2  | 1 | 1 | 1 |
| Acrobatidae    | Acrobates pygmaeus               |   |    | Х |   | X |
| Muridae        | Conliurus albipes                |   | Х  | Х |   | X |
|                | Mastacomys fuscus                |   | X* | Х | X | X |
|                | Pseudomys sp. cf. P. gouldii     |   |    |   | X | X |
|                | Pseudomys sp. cf. P. fumeus      |   |    |   | X | X |
|                | Pseudomys sp. indet.             |   | X* | Х | X |   |
|                | P.apodemoides                    |   |    | Х | X | X |
|                | P. apodemoides/novaehollandieae  |   | X* |   |   |   |
|                | P. australis                     |   | X* | Х | Х | X |
|                | P. gouldii                       |   | X* | Х | X |   |
|                | P. shortridgei                   |   | X* | Х | X | Х |
|                | P. auritus                       |   | X* | Х | Х |   |

|                     | P. fumeus                        |   | X* | Х  | X  |    |
|---------------------|----------------------------------|---|----|----|----|----|
|                     | Rattus fuscipes                  |   | Х  | Х  | X  | X  |
|                     | R. tunneyi                       |   | X* | Х  | X  | X  |
|                     | R. lutreolus                     |   | Х  | Х  | X  |    |
|                     | Notomys mitchelli                |   | Х  | Х  | X  | X  |
|                     | Hydromys chrysogaster            |   |    | Х  | X  | X  |
|                     | Species richness                 |   | 12 | 13 | 13 | 12 |
| Miniopteridae       | Miniopterus sp. cf. schreibersii |   |    |    | X  |    |
| Total small mammals | Species richness                 |   | 27 | 37 | 34 |    |
| Tachyglossidae      | Tachyglossus aculeatus           |   |    | Х  | X  | X  |
|                     | Megalibgwilia ramsayi            |   |    |    |    | X  |
|                     | Species richness                 | 0 | 0  | 1  | 1  | 2  |
| Thylacinidae        | Thylacinus cynocephalus          | Х |    | Х  | X  | X  |
| Phascolarctidae     | Phascolarctos cinereus           |   |    |    | X  | X  |
|                     | Phascolarctos stirtoni           |   |    | Х  |    |    |
|                     | Species richness                 |   |    | 1  | 1  | 1  |
| Diprotodontidae     | Zygomaturus trilobus             |   |    | Х  | X  | X  |
| Palorchestidae      | Palorchestes azael               |   |    | Х  |    | X  |
| Vombatidae          | Vombatidae gen. et sp. indet     |   |    | Х  |    |    |
|                     | Lasiorhinus latifrons            |   |    | Х  |    | X  |
|                     | Lasiorhinus krefftii             |   |    | Х  |    | X  |
|                     | Vombatus ursinus                 | Х |    | Х  | X  | X  |
|                     | Species richness                 |   | 1  | 3  | 1  | 4  |
| Thylacoleonidae     | Thylacoleo carnifex              | Х |    | Х  | X  | X  |
| Macropodidae        | Macropodidae sp. indet.          |   | X* |    |    |    |
|                     | Macropus giganteus               | Х | Х  | Х  | X  | X  |
|                     | M. fuliginosus/giganteus         |   |    |    | X  |    |
|                     | M. fuliginosus                   |   |    |    |    | X  |
|                     | M. rufogriseus                   | Х |    | Х  | X  | X  |
|                     | Macropus sp. cf. M. titan        | Х |    |    |    |    |
|                     | Macropus sp. indet.              | Х | X* | Х  | Х  |    |
|                     | Macropus sp. nov.                |   |    | Х  |    |    |
|                     | M. greyi                         |   |    | X  | X  | Х  |
|                     | M. eugenii                       |   |    |    |    | Х  |
|                     | Protemnodon roechus              | Х |    |    |    | Х  |
|                     | Protemnodon sp. cf. P. anak      | X |    |    |    |    |
|                     | Protemnodon sp. cf. P. brehus    |   |    | Х  | X  |    |

|                     | Onychogalea lunata                |    |    | Х  |    |    |
|---------------------|-----------------------------------|----|----|----|----|----|
|                     | Lagorchestes leporides            |    |    | Х  |    | Х  |
|                     | Thylogale sp. indet.              | Χ^ |    |    |    |    |
|                     | Wallabia bicolor                  |    | X* | Х  | Х  | Х  |
|                     | Lagostrophus fasciatus            |    |    |    |    | Х  |
|                     | 'Procoptodon' goliah              |    |    | Х  |    | Х  |
|                     | 'Procoptodon' sp. cf. 'P'. goliah |    | X* |    |    |    |
|                     | 'P.' browneorum                   | Х  |    | Х  | Х  | Х  |
|                     | 'P.' gilli                        | Х  |    | Х  | Х  | Х  |
|                     | Simosthenurus baileyi             | Х  |    |    |    | Х  |
|                     | S. pales                          |    |    | Х  |    | Х  |
|                     | S. maddocki                       | Х  |    | Х  | Х  | Х  |
|                     | S. occidentalis                   | Х  |    | Х  | Х  | Х  |
|                     | Simosthenurus sp. cf. S.          |    |    |    |    |    |
|                     | occidentalis                      |    | X* |    |    |    |
|                     | Sthenurus sp. indet.              |    | X* |    | Х  |    |
|                     | S. andersoni                      |    |    | Х  | Х  | Х  |
|                     | Sthenurus sp. cf. S. andersoni    |    | X* |    |    |    |
|                     | Metasthenurus newtonae            |    |    | Х  | Х  | Х  |
|                     | Species richness                  |    | 11 | 17 | 12 | 18 |
| Total large mammals | Species richness                  |    | 13 | 25 | 17 |    |

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