Island Biodiversity and Human Palaeoecology in the Philippines:

A zooarchaeological study of Late Quaternary faunas

Janine Ochoa

Newnham College

University of Cambridge

May 2019

This thesis is submitted for the degree of Doctor of Philosophy

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit for the relevant Degree Committee.

Island Biodiversity and Human Palaeoecology in the Philippines:
A zooarchaeological study of Late Quaternary faunas
Janine Ochoa

Abstract

This thesis is a zooarchaeological analysis of Late Quaternary faunal assemblages from the Philippines, *ca*. 25,000 to 2,000 years ago. The research utilises several approaches within a broad ecological framework. The first element of the ecological approach is informed by zooarchaeology's niche in palaeoecology and its application to modern biodiversity conservation. This approach is crucial for a tropical faunal region known for its exceptionally high levels of biodiversity and endemism but that also has a relative paucity of fossil studies. In this regard, the thesis aims to investigate the evolutionary and biogeographic history of these faunas. The second element of the framework uses the faunal subsistence record to explore human palaeoecology in the Philippines and its relevance to understanding indigenous ecological knowledge systems in the past.

Using archaeofaunal material from Luzon and Palawan Islands, the study presents important fossil discoveries and palaeoecological insights into the dynamics of faunal change in the Philippines. The faunal analyses also allow the first attempt to construct Late Quaternary biostratigraphic sequences for the archipelago. For Palawan Island, the thesis presents an MIS-2 (25,000-20,000 cal BP) faunal record based on the re-excavation and re-dating of Pilanduk Cave. This record provides evidence for the presence of the tiger on Palawan during the Last Glacial Maximum and morphological confirmation of the presence of two locally extinct deer taxa. For Luzon Island, the study presents evidence from Minori and Musang Caves for previously unknown and extinct endemic giant cloud rats, as well as for the human translocation of macaques and palm civets. In line with the second element of the framework, the zooarchaeological analyses also provide foraging histories of local human populations in tropical island environments. The subsistence data present the responses and possible roles of humans in observed faunal and environmental changes. Human impacts are possibly implicated in the Late Holocene extirpation of the hog deer of Palawan and two endemic cloud rat species on Luzon. The subsistence records also present island-specific strategies for tropical rainforest foraging across the Holocene. Taken together, the findings offer diachronic perspectives on indigenous ecological knowledge systems as manifested in these changing local settings.

Preface

Various chronological and taxonomic terms appear throughout the thesis and their usage and definitions are clarified here. Abbreviations used are also listed below.

Chronological Terms

Geological time divisions used in the text follow the International Commission on Stratigraphy (ICS; www.stratigraphy.org). Radiocarbon ages within the text are typically given as calibrated calendar years before present and present is designated as 1950 CE. The main exceptions are for citing ages as reported by original authors in their publications, in which case dates in BP (uncalibrated), BC and cal BC are provided. The ICS defines the start of the Quaternary Period at 2.58 Ma, the Late Pleistocene at 0.126 Ma, the Early Holocene at 11,700 yr b2k (before AD 2000), the Mid Holocene at 8326 yr b2k, and the Late Holocene at 4250 yr b2k. The informal term Late Quaternary is used to refer to the duration of the Late Pleistocene to the Holocene.

Abbreviations

AD	anno Domini
BP	before present, present referring to 1950 CE
BC	before Christ
^{14}C	radiocarbon
BMNH	British Museum of Natural History
ca.	*circa*
cal BP	calibrated years before present
CE	Common Era
CT scanning	computed tomography scanning
FFI	Freshness Fracture Index
FMNH	Field Museum of Natural History
FUI	Food Utility Index
GIS	Geographic Information System
HBE	human behavioural ecology
IEK	indigenous ecological knowledge
IK	indigenous knowledge
ISEA	Island Southeast Asia
IUCN	International Union for Conservation of Nature
LGM	Last Glacial Maximum
LGP	Last Glacial Period
Ma	Mega-annum, one million years
MAU	minimum animal unit
mbpsl	meters below present sea level
MCZ	Museum of Comparative Zoology, Harvard University
MIS	Marine Isotope Stage

MNE	minimum number of elements
MNI	minimum number of individuals
N	number of specimens
NISP	number of identified specimens
NMP	National Museum of the Philippines
OFT	optimal foraging theory
ORAU	Oxford Radiocarbon Accelerator Unit
OUMNH	Oxford University Museum of Natural History
PAIC	Pleistocene aggregate island complexes
PIPRP	Palawan Island Palaeohistoric Research Project
r	Pearson's r or Pearson correlation coefficient
R^2	coefficient of determination
r_s	Spearman's rho
SEA	Southeast Asia
sp.	species
spp.	*species pluralis*, multiple species
SST	sea surface temperature
TNF	total number of fragments
TEK	traditional environmental/ecological knowledge
UP	University of the Philippines

Taxonomic Names and Common Names

Scientific Name	English Common Name	Vernacular Names
Aonyx cinereus	Oriental small-clawed otter	dingguin
Arctictis binturong	bearcat, binturong	binturong, manturon
Axis calamianensis	Calamian hog deer	pilanduk, usa
Batomys sp.	hairy-tailed rat	
Bubalus bubalis	domestic water buffalo; carabao	kalabaw
Bullimus luzonicus	large Luzon forest rat	
Canis lupus familiaris	domestic dog	aso
Carpomys sp.	dwarf cloud rat	
Chiropodomys calamianensis	Palawan pencil-tailed tree mouse	
Crateromys sp.	Luzon bushy-tailed cloud rat	bu-ot
Cuora amboinensis	Malayan box turtle	bakoko, bao, pagong
Cyclemys dentata	Asian leaf turtle	bakoko, bao, pagong
Herpestes brachyurus	short-tailed mongoose	
Hipposideros cf. *ater*	roundleaf bat	kabat-kabat, kabag
Hipposideros diadema	diadem roundleaf bat	kabat-kabat, kabag
Homo luzonensis	Luzon human	
Homo sapiens	modern human	tao
Hylopetes nigripes	arrow-tailed flying squirrel	bia'tat, tapilak
Hystrix pumila	Palawan porcupine	dugyan, durian
Macaca fascicularis	long-tailed macaque	bakes, amu, unggoy
Manis culionensis	Palawan pangolin	balintong
Maxomys panglima	Palawan spiny rat	daga
Mydaus marchei	Palawan stink badger	pantot
Panthera tigris	tiger	tigre
Paradoxurus philippinensis	palm civet	musang
Phloeomys cumingi	southern Luzon giant cloud rat	bugkun
Phloeomys pallidus	northern Luzon giant cloud rat	bu-ot
Prionailurus philippinensis	leopard cat	maral
Rattus everetti	Philippine forest rat	daga
Rattus tiomanicus	Malaysian field rat	daga
Rhinoceros phillipinensis	rhinoceros	
Rusa marianna	Philippine brown deer	usa
Stegodon luzonensis	stegodon	
Sundasciurus spp.	tree squirrel	bising, laksoy
Sus ahoenobarbus	Palawan bearded pig	babuy, byak
Sus philippensis	Philippine warty pig	babuy
Sus scrofa	domestic pig	babuy
Varanus spp.	monitor lizard	bayawak, biawak

Acknowledgements

This research would not have been possible without the support and kindness of many people and institutions. First and foremost, I thank my supervisors, Professor Graeme Barker and Dr. Preston Miracle, for their guidance and encouragement throughout the PhD journey.

My research in the Philippines was made possible by the support of the National Museum. My earnest thanks go to Director Jeremy Barns, Dr. Anna Labrador, and Dr. Mary Jane Louise Bolunia. I am indebted to Dr. Ame Garong for graciously directing the excavation of Pilanduk Cave. Many thanks also go to Antonio Peñalosa, Gerard Palaya, Clyde Jago-on, Nida Radam, Larry Pronto, Jonathan Jacar, Marian Reyes, Maricar Belarmino, Alexandra de Leon, Timothy James Vitales, and Bobby Orillaneda.

I am grateful for the kind support of the local government of Quezon and Barangay Maasin during our fieldwork in 2016, especially Mayor Joselito Ayala, Barangay Captain Nelson Cabrestante and IPMR Narciso Seniaga. My heartfelt gratitude goes to the local members of our research team: Panglima Eddie Seniaga, Councillor Gaddy Narte, Jofer Seniaga, Rayban Seniaga, Joseph Toledo, Larry Pagdato, Jessie Billones, Jojo Nuñez and Janice Nuñez.

The Pilanduk Cave archaeological project came to fruition through the help of friends and colleagues at the University of the Philippines. To Jane Carlos, Myra Lara, Rebecca Ferreras, Jeanne Ramos, Llenel de Castro, Dante Manipon, and Lursh Almojano, thank you for joining me on this project and going on the daily hike up the cave, even amidst one of the strongest typhoons of that year. A special thanks must go to the research assistants of the project: Patricia Cabrera and Trishia Palconit. This brilliant and extraordinary duo was indispensable to the research: from digging and accessioning, to bone analysis, photography and graphics editing. Thank you also to the PIPRP through Dr. Victor Paz for his support and for lending archaeological equipment. The maps in this thesis and for the Pilanduk project were made by Jon Villasper. The Pilanduk site plan was made by Myra Lara and Antonio Peñalosa. Identification of Pilanduk macrobotanical specimens was conducted by Jane Carlos. Lithic analysis was conducted by Dante Manipon and the pottery analysis by Alexandra de Leon. Bernadette Almanzor and Loraine Xian Claver also assisted me during the early stages of the field research. I followed the footsteps of Jonathan Kress, and gratefully acknowledge that without his work, my Palawan research would not have been conceived. In Peñablanca, I am also grateful for the help of Bonifacio Pacion, Domingo Pagulayan, Dominic Pagulayan and Jerome Tumbali.

Financial support for the PhD was provided by the University of the Philippines Doctoral Studies Fund through the UP Office of the President. Financial support for the research was provided by the University of Cambridge HSPS Fieldwork Funding, Wenner Gren Foundation Dissertation Fieldwork Grant, Evans Fund, Anthony Wilkins Fund, Newnham College Travel and Research Grants and Ridgeway Venn Fund. My sincerest thanks also go to the UP Department of Anthropology, particularly to Chancellor Michael Tan, Dr. Soledad Natalia Dalisay, and Dr. Nestor Castro for their kind support and understanding.

My gratitude also goes to my UP friends and colleagues. Apart from the UP excavation team who joined us at Pilanduk, I must also thank Agatha Villaluz, Edwin Valientes, Omar Choa, Kat Manalo, Leee Neri, Michael Herrera, Michelle Eusebio, Mindy Ceron, Mylene Lising, Eliza Romualdez, Noel Amano, Deyya Cosalan, Anna Pineda, Danny Galang, Aida Tiama, Digna Jacar and Ramil Mainot. Many thanks to Dr. Armand Mijares for permission to access materials and equipment at the UP ASP. Sincerest thanks also to Dr. Grace Barretto-Tesoro and Archie Tesoro for their support at ASP and for our restorative mountain hikes.

My journey in academia was inspired by my archaeology mentor, Dr Victor Paz. I must thank Sir Vic and Dr. Helen Lewis for allowing me to work in the Dewil Valley and on Ille and Pasimbahan material. Victor and Grace also motivated me to follow their footsteps and apply at Cambridge. I also owe a debt of gratitude to my zooarchaeology mentor, Dr. Philip Piper – thank you Phil for opening my eyes to the world of vertebrate biodiversity.

The research relied on the support and collections of several museums. My gratitude goes to Matt Lowe at the Cambridge University Museum of Zoology, Mark Carnall at the Oxford University Museum of Natural History, and Roberto Portela Miguez and Louise Tomsett at the Natural History Museum. My research on Philippine mammals has long been inspired by the work of Lawrence Heaney and Danilo Balete and facilitated by the Mammal Collection at the Field Museum of Natural History. Many thanks also to Larry, Terry, Lilo and Zeb for letting me into their Evanston home.

In Cambridge, I must thank the Grahame Clark Lab, headed by Dr. Preston Miracle and Jessica Rippengal. Among many things, Jess enabled me to get fieldwork-ready with equipment and permits and get my research materials to Cambridge. The lovely Emily Tilby, Leah May Damman and Marjolein Bosch make our lab life lively, keeping me sane with our tea breaks, baby visits and sage osteological advice. In the early days of the PhD, I was welcomed to the Lab by Ningning Dong, Yiru Wang, Minghao Lin, Pia Spry-Marques and Professor Haskell Greenfield. I am deeply thankful to my Cambridge friends for sharing this journey with me: Akshyeta Suryanarayan, Ian Ostericher, Hermine Xhauflair, Alice Lepleongeon, Samantha

Leggett, Natalie Morningstar, Mat Dalton, Lucy Farr, Emma Lightfoot, Jeremy Bennett, Chris, Stimpson, Ben Utting, Ankica Oros Srsen, Ah Tshen, Callie Vanderweile, Jess Thompson, Danika Parikh, Katerina Mourelatou, Srishti Krishnamoorthy, Amiel Clarke, Yoanna Shams, Anna Rowell, and Pamela McDuff – you all touched my Cambridge life in some way. Thank you also to Rachel Ballantyne and Catherine Kneale for lending me their microscopy time and skills. Kind thanks to the Cambridge Pinoy crew: Reg Lagaac, Ranier Macatangay, Patrick Perillo, James Gabrillo, Nelzo Ereful, Tanya Recalde, Joji Mendoza, Sharmila Parmanand, Carlo Sandoval and Chai Apale. My deepest thanks must also go to my Cambridge girls, Ica Fernandez and Danica Cervantes – thank you for being there during the good and the bad. I also thank Dr. Elizabeth English for starting me on the path of mindfulness meditation. To my girlfriends Marilyn, Elaine, Rona and Jennifer, thank you for your constant support.

Finally, I would like to dedicate this work to my family and thank them for their unconditional love and kindness throughout this lengthy venture: my parents Romana and Jason, my Ate Jannie and Kuya Matt, Johnnie, Kuya Jay, Isay, Casey and Cathryn. Last, but not least, I also dedicate this work to my husband Andy for his unstinting support, technical knowhow and for embarking upon this Cambridge journey with me. This work would not have reached completion without you.

Contents

List of Figures

List of Tables

Chapter 1 Introduction

This thesis is an investigation of biodiversity changes, palaeoecological histories, and human-environment interactions in the Philippine archipelago from *ca*. 25,000 to 2000 years ago. The research utilises ecological perspectives to investigate the history of faunal communities and of human subsistence in tropical island environments. More specifically, the thesis explores the structure of local fossil faunas, examines how these animal communities change through time, and considers how such changes relate to local environments and palaeohistoric economies. The Philippines presents a unique evolutionary and ecological laboratory for understanding island biodiversity changes in Southeast Asia. The archipelago also provides long archaeological sequences that offer early records of human occupation in the island tropics. To explore specific ecological and archaeological histories in the region, I turn my focus to two large Philippine islands: Luzon and Palawan.

The low-latitude wet tropics are known to contain the most diverse of terrestrial habitats (Gentry 1992; Myers 1988; Pimm and Raven 2000; Slik et al. 2015; Barlow et al. 2018) and Southeast Asia (SEA) indeed harbours tremendous biodiversity (Gower et al. 2012). Island Southeast Asia (ISEA) notably consists of three biodiversity hotspots: Sunda, Wallacea and the Philippines (Figure 1.1). In conservation biology, 'hotspots' are described as areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of biodiversity (Myers 1988; Myers et al. 2000). The Philippines is one of only three countries on earth that, in its entirety, is considered a biodiversity hotspot. It is recognised not only as highly biodiverse but 'megadiverse'. Megadiversity countries refer to the world's top biodiversity-rich countries (Mittermeier et al. 1997). The conservation of living species in these megadiverse hotspots is imperative to preserve and maintain the earth's biodiversity.

Many island faunas are often characterised as depauperate, unbalanced and disharmonic because of the absence or low diversity of certain taxonomic groups that have low dispersal capabilities over ocean crossings (Morwood 2014; van der Geer et al. 2010). In the case of the Philippines, a dominant biogeographical perspective for most of the 20th century viewed it as a 'fringing archipelago' (Brown and Alcala 1970; Dickerson et al. 1928). In this view, archipelagos near a continental source are expected to show an 'immigrant pattern' of faunal distributions. Islands like Palawan are considered as dispersal corridors whereas islands like Luzon are viewed as the tail ends of island chains and are expected to be depauperate (see discussion in Brown et al. 2013a; Diamond and Gilpin 1983). Nonetheless, recent studies of Southeast Asian islands show unexpectedly high levels of diversity and endemism. Islands vary considerably due to their geological histories, and unbalanced island faunas do not necessarily mean that they are species poor. Indeed, several large tropical islands have been recognised as highly biodiverse. Such is the case for Luzon, Mindanao and Sulawesi (Achmadi et al. 2013; Brown et al. 2013b; Heaney et al 2016a; Rowe et al. 2016). In Luzon alone, half (n=28) of the known native non-volant mammals (n=56) only became known to science in the last two decades (Heaney et al. 2016b). The herpetological diversity of Luzon is also high at over 380 species known, 74% and 80% of which are endemic for reptiles and amphibians, respectively (Brown et al. 2013b). It is also projected that more than 100 species await discovery and description with ongoing reptile and amphibian studies in the archipelago (Brown et al. 2013a). These findings indicate a very high rate of species discovery that is said to match discovery rates in Brazil and Peru, areas that are significantly larger than the Philippines.

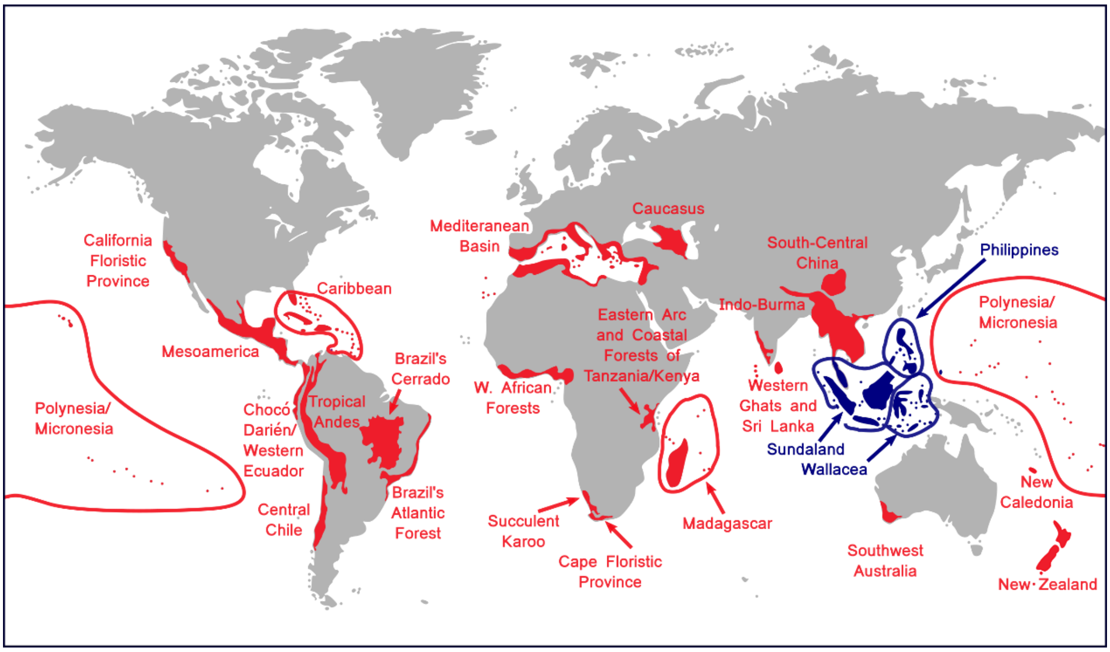


Figure 1.1 Map of the world's 25 biodiversity hotspots highlighting the three hotspots in Island Southeast Asia: Sundaland, Wallacea and the Philippines (after Myers et al. 2000).

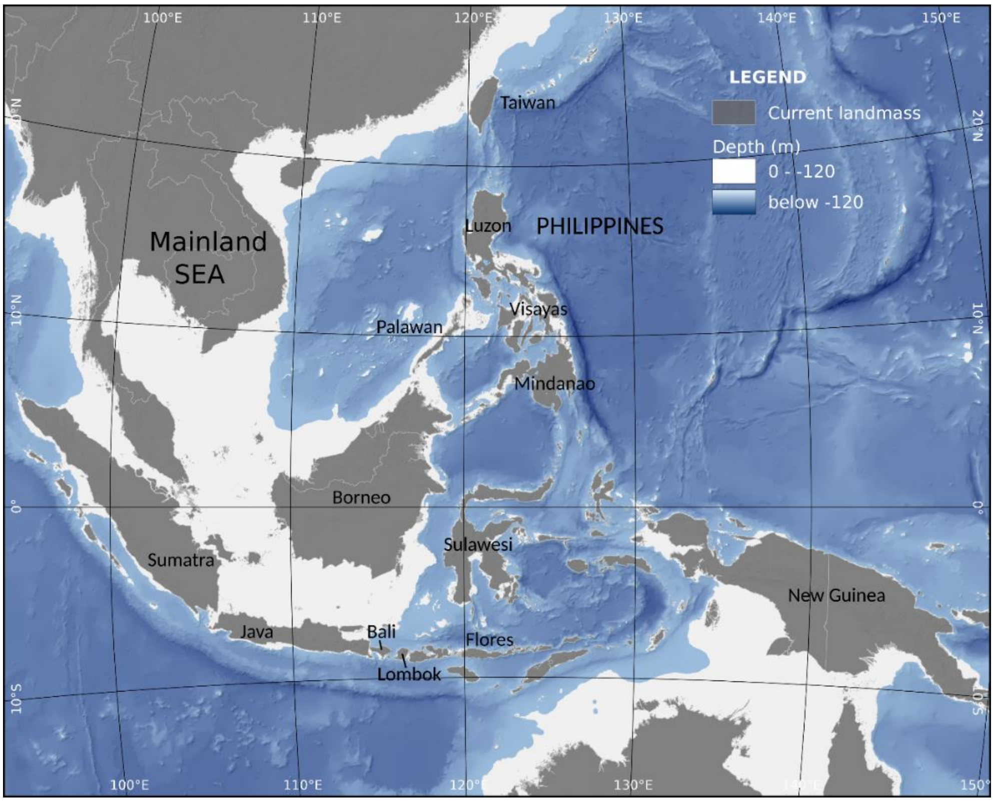


Figure 1.2 Map of Southeast Asia (SEA) showing Luzon and Palawan Islands in the Philippine archipelago. Drawn by J. Villasper.

Given this potential for studying large tropical islands, the thesis focuses on two Philippine islands: Luzon and Palawan (Figure 1.2). Luzon is an oceanic island whereas Palawan is a continental shelf island. Luzon (18° to 12° N and 119° to 123° E) is the largest and most populous island with a land area of 104,688 km^2. Palawan Island (11° to 8° N and 117° to 120° E) is the fifth largest island measuring 11,785 km^2. The two islands present contrasting tales: Palawan presents continental (Sundaic) faunal affinities, while Luzon has a true oceanic island fauna. The Philippine archipelago is located at the interface of the Asian and Australasian faunal zones, where biogeographers contend is the sharpest faunal demarcation on the planet (Brown et al. 2013; Lomolino et al. 2016). A classic biogeographic description comes from Alfred Russell Wallace's (1881: 4) *Island Life* where he illustrates the conspicuous contrast between the faunas of Bali and Lombok (Indonesia):

"*But here are some more striking cases even than this, of the diversity of the productions of countries not far apart. In the Malay Archipelago there are two islands, named Bali and Lombok, each about as large as Corsica, and separated by a strait only fifteen miles wide at its narrowest part. Yet these islands differ far more from each other in their birds and quadrupeds than do England and Japan… Bali has red and green woodpeckers, barbets, weaver-birds and black-and-white magpie-robins, none of which are found in Lombok, where, however, we find screaming cockatoos and friar-birds, and the strange mound-building megapodes, which are all equally unknown in Bali.*"

These comparisons typify the differences between the faunas of Sunda (Bali) and Wallacea (Lombok), and the water gap between the two islands forms the southernmost boundary between the two regions. Further north, the story of the transition between Palawan and the oceanic Philippines is lesser known. Nonetheless, this is an equally compelling story, and the contrast between Luzon and Palawan is striking. These two large islands harbour impressive biodiversity and endemism due to their larger land area and topographical complexity. These factors, among others, produced the megadiversity that is now known for the Philippines (Brown et al. 2013b; Heaney 2001; Heaney et al. 2016a; Rickart et al. 2019). The story also grows more interesting as new living species continue to be described for both islands (e.g. Balete et al. 2015; Hutterer et al. 2018; Welton et al. 2010). In the latter regard, the fossil record of these remarkable faunas is little known, and the zooarchaeological record has the potential of providing insights into the evolutionary and ecological histories of these faunal communities.

Much of our understanding of these faunas relies on data on modern biotas. However, various authors have already observed that many modern faunas are heavily transformed faunas, largely due to human impacts (Helmus et al. 2014; Steadman 2006; Zalasiewicz et al. 2011). In this light, palaeozoological records are necessary for understanding not only the history of these faunas but also the biological patterns and processes prior to the Late Pleistocene colonisation of *Homo sapiens.* There has been greater recognition that fossil records are necessary for assessing baseline faunal structure and assembly, and these have implications for modern conservation planning (Barnosky et al. 2011; van der Geer et al. 2017; Lyman 2012; Stegner and Holmes 2013). Baseline ecological data include the confirmation of native versus non-native species, which can be ascertained by archaeological evidence for animal translocation (e.g. Heinsohn 2003, 2010). Such records are also critical for understanding the processes of defaunation that now pervade the Anthropocene (Dirzo et al. 2014).

The archaeological and archaeofaunal records of ISEA are also important because they provide exemplary case studies on human adaptations in tropical rainforest and equatorial island environments. Tropical rainforests have been previously viewed as hinterland habitats or even barriers for human occupation (Bailey et al. 1989; Boivin et al. 2013; Headland and Bailey 1991; Hutterer 1983). Archaeological evidence from Southeast Asia, South Asia and Melanesia demonstrates that modern humans occupied tropical rainforests during its expansion beyond Africa during the Late Pleistocene from at least 49,000 years ago (Barker et al. 2007; Roberts and Petraglia 2015a; Roberts et al. 2015; Summerhayes et al. 2010). Beyond this recognition, there is a need to investigate human behavioural repertoires amidst the variety of habitats within tropical rainforest and tropical island environments. The view of tropical rainforests as primeval and unchanging has previously permeated archaeological and anthropological literature (see Mercader 2002), whereas ecologists have long recognised the complexity of habitats within tropical rainforests (Richards 1996; Whitmore 1992). Moving beyond notions that such environments were barriers to occupation, we can now re-frame the discourse to explore the complexity of adaptations entailed in the human colonisation of these 'forests of plenty' (Mercader 2002; Roberts 2017). The Pleistocene colonisation of Island Southeast Asia and Melanesia also presents important thresholds for our species, such that these colonists are referred to as 'first mariners' (Connor and Veth 2000) or 'first islanders' (Bellwood 2017). To these ends, Luzon and Palawan offer some of the oldest records of human occupation in ISEA, which lend substance to the exploration of these research themes.

To summarise, the study of Late Quaternary faunal assemblages of the Philippines contributes to a number of palaeoecological, biogeographic and archaeological questions. The rationale for choosing the Philippines – and Luzon and Palawan Islands, in particular – is as follows:

1. Philippine faunal assemblages provide an opportunity to investigate the biogeographic and evolutionary history of an archipelago recognised as one of the world's richest hotspots of biological diversity, as well as harbouring the highest concentration of endemic terrestrial vertebrates per unit land area on Earth (Brown et al. 2013b, Heaney et al. 2016b). The tropics are known to disproportionately harbour a large amount of global biodiversity (Barlow et al. 2018), and this has partly to do with high diversity coupled with high endemism, such as that observed for the terrestrial faunas of the Philippines (Heaney et al. 2016b; Justiniano et al. 2015; Lomolino et al. 2016). The zooarchaeological analysis aims to contribute to the understanding of diversity and endemism patterns observed today in the archipelago.

2. The focus on Luzon and Palawan Islands particularly illuminates on the palaeoecological comparison of oceanic (Philippine/Wallacean) and continental (Sundaic) island faunas, respectively.
3. Luzon and Palawan Islands also hold the longest archaeological sequences in the archipelago, and as such the periodisation of Philippine archaeology has been based on these two islands. The sites chosen for this study serve to fill in certain temporal gaps in the Late Quaternary faunal and archaeological sequences of the archipelago.
4. The Philippines also provides long sequences of human occupation in the island tropics of Southeast Asia. These sequences offer long records of environmental change, and in this thesis, emphasis is placed on the Last Glacial Maximum, the Pleistocene-Holocene transition and the Late Holocene. These sequences also provide human subsistence records in tropical island environments and tropical rainforests, as well as evidence for long-term human impacts in these ecosystems. The focus on two islands of Luzon and Palawan can also offer insights into local trajectories of human behaviour in these island settings.
5. The study of human impacts on tropical islands across the Holocene builds upon the author's previous research on large mammal extinctions on Palawan Island (Ochoa 2009; Ochoa et al. 2017; Piper et al. 2008, 2011). This current study further examines extinction dynamics and other impacts such as the translocation of Sundaic mammals to an oceanic island (Luzon).

1.1 Research Questions

Based on these biogeographic, palaeoecological and archaeological premises, the thesis asks two main research questions:

1. What are the processes that influence Late Quaternary biodiversity changes in tropical island ecosystems of Southeast Asia?

2. What were the behavioural responses and environmental impacts of human groups living in the tropical island environments of Southeast Asia?

The thesis aims to explore long-term ecological and evolutionary histories as may be evident in the faunal record. More particularly, it aims to analyse palaeoecological dynamics as they relate to local faunas, human adaptation, and human ecological knowledge systems in the past. To these ends, the thesis will consider the theoretical interface of 'ecological' disciplines that inform zooarchaeology. At one end of the spectrum are palaeoecology, biogeography and conservation biology, while on the other end are human behavioural ecology and ecological/environmental anthropology.

The first research question forms the *palaeoecological* component of this research. Firstly, the investigation of biodiversity dynamics and changes must tackle the baseline query relating to the composition and structure of local faunal communities. From these data, we can ask: what insights can zooarchaeological records of ISEA shed on fundamental biogeographic and evolutionary processes in island environments? With previous Holocene records of large mammal extinctions reported from Palawan Island (Ochoa and Piper 2017, Piper et al. 2011), it is of interest to investigate whether Philippine terrestrial vertebrate biodiversity decreases after the Pleistocene-Holocene transition at ca. 11,700 years ago. During the Holocene, one driver of faunal change was the human introduction of non-native taxa into island environments (Heinsohn 2003; Pimm et al. 2014; Tershy et al. 2015), yet these processes remain largely unresolved for the biodiversity hotspots of SEA. This factor, in turn, relates to the second research question, which aims to probe possible human impacts on local faunal communities. More broadly, the second question relates to the *human ecological* component of the research. The analysis of long-term subsistence records aims to examine the behavioural responses and adaptive repertoire of modern humans colonising and occupying the changing tropical environments of ISEA.

1.2 Thesis Structure

The thesis is divided into nine chapters. Chapter Two lays down the research context and intellectual landscape in which the thesis took root and evolved. This chapter tackles the biogeographic data for the Philippine archipelago and the palaeoenvironmental background for ISEA from the Late Pleistocene to the Holocene. Chapter 2 also delves into the archaeological record of modern humans in ISEA. This discussion begins with the earliest evidence of modern human occupation of the region and surveys the tropical subsistence record of ISEA. The chapter ends with a discussion of the concepts of indigenous knowledge (IK) and indigenous ecological knowledge (IEK), as they are applied in archaeology.

Chapter Three outlines the research framework, materials and methods chosen for this thesis. The *ecological framework* used here hinges on four ecological perspectives employed across the disciplines of biology, archaeology and anthropology. To operationalise this framework, I present the zooarchaeological materials and toolkit of the thesis, consisting of the study sites, vertebrate assemblages and faunal analytical methods.

Chapter Four provides the archaeological background for the Philippines, with particular focus on Luzon and Palawan Islands. This chapter describes the three main study sites – Pilanduk, Minori and Musang Caves – and presents how these sites are apt for the ecological agenda of the research. Comparative sites in both islands are also presented, along with an overview of the faunal assemblages within these sites. The chapter also provides the first set of results of the thesis, with the re-excavation and re-dating of Pilanduk Cave.

Chapters Five and Six present the core zooarchaeological and morphological data for the vertebrate assemblages of Palawan and Luzon, respectively. The results are presented in the format of an *account of species*, which facilitates the discussion of the relevant biogeographic and archaeological significance of mammal taxa identified in the assemblages.

Chapter Seven provides a biogeographic synthesis of the archaeofaunal data and addresses the research question pertaining to Late Quaternary biodiversity changes. The chapter combines the zooarchaeological data from the three study sites with published faunal studies to present biostratigraphic sequences for the Philippines. The chapter examines in detail the ecological processes contributing to faunal and palaeoecological changes across the Holocene.

Given the palaeoecological data presented in Chapters Five to Seven, Chapter Eight provides the zooarchaeological subsistence data for the three assemblages. A zooarchaeological synthesis is also provided by augmenting the primary data with published data from Philippine comparative sites.

The thesis concludes with Chapter Nine, in which a summary of the palaeoecological and zooarchaeological findings and conclusions are presented. These are appraised within the broader regional and theoretical setting of the research. To end, avenues for future work are offered.

Chapter 2 Biogeography, Palaeoenvironments and Human Palaeoecology in Island Southeast Asia

2.1 Introduction

This chapter provides the broad research context in which this thesis has developed. The first section presents the background for the biogeographic, palaeoenvironmental and geologic history of the Philippines and Island Southeast Asia. The second section deals with the archaeological record of modern humans in the region, along with evidence for foraging practices across different tropical environments. Based on the subsistence record of ISEA, the last section brings in the concept of indigenous ecological knowledge, with an overview of its theoretical context within anthropology, conservation and development studies.

2.2 Sunda, Wallacea and the Philippines

Island Southeast Asia is comprised of over 26,000 islands spanning across modern-day Malaysia, Indonesia, Papua New Guinea, the Philippines and Taiwan. These islands fall into three main biogeographic divisions: Sunda, Wallacea and Sahul (Figure 2.1). The Sunda region consists of the Southeast Asian mainland and islands lying on or attached to the Sunda shelf. Covering over 1.8 million square kilometres, Sunda is known as the largest area of shallow submerged continental shelf outside of the polar regions (Hanebuth 2000; Molengraaff 1921). Maximum exposure of the shelf is estimated to have occurred during Pleistocene glacial maxima and this exposed land mass is called Sundaland (Molengraaff 1921; Voris 2000). To the east, the Sahul shelf forms another shallow and drowned continental mass, consisting of the Australian continent and New Guinea. Between these two continental shelves are the oceanic islands of Wallacea. In general, Sunda has an Asian placental mammal fauna, Sahul has an Australasian marsupial fauna, and Wallacea has endemic oceanic faunas with a mixture of Asian and Australasian influence.

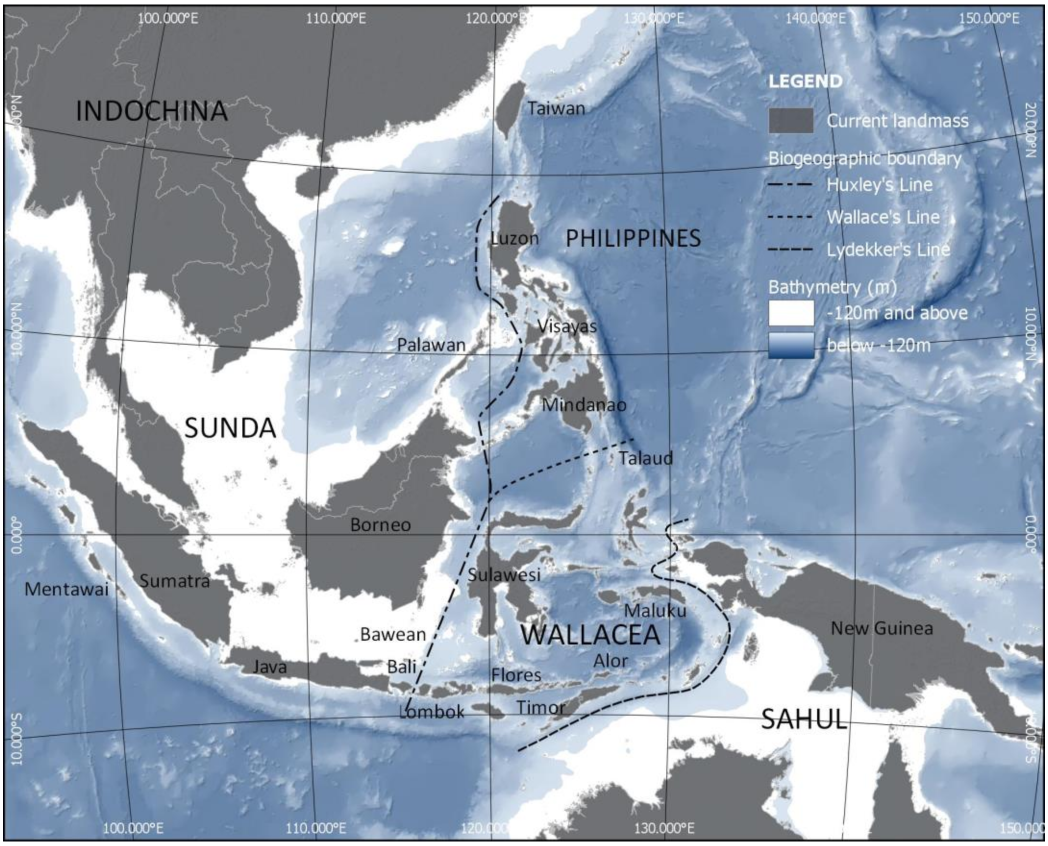


Figure 2.1 Map of Southeast Asia showing present-day land distribution, biogeographic regions, biogeographic boundaries and the major islands mentioned in the text. The -120 m isobath approximates the possible extent of land masses during the Last Glacial Maximum. Map drawn by J. Villasper.

The biota of ISEA has long fascinated scientific communities, particularly since Alfred Russel Wallace's explorations and narratives of the region (Wallace 1859, 1869, 1876). Such was the impact of Wallace on classical zoogeography that one of these regions – Wallacea – was subsequently named after him (Dickerson et al. 1928). Huxley (1868) also coined the term Wallace's Line, which was originally drawn by Wallace crossing through the Makassar Straits and across the Celebes Sea between Mindanao Island (of the Philippines) and the Talaud Archipelago (of Indonesia). Huxley's modification (Huxley's Line) of the original line drawn by Wallace grouped the oceanic portion of the Philippines in Wallacea, but apportioned Palawan Island westward of this line to the Sunda region. As a consequence of these drawn boundaries and depending on the faunal classes used, the Philippines is sometimes considered as its own zoogeographic region separate from Wallacea, whereas in other instances, it is considered a part of Wallacea.

The physical and environmental setting of the Philippine archipelago lies in the wet tropics and characterised by the biome of tropical and subtropical moist broadleaf forests (Wikramanayake et al. 2002). Seasonality is largely influenced by rainfall and can vary across islands. Luzon and Palawan has a mean annual rainfall of 1500-3000mm (Baillie et al. 2000; Heaney et al. 2016a). Two prevailing wind systems bring heavy rains to the archipelago: the northeast monsoon (October–March) and the southwest monsoon (July–September) (Yumul et al. 2011). Temperature varies with increasing elevation, but in the lowlands, it averages from 26 to 28°C. The dry season typically lasts from December to April but the duration can vary across the archipelago. Prior to extensive anthropogenic disturbance, lowlands were dominated by evergreen dipterocarp rainforest. On Palawan, the eastern half of the main island is in a rainshadow and contains moist semi-deciduous forests, along with specialised forest types in ultramafic soils, limestone and coastal areas (Wikramanayake et al. 2002). Similar specialised lowland forest habitats are also found in Luzon. With increasing elevation, montane and mossy forests are also found in the mountain ranges of Luzon.

2.2.1 Philippine Biogeography and Geologic History

The Philippines is a volcanic island archipelago that consists of five major faunal regions (Figure 2.2), all of which display substantial levels of diversity and endemism (Brown and Diesmos 2001; Heaney 1985). Biogeographic syntheses suggest that the archipelago may have the highest concentration of endemic terrestrial vertebrates per unit land area on Earth (Brown and Diesmos 2009; Brown et al. 2013; Catibog-Sinha and Heaney 2006; Heaney et al. 2016). The exceptional rates for endemism within Philippine faunas by themselves necessitate the study of these highly diverse components of the earth's biodiversity that are found nowhere else. The study of fossil faunas from Luzon and Palawan involves not just studying two island faunas; instead, it encompasses two distinct faunal regions within the Philippines that harbour unique and highly speciose ecological communities that have been generated by different processes of evolutionary diversification. From this evolutionary standpoint, the Philippines has been regarded as a model island archipelagic system that is valuable for understanding general patterns of faunal assembly and diversification (Brown et al. 2013; Heaney et al 2016a). From the palaeoecological standpoint of this thesis, the analysis of the faunal composition and structure of these island faunas form the baseline by which we can examine patterns of biodiversity distribution and faunal change during particular segments of the Late Quaternary.

A synopsis of Philippine mammals by Heaney et al. (2010, 2016a) describes at least 215 native species, 150 (70%) of which are endemic. The non-volant (non-flying) mammals comprise 103 species, 93 (90%) of which are unique to the Philippines. Endemicity is also exceptional at the generic level, with 24 of 84 genera endemic to the archipelago. Further land vertebrate summaries across the archipelago show that there are at least 440 native resident bird species (56% endemic), 111 amphibians (80% endemic) and 27 reptiles (74% endemic) (Brown et al. 2013). These high rates of diversity and endemism are constrained within a land area of only 300,000 km^2, and more species are being discovered and described. Half of the extant native mammals species (n=28) on Luzon have only been described in the last two decades, indicating a very high rate of species discovery (Heaney et al. 2016b). This rate of species discovery by modern biologists is said to be matched only by discoveries in Peru and Brazil, areas that are more than ten times the size of the Philippines.

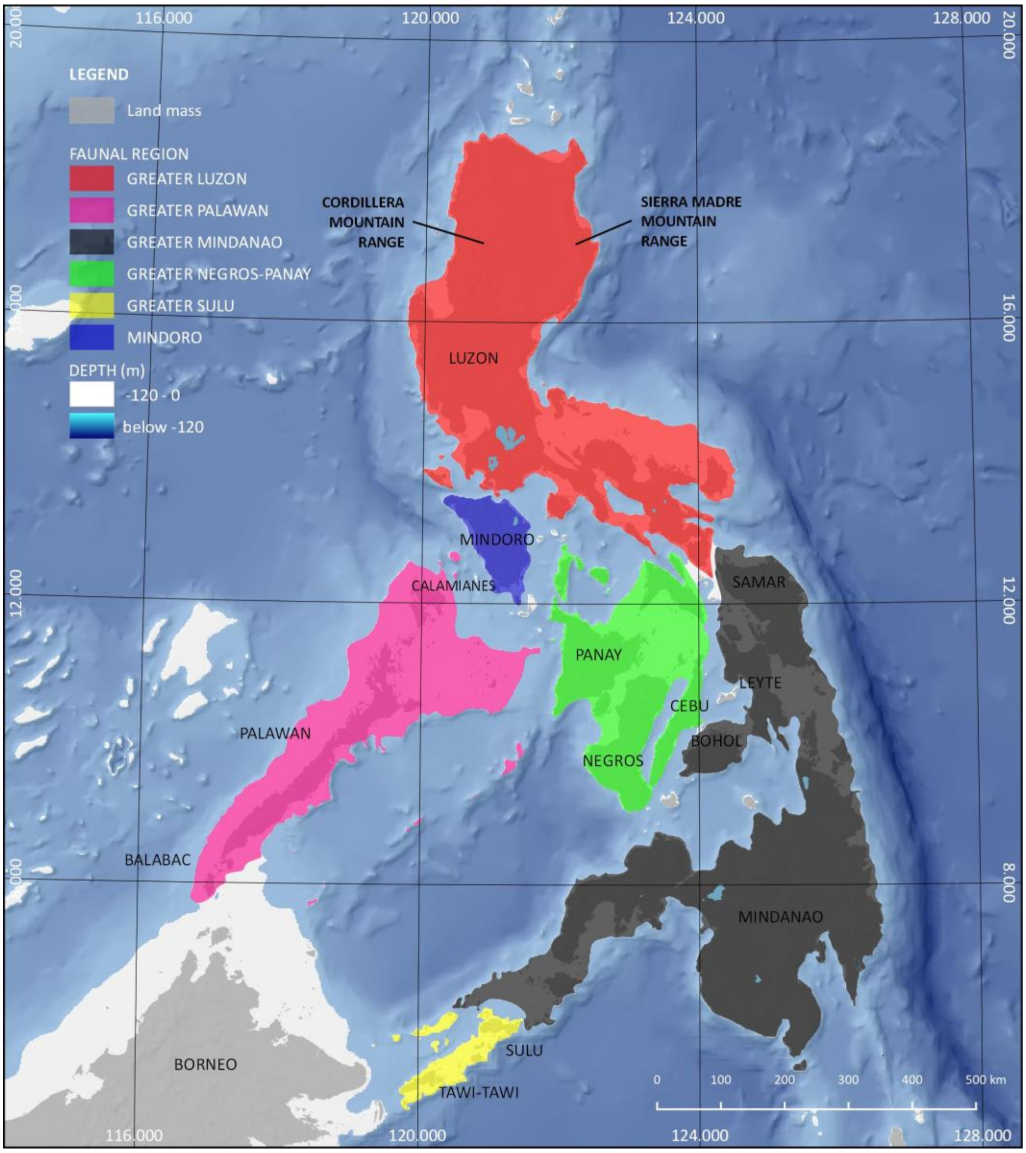


Figure 2.2 Map of faunal regions in the Philippines following Heaney (1985, 1986) and demarcated using the -120m isobath to show the maximum extent of islands during the Last Glacial Maximum. The approximate location of the major mountain ranges of northern Luzon are also shown. Map drawn by J. Villasper.

The present-day configuration of Philippine faunal regions is shaped by the geology and palaeogeography of the archipelago. The boundaries of the faunal regions correspond to the maximal extent of land exposed and connected by land bridges during Pleistocene sea-level lowstands (Figure 2.2). The Calamianes, Cuyo and Balabac group of islands would have been connected to Palawan, forming what is labelled as the Greater Palawan faunal region. In the case of Luzon, most of the coastlines would have advanced during sea-level lowstands, and several islands off the south and east coast would have been connected to form what is called Greater Luzon. As biogeographic sub-units, these connected land areas are also called Pleistocene aggregate island complexes (PAICs) (Brown and Diesmos 2001). In this study, Heaney's (1985) original labelling of Greater Palawan and Greater Luzon are used for the two PAICs.

The observed patterns of diversity and endemism on these island complexes are set against the complex geological history of the region (Hall 2013; Heaney et al. 2016a). The Philippines is situated in one of most geologically active places on earth that is often dubbed as the 'Pacific Ring of Fire'. It is an island arc system bounded on both sides by trench systems (the Manila Trench and Philippine Trench) and transected by a major strike–slip fault zone (Philippine Fault Zone) (Figure 2.3). On the east of the archipelago lies the Philippine Sea Plate and, on the west, the Sundaland-Eurasian Plate. The archipelago itself is composed of two major geologic blocks: the aseismic Palawan microcontinental block and the seismically-active Philippine Mobile Belt (PMB). The geologic history for Palawan that is provided here comes from the review by Yumul et al. (2009) and Suzuki et al. (2000). Within Palawan, two primary geological units or terranes are recognised: the North Palawan Continental Terrane (NPCT) and the South Palawan Terrane (SPT). Terranes are older tectonic fragments incorporated into younger orogenic systems (Roeder 2012). The NPCT consists of sedimentary and metamorphic formations derived from the Asian continent. Its northernmost tip and portions of the Calamianes contain the oldest reported sequences in the archipelago, which are of Upper Palaeozoic to Mesozoic in age (300 – 60 Ma). The sedimentary sequences in the NPCT are of Late Cretaceous to Eocene age (100 – 33 Ma). The NPCT was originally attached to what is now Southern China and rifted during the opening of the South China Sea basin during the Early Oligocene to Early Miocene (33 – 20 Ma). The SPT, on the other hand, primarily consists of oceanic-derived rock formations that includes the Palawan Ophiolite Complex. The major collision between the Palawan block and the PMB is estimated to have occurred during the Early Miocene to early Middle Miocene age (20–16 Ma) (Yumul et al. 2003) and reached its current position at about 5 Ma (Hall 1998; 2013). Uplift of the current mountains possibly occurred not more than 5 Ma, with

Mt. Mantalingahan (its highest peak) and other Palawan high peaks reaching their current elevations more recently.

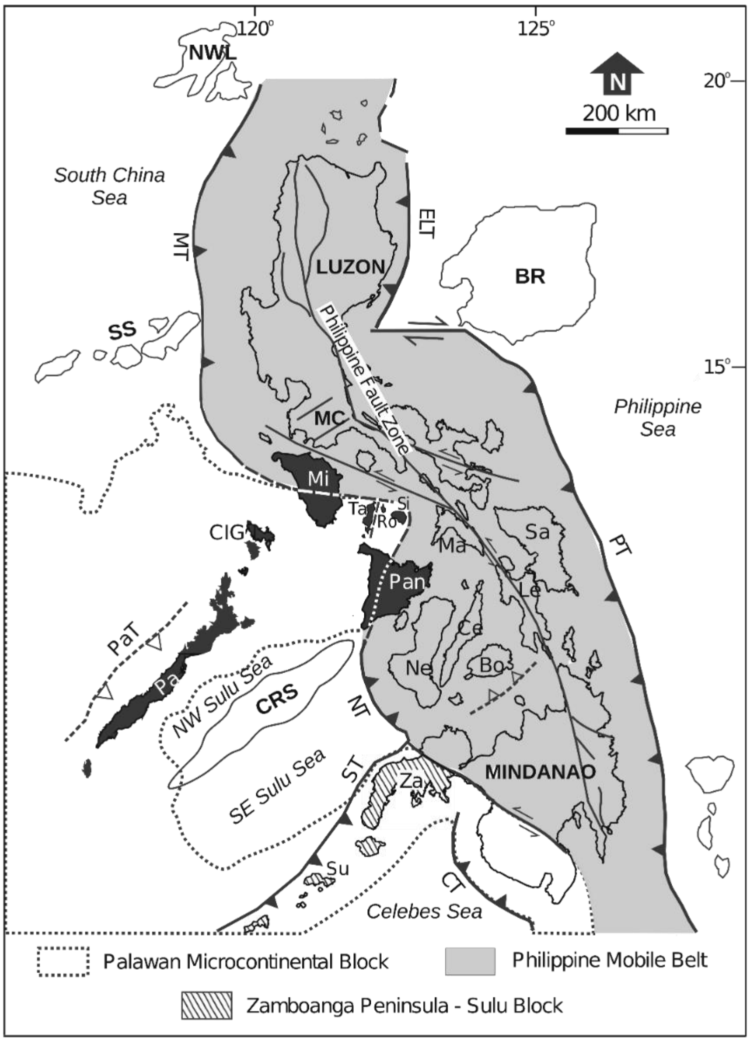


Figure 2.3 Map of the Philippine Island arc system from Yumul et al. (2009), showing the two major tectonic regions in the archipelago: the Palawan Microcontinental Block and the Philippine Mobile Belt. Legend (relevant for the discussion): MT = Manila Trench, PT = Philippine Trench, Pa = Palawan, CIG = Calamian Island Group.

Luzon Island occupies the northern portion of the Philippine Mobile Belt. The PMB is composed of Cretaceous to early Paleogene basement rocks and middle Paleogene to Quaternary sedimentary and volcanic cover (Suzuki et al. 2017). The PMB also consists of some proto-Philippine Sea Plate fragments and the major components of the basement rocks are ophiolite complexes. Based on paleomagnetic data, Luzon and other islands in the PMB have been translated northwestward and consequently, rotated clockwise (Hall 2002). The oldest geological unit in the island that existed above sea level is the Central Cordillera of the Luzon volcanic arc, emerging as a set of scattered islands during the late Oligocene to the Early Miocene (26-20 Ma). The Central Cordillera was the only portion of Luzon that had a substantial highland area from the period of 15 to 7 million years ago. The Northern Sierra Madre coalesced around 5 million years ago and much of the other areas of Luzon would join together mostly within the last three million years.

This broad outline of the geological history and configuration of the archipelago sets the stage for evolutionary processes of diversification within the Philippines. Brown and colleagues (2013: 413-414) summarise four major processes that have produced and maintained Philippine biodiversity: a) isolation of ancient colonists that diversified in precursor palaeoislands over the past 5-30 Ma; b) recent arrival of mainland-derived colonists through Pleistocene land bridges and island chains; c) stratification and *in situ* diversification along elevational gradients; and d) "species pump" action of oscillating sea levels resulting in the repeated formation and fragmentation of PAICs.

The present-day mammal fauna of Palawan Island is composed of at least 63 native species (Esselstyn et al. 2004; Heaney et al. 2010; Hutterer et al. 2018). Fourteen species (22%) are endemic to the island, 13 of which are non-volant (non-flying) taxa. Heaney (1986) observed that over 90% of Palawan's mammalian genera are shared with Borneo and that most species have their closest relatives on the Sunda Shelf. More recently, other authors have also explored Palawan's affinities with the oceanic faunas of the Philipppine archipelago. Most Palawan vertebrate taxa are indeed shared with the Sunda Shelf only, or with both the Sunda Shelf and the Philippines, but there are also vertebrate lineages that are most closely shared with the oceanic Philippines (Esselstyn et al. 2010). The latter includes, for instance, the Palawan spotted stream frog (*Rana moellendorffi*), the Palawan spadefoot toad (*Leptobrachium tagbanorum*), and the Palawan bearded pig (*Sus ahoenobarbus*) (Brown and Guttman 2002; Brown et al. 2009; Lucchini et al. 2005).

Luzon Island presents a very different composition from Palawan – an oceanic island fauna with exceptionally high levels of endemism brought about by speciation and *in situ* diversification. The mammal fauna supports at least 56 species of native non-volant species, of which 51 (93%) are endemic to the island (SIEs or single island endemics; Heaney et al. 2011, 2016a). Of these SIEs, 42 species (76%) are single-area endemics (SAEs, i.e., endemic to a single subcentre of endemism within the island). Due to its size and geological complexity, Luzon harbours eight known local subcentres of endemism (Heaney et al. 2016a; Rickart et al. 2011). They are often referred to as 'sky islands' because they are isolated mountain ranges or mountain tops that harbour distinct habitats and species. Biologists currently working on Luzon observe that no other location has as many endemic species of mammals in an area equal to or smaller than Luzon, and that no region contains as many centres of endemism (Heaney et al. 2016a). Murids comprise 84% of non-volant mammal diversity on Luzon (47 out of 56 species). Within the Philippine Muridae, two ancient clades (collectively referred to as 'Old Endemics') have diversified into an extensive range of morphological and ecological specialisations (Heaney et al. 2010; Jansa et al. 2006; Musser and Heaney 1992). Among herpetiles (amphibians and reptiles), diversity and endemism is also very high: at least 110 species are recognized, 70% of which are endemic (Brown et al. 2013).

The production of this diversity has been driven by *in situ* speciation as well as vertical diversification along elevational gradients within 'sky islands' across the archipelago. It has been observed that the species richness of non-volant small mammals increases with elevation, peaking at the transition zone from montane to mossy forest (Heaney 2001). This pattern has been observed in several mountains in different Philippine Islands that each harbour several SAEs (e.g. Balete et al. 2011; Heaney et al. 1999; Hutterer et al. 2018; Rickart et al. 2016). Philippine amphibian and reptile diversity peaks at lower elevations, at 700 - 900 m (Brown et al. 2013). This unimodal pattern of increasing biological diversity up to an intermediate elevation is a general trend observed in many studies of elevational gradients in diversity (Lomolino et al. 2016).

Pleistocene glacial-interglacial cycles comprise another factor amongst mechanisms of diversification. These cycles produced alternating episodes of isolation and connection and have long been recognized as a main driver in the evolution and assembly of Philippine biodiversity within the PAIC paradigm (Brown and Diesmos 2001; Dickerson 1928; Heaney 1985; Kloss 1929). However, within-island shifts of ecological ranges and barriers also promoted divergence and speciation, creating what is labelled as a 'species pump' mechanism (Heaney 1985; Esselstyn and Brown 2009; Lomolino et al. 2016; Siler et al. 2009). This is evidenced from deep phylogenetic splits among terrestrial vertebrate lineages and species diversity within-PAICs (=within faunal regions), suggesting that ecological factors apart from coastline and land-bridge connections are at play (Brown et al. 2013; Siler et al. 2010; Welton et al. 2010). There have been several calls to go beyond the PAIC paradigm to further understand the scale and dimensions of Philippine biodiversity (Brown et al. 2013; Esselstyn et al. 2011; Siler et al. 2009; Vallejo 2011). The PAIC theory is able to explain speciation of Philippine taxa within the last 5 million years and speciation within the geologically younger islands such as Negros and Panay; however, the paradigm finds certain difficulties for deeper phylogenetic relationships (Vallejo 2014). Although many of these processes operate within long evolutionary timescales, they give shape to the biodiversity and ecological patterns observed in the faunal regions across the Late Quaternary.

This biogeographic overview sets the stage for the analysis of terrestrial vertebrate fossils in the archaeological record (Chapters 5 and 6). It also puts into context the relevant biogeographic patterns and observations derived from the faunal analysis (Chapter 7). As described above, the zoogeography and faunal composition of Palawan Island vary significantly from that of Luzon Island, primarily due to their differing geological histories. Palawan is in fact distinct within the archipelago for its high levels of Sundaic affinities, whereas the fauna of the rest of the archipelago is truly oceanic. It is this contrast that provides for a valuable comparison of the two island faunas. Such a contrast is useful for understanding patterns of biodiversity and faunal changes in tropical island ecosystems of the region. It also allows the examination of varying human impacts in these differing settings.

2.2.2 Southeast Asian Palaeoenvironments and Sea Level Change

The archaeological records covered in this study span the last ca. 67,000 years and are subsumed under Marine Isotope Stage (MIS) 4 to MIS-1. A number of marine and terrestrial sediment cores in SEA cover MIS-4 and MIS-3. Two deep-sea cores off the island of Sumatra document the environment of the island for the last 100,000 years (van der Kaars et al. 2010, 2012). Multi-proxy palaeoecological data indicate that the environment predominantly consisted of closed-canopied complex lowland rainforest and that climatic conditions were principally everwet. MIS-4 conditions on the island were drier, with fire activity and herbaceous cover increased, and a generally weaker monsoon. Such patterns are said to persist until the onset of MIS-1. Both cores also show that the vegetation in Sumatra was most open during MIS-3 and that this phase was the driest of the last glacial rather than MIS-2. In contrast, other marine pollen records in the region identify the period between 50,000 and 45,000 as the driest phase (e.g. Makassar Strait record from Morley et al. 2004; Halmahera Island record from van der Kaars 1991; Banda Sea record from van der Kaars et al. 2000). Such incongruities imply that there are no direct links between maximum global aridity and the extent of herbaceous taxa in these records (van der Kaars et al. 2010). Another record that covers this time period comes from intramontane sediment cores from the Bandung Basin of West Java spanning the last 135,000 years (van der Kaars and Dam 1995, 1997). The coldest climatic conditions in these records span from *ca*. 52,000 to 16,000 years, reportedly characterised by the decrease of lowland trees and the expansion of montane trees.

In Niah Cave in Borneo, the 50,000-year old sequence show alternating phases where lowland forest taxa and open-ground/montane taxa varyingly dominate pollen assemblages (Barker et al. 2007; Hunt et al. 2012). The earliest part of the Niah Cave record (>46,000 BP) shows pollen zones belonging to interstadial phases. In certain pollen zones interpreted as corresponding to thermal maxima, taxa typical of lowland and swamp forests have been identified (Hunt et al. 2012). Another pre-LGM terrestrial proxy comes from Tabon Cave in Palawan Island (see Chapter 2.2.3). Re-dating of assemblages and stable isotope analysis of guano sequences by Choa (2018) has revealed that the earliest occupation levels are of MIS-3 age (ca. 39,000 BP) and that the cave environs were characterized by closed forest during this period.

Climate-driven marine transgressions and regressions have repeatedly exposed and drowned the Sunda Shelf. The Southeast Asian tropics were less prone to extreme temperature shifts during glacial-interglacial cycles, but these glacio-eustatic changes produced dramatic geographic remodeling of the region (Sathiamurthy and Voris 2006; Voris 2000). During periods of glacial maxima, the Sunda Shelf would have been exposed and islands such as Java, Sumatra and Borneo were connected to the mainland. At the LGM, the sea-level lowstand is estimated at -123 ± 2 mbpsl (meters below present mean sea level) (Hanebuth et al. 2009). Bathymetric reconstructions using Geographic Information Systems (GIS) show that Sundaland doubled in size, with an additional 2.3 million km^2 exposed during the terminal phase of the LGM (Sathiamurthy and Voris 2006). In Wallacea, numerous oceanic islands were also enlarged and/or connected to one another, such as in the Maluku Islands, Lesser Sundas and the Talaud archipelago (O'Connor et al. 2017). LGM reconstructions of Sundaland also depict a broad plain of low relief that is drained by several complex river systems (Sathiamurthy and Voris 2006; Voris 2000). Amongst these, the North Sunda River is the largest palaeoriver system identified, and it flowed and drained to the northeast (Tjia 1980).

The epicontinental seas surrounding SEA are part of the Indo-Pacific Warm Pool (IPWP), which is a major source of heat and driver of global oceanic circulation and atmospheric processes (Bird et al. 2005; Gagan et al. 2004; Webster 1994). With the exposure of the Sunda Shelf, a reorganisation of oceanic currents and heat and moisture transport systems would have been in effect in the region (De Deckker et al. 2003). It is estimated that sea surface area was only 1.6 times the size of land exposed during the LGM, whereas it is 4.1 times at present. Reconstruction of sea surface temperatures (SSTs) in the IPWP during the LGM shows a decrease of 2°- 3°C compared to the present (De Deckker et al. 2003; Gagan et al. 2004). This lowering would have led to a drier atmosphere, diminished level of cloud cover and a further cascade of atmospheric changes that would have forced the tree line to drop.

These climatic, sea-level, and geographic changes would have consequently shaped vegetation patterns across the region. From the Khorat Plateau in Thailand to the islands of Sulawesi and Java, many pollen records across the region show that it had a drier environment during the LGM (e.g. Dam et al. 2001; Hunt et al. 2016; Morley 1981; van der Kaars and Dam 1995; Wurster et al. 2010; Yang and Grote 2018). The absence of lowland peat accumulation in the region during this period also supports drier environmental regimes (Anshari et al. 2004; Dommain et al. 2014). Such data have been used to support the hypothesis that a savanna corridor existed in the central region of Sundaland, as well as on the western flank of the Philippine archipelago, following Heaney (1991). Pollen, geomorphological and other environmental proxies for the LGM appear to support such a scenario, along with the contraction of closed forests (Bird et al. 2005; Gathorne-Hardy et al. 2002). It has been pointed out, though, that comparable palynological studies in the central part of the Sunda Shelf are lacking, and so it remains open to interpretation whether such a savanna corridor existed (Morley 2018). Among available LGM proxies, rainforest refugia are argued for several regions such as Sumatra (Stuijts et al. 1988; van der Kaars et al. 2012), Borneo (Gathorne-Hardy et al. 2002; Hunt et al. 2012) and the northern edge of the Sunda Shelf (Sun et al. 2000). Climate modelling (Cannon et al. 2009) and tree population modelling for dipterocarps (Raes et al. 2014) propose that the climate of central Sundaland was possibly suitable to sustain dipterocarp rainforest, contrasting with the hypothesis of a transequatorial savanna corridor. Morley (2018) suggests that more seasonally dry vegetation types, such as semi-evergreen and deciduous forests, may have been possible instead of open savanna vegetation. More recently, stable carbon isotope records from bat guano sequences in Saleh Cave lend support to the presence of savanna vegetation in equatorial Borneo for much of the last 40,000 years (Wurster et al 2019), contrasting with other environmental proxies on the island indicating rainforest refugia.

The warming trend after the Pleistocene led to a suite of palaeoenvironmental changes including sea level transgression, a strengthening of the Asian monsoon, and the expansion of forested environments (e.g., van der Kaars and Dam 1997; van der Kaars et al. 2000; Kershaw et al. 2007; Wang et al. 2008). This shift from cold/dry to very warm/humid conditions is supported by speleothem records from Borneo (Partin et al. 2007) and Flores (Griffiths et al.

2009) showing evidence for an increase in precipitation. The sea continued to rise and inundate the Sunda shelf: at the beginning of the Holocene, sea levels were at around -48 m and the rise continued to levels even higher than present during the mid-Holocene high-stand (Horton et al. 2005; Maeda et al. 2004; Tjia 1996). An accelerated increase of sea levels in Southeast Asia is recorded during 14,300 -13,100 BP at 1.33 m /100 years during meltwater pulse IA (Hanebuth et al. 2000). Within this period, the most rapid record of flooding is estimated between 14,600 and 14,300 BP, when sea level rose from −96 to −80 m at an accelerated rate of 5.33 m per 100 years.

2.2.3 Palawan Island Palaeoenvironments

A number of palaeoenvironmental records from Palawan Island provide a picture of vegetation, climate and palaeogeography from MIS-3 to MIS-1 (Figure 3.1). As mentioned above, Choa's (2018) re-dating of Tabon Cave Flake Assemblages II and III (*sensu* Fox 1970) pushes the age range of these layers to 33,000 – 39,000 cal BP (see Chapter 4). Tabon Cave is located in the southern portion of the Island. Choa's (2018) stable isotope analysis of three phases of ancient cave guano deposits reveals environments that are predominantly characterised by closed forest. The youngest of these sequences corresponds in age with Flake Assemblage III at *ca*. 39,000 cal BP. It is suggested that during this period, conditions were drier than at present, with possible clearings and other open areas, although the environment was still generally characterised by closed forest.

From the LGM to the onset of the Holocene, two cave sites present evidence for changing vegetation communities on the island based on stable carbon isotope analysis of guano sequences. The first methodological attempt to obtain a proxy environmental record using tropical cave guano was applied in Makangit Cave in El Nido, northern Palawan (Bird et al. 2007). Results show that carbon-isotope values in ancient guano deposited during the LGM are indicative of a C_4-dominated grassland around the cave at this time. The data also suggest that the climate of northern Palawan was substantially drier at the LGM than at present. By the mid-Holocene, the open vegetation was replaced by C_3-dominated closed tropical forest, similar to that of the present. The same method was applied in Gangub Cave in southern Palawan (Wurster et al. 2010). The Gangub Cave guano sequence shows that closed forest was present in the area *ca*. 50,000 – 33,000 BP. Thereafter, a substantial increase in $\delta^{13}C$ values is recorded during the LGM, indicating the presence of open savanna (C_4) vegetation. Closed rainforest is said to have expanded again by *ca.* 13,500 BP. Together, the ancient guano profiles from Makangit and Gangub Caves show that the north and south of Palawan were dominated by open savanna during the LGM and rainforest refugia proposed by other authors (Meijaard 2003; Cannon et al. 2009) must have been severely reduced (Wurster et al. 2010: 15510).

Marine cores off the coast of the southern Philippines present further palaeoenvironmental evidence from MIS-2 to the present. The first is a high-resolution planktonic $\delta^{18}O$ record from the Sulu Sea, which provides a record of SST change in the last ca. 25,000 years (Rosenthal et al. 2003). The data suggest that SST during the LGM were cooler by 2.3 ± 0.5°C and that this rose to approximately modern levels by the beginning of the Holocene.

A marine pollen record from the Davao Gulf off the southern coast of Mindanao Island also provides evidence for the last *ca.* 30,000 years (Bian et al. 2011). The base of this record indicates that vegetation cover was dominated by tropical upper montane and lowland rainforests, although the lower montane rainforest was suppressed, along with open herbaceous swamp and mangrove vegetation. The pollen record further suggests that upper montane vegetation expanded to lower altitudes, with a concomitant increase of herbaceous cover. The data are consistent with other Palawan and regional proxies reflecting cooler and drier conditions during the LGM. By the Early Holocene, there is a recorded reduction in montane and herbaceous taxa, suggesting the onset of warmer and wetter climatic conditions. Relatively high levels of herbaceous pollen are recorded during the Late Holocene, which suggests a more open environment than in the Early Holocene. However, the area was still generally covered by tropical lowland rainforest at this period.

The only terrestrial pollen record for Palawan comes from the >5000-year Makinit peat sequence in El Nido, northern Palawan (O'Donnell 2016). This record shows evidence of marine regression and hydrological fluctuations that are likely related to ENSO cyclicities. In contrast to the Holocene guano sequences described above, this pollen record details the persistence of open landscapes in northern Palawan during the last 5000 years, with minor evidence of closed forest after 2750 cal BP. Such data may relate to other palaeoclimatic proxies indicating ENSO (El Niño - Southern Oscillation) intensification from *ca.* 3000 cal BP (Gagan et al. 2004). However, O'Donnell (2016) does not speculate further on anthropogenic versus natural causes of open vegetation regimes due to problems of equifinality of pollen signatures.

The geographic configuration of Palawan during the Late Quaternary is also crucial in building the palaeoenvironmental history of the island. Like many other islands in ISEA, the maximum exposure of Greater Palawan during the Pleistocene occurred during sea-level low-stands. Because of the Sundaic affinities of its fauna, the question of a land bridge with Borneo is also of long-standing interest. The maximum depth separating Palawan from Borneo is measured at 145 m across the Balabac Strait, making it unlikely that a connection existed during the LGM when sea levels were lowered to -116 to -123 m. GIS-based reconstructions of Palawan's palaeocoastlines by Robles et al. (2015) suggest a minimal connection may have been present in the Middle Pleistocene at *ca*. 420,000 BP. This is based on the data from Rohling et al. (1998) suggesting that ice volumes during the glacial period at *ca*. 450,000 BP may have been ~15% greater than at the LGM and greater than at any time during the last 3 million years (Bird et al. 2007; Lambeck et al. 2002). Along with biogeographic and fossil evidence (Heaney 1985, 1986; Piper et al. 2011; Reis and Garong 2001), the most recent data indicate that this episode in the Middle Pleistocene may have been the most recent time a land connection existed between Borneo and Palawan. The GIS reconstructions (Robles et al. 2015) also estimate that post-LGM transgression from 19,000 to 14,500 BP would have drowned approximately 4033 km^2 of Greater Palawan (at a rate of ~92 km^2/100 yrs). The onset of the Holocene, when sea levels stood at about -48 m, is possibly marked by a change in the local hydrological regime of Ille Cave, as reflected in its geoarchaeological history. At *ca.* 13,000-12,000 BP, a long phase of stream deposition ceased and cave deposits became more organic and dry (Lewis et al. 2008). The GIS coastline reconstructions also further show that the appearance of mid-Holocene shell middens in several Palawan sites was brought about by the formation and proximity of mangrove forests during the sea-level high-stand.

2.2.4 Luzon Island Palaeoenvironments

For Luzon Island, there are fewer palaeoenvironmental proxies available. Two terrestrial pollen records are known (Figure 3.1). The first comes from a 7000-year core from Paoay Lake in the northwestern portion of the island (Stevenson et al. 2010). This record reflects vegetation changes in the surrounding coastal plain and the adjacent Central Cordillera range and Ilocos mountains. There is no direct pollen record available for the archaeological assemblages covered in the study, which are located in the northeast portion of the island and at the foothills a separate mountain range, the North Sierra Madre. At *ca.* 6500-5000 BP, submontane forest disturbance is observed in the Paoay record, characterised by high values for *Pinus*. Charcoal is abundant throughout the Paoay record, but its highest values appear to coincide with the *Pinus*-related disturbance during the mid-Holocene. *Pinus* values increase once again after 4200 BP, but the percentage input does not return to values recorded in the pre-5000-year levels until after 1000 BP.

The only other Luzon pollen record comes from Laguna de Bay (Ward and Bulalacao 1999). This lake is situated at the southwest section of the island and also southward of the Central Cordillera. There is minimal representation of pine pollen in this record, since the prevailing southwest monsoon prohibit accumulation from pine forests in the Central Cordillera. The Laguna de Bay record indicates forest decline at *ca.* 5000 BP, which parallels with the Paoay record. The results from both pollen studies are interpreted as climate-driven changes, possibly during a period of higher temperature and lower rainfall in the mid-Holocene. For the Paoay record, it is suggested that forests appear to have slowly recovered in the succeeding 3000 years. In contrast, forest recovery is not observed in the Laguna de Bay record; instead, grass and charcoal concentrations continue to increase after 2500 BP.

Related to the palynological data are sea surface salinity records developed from fossil and modern coral data from the South China Sea (SCS) (Yokoyama et al. 2011; see Figure 3.1). This 6600-year old record was taken off the Currimao coast of northwest Luzon, approximately 50km to the south of Paoay Lake. The data suggest an increase in salinity that is attributable to less precipitation in the northern SCS. The cooler and drier SCS, in turn, is connected to the enhanced Asian Monsoon and the northward shift of the inter-tropical convergence zone. The analysis by Yokoyama and colleagues runs parallel with studies near Hainan (west coast of SCS) (Sun et al. 2005) and in the Great Barrier Reef (Gagan et al. 1998) that higher sea surface salinity is recorded across the IPWP region at least until 4400 BP.

These palaeoenvironmental records are crucial for understanding the ecological histories of the island faunas (see Chapter 7). They also form the broad canvas for human occupation and adaptation in the region from the Late Pleistocene to the Holocene. The overview that follows begins from the earliest modern human colonisation of ISEA and continues into the Holocene.

2.3 Modern Human Adaptations and Tropical Foraging in Island Southeast Asia

The behavioural repertoire and technological flexibility of *Homo sapiens* is given breadth by the Late Pleistocene records of Southeast Asia in the form of tropical foraging strategies and maritime adaptations. Mounting evidence has come to light, particularly in the last decade when there has been an upsurge in Palaeolithic research in the region. This regional record is providing a more diverse picture of human adaptability and alternative views on human 'modernity'. SEA has not traditionally been in the forefront of discussions on the Upper Palaeolithic, largely because of persisting descriptions of 'primitive' and 'conservative' lithic industries that date back to the descriptions of Movius (1948). Southeast Asian and Australasian lithic tools do not conform to formal types known from other regions of parallel ages and currently do not permit differentiation of human groups or tool traditions in the region (Moore and Brumm 2007; Pawlik 2009; Xhauflair et al. 2016). Some authors explain this phenomenon based on the loss of technological diversity with distance from Africa owing to stochastic effects and founder effects (Lycett and Norton 2010; Mellars 2006). Others see this as a refutation of the perceived inevitability of the technological sequence seen in Africa and Eurasia (Moore and Brumm 2007). Further explanations suggest that technological developments happened in other media – such as in plants, in the form of the 'bamboo hypothesis' (e.g. Pope 1989; Solheim 1972; Xhauflair et al. 2016), and in shell tools (Szabo et al. 2007). The 'Upper Palaeolithic' evidence in the region comes from a variety of tropical environments, ranging from the caves of continental Borneo, Java and Vietnam, to the oceanic islands of the Philippines and Timor, and further afield to the highlands of New Guinea (Barker et al. 2007; O'Connor and Bulbeck 2014; O'Connor 2015; Rabett 2012; Summerhayes et al. 2010). This regional record has consequently challenged conventional assumptions regarding the behavioural modernity of our species and is providing insights into the lifeways of foragers that successfully colonised and inhabited these diverse environments.

2.3.1 Modern Humans in Island Southeast Asia

The earliest unambiguous fossil evidence for modern humans in Island SEA is the ‘Deep Skull’ from Niah Cave in Borneo, dated at 45,000–39,000 cal BP (Barker et al. 2007; Barker and Farr 2016). In mainland SEA, Demeter et al. (2017) report cranial remains attributed to *Homo sapiens* from Tam Pa Ling Cave (Laos), with an age range of 63,000 to 44,000 BP. In the Philippines, human remains from Tabon Cave are suggested to be of similar age, having been dated by uranium-series techniques to 47,000 +/- 11,000 years ago (Detroit et al. 2004). On Luzon Island, Callao Cave produced a single human third metatarsal fossil of greater antiquity and was provisionally ascribed to *H. sapiens* (Mijares et al. 2010). The fossil is associated with hunted faunal remains showing cutmarks and is dated by uranium series and electron spin resonance methods to between 67,000 and 52,000 years ago. More recently, additional fossils have been described and this fossil human has been ascribed to a novel species, *Homo luzonensis* (Detroit et al. 2019). In this thesis, the focus is on modern humans, but the Pleistocene record of Callao Cave also presents an opportunity to examine subsistence modes of an endemic island hominin and compare this to *H. sapiens*.

Claims for a much older presence of modern humans come from the continental island of Java, specifically from the Punung locality where a human premolar is designated as *H. sapiens* (Storm et al. 2005). The Punung III breccia, and consequently the tropical rainforest Punung fauna, has been dated to 128 – 115 ka BP (Westaway et al. 2007), suggesting that *H. sapiens* may have arrived in Southeast Asia during the last interglacial. This MIS 5e age coincides with several fossil finds from southern China. In Tongtianyan Cave, Liujiang, a modern human cranium is reported to have an age between 111–139 ka (Shen et al. 2002). Zhiren Cave in Guangxi Zhang also produced dental remains ascribed to modern humans with a minimum age of 113-100 ka (Liu et al 2010). More recently, a larger fossil sample of teeth (N=47) from Fuyan Cave, Daoxian is more definitively ascribed as *H. sapiens* (Liu et al. 2015). The age of the fossils is bracketed between 120,000–80,000 year ago based on dating of speleothems and biostratigraphic association.

2.3.2 Subsistence Strategies in Island Southeast Asia

The current corpus of archaeological data for the region provide greater detail into the lifeways and technologies of *Homo sapiens* populations by *ca*. 50,000 years ago. In this review, I turn my focus specifically to the earliest records found in Island Southeast Asia. As noted by O'Connor and Bulbeck (2014:11), tools made of organic materials and subsistence remains demonstrate the use of sophisticated composite tools, plant exploitation strategies, and capture technologies for prey taxa. This is exemplified by the 50,000-year old record of Niah Cave in Borneo, which shows evidence from the earliest occupation levels of habitat-tailored foraging, trapping and projectile hunting technologies for terrestrial fauna, tuber digging, plant detoxification and forest burning (Barker et al. 2007; Barker and Farr 2016). It also provides one of the oldest dated examples of unequivocal rainforest foraging in the Indo-Pacific region. Gathered plants included a wide range of rainforest taxa of roots, tubers, palms, fruits and nuts, including toxic varieties which needed leaching techniques prior to consumption (Barton et al. 2016; Barton 2005; Paz 2005). The diverse terrestrial vertebrate taxa also indicates a variety of hunting and trapping methods used to exploit different habitats surrounding the cave system (Barton et al. 2009; Rabett et al. 2006). Bone tools also appear at the base of the Niah cultural deposits (N=3), and become much more abundant (N=77) in the Terminal Pleistocene and Early Holocene (Rabett 2005; Piper and Rabett 2009).

The work in Niah has also extended into several sites in the Kelabit highlands of central Borneo (Barker et al. 2017; Jones et al. 2013; Hunt and Premathilake 2012). From ca. 7000 years ago to the second millennium AD, there is evidence of pollen changes and disturbances that are indicative of forest clearance, sago management and, later on, mound building. At 10,000 years ago, there is also early evidence of the translocation of *Metroxylon*, a sago taxon native to New Guinea (Hunt and Rabett 2014). The long histories present link to the present, particularly to the *molong* system of plant management and forest stewardship of the Penan foragers and to antecedent farming practices and mound-building among the Kelabit (Brosius 1991; Janowski and Langub 2011). Nonetheless, the extensive record also shows practices that have no known modern analogues. Such a case is presented in the differential butchery practices of viverrids and monkeys at Niah (Piper and Rabett 2016) and the possible translocation of sago palms from upland ridges to valley bottoms in the Late Holocene (Barker et al. 2017).

In the oceanic islands of Wallacea, complex maritime technologies are necessary for colonisation and there is growing evidence for it. The occupation of Wallacea, Near Oceania and Australia necessitated separate open-sea crossings from a few tens to a few hundred kilometres. Actual remains of ancient watercraft technologies have not yet been reported; however, what has been archaeologically visible is evidence for coastal and marine resource exploitation, especially in places where coastlines were relatively stable throughout the Late Pleistocene (Erlandson 2001; Robles et al. 2015). Earliest examples derive from Jerimalai and Lene Hara in East Timor (O'Connor et al. 2002, 2011) and Leang Sarru in Talaud Island (Ono et al. 2009). In Jerimalai rockshelter, evidence for pelagic fishing is traced back to 42,000 years, and earliest fish hook manufacture is dated between 23,000 and 16,000 years BP (O'Connor et al. 2011). Such early dates are significant not only for the region, but for the global seafaring record of *Homo sapiens.*

In terms of aquatic resources and tool technologies, the molluscan record plays a central role. The Jerimalai fish hooks are made of sea snails of the genus *Trochus*. Early shell artefact production is also present in Golo Cave (Gebe Island) by 32,000-28,000 BP, where it is observed that the knappers were producing more sophisticated tools from *Turbo* opercula compared to their lithic counterparts in the same site and period (Szabo et al. 2007). The exploitation of molluscs as food expands in the record of SEA by around 40,000 years ago, with variable habitats being explored throughout the Pleistocene and Holocene (Szabó and Amesbury 2011). Another notable example is from the 35,000-year old site of Leang Sarru rockshelter in the Talaud Islands. The faunal record of the Pleistocene is exceptional in that it consists solely of marine shellfish, with no fish or terrestrial remains (Ono et al. 2009).

Further into Melanesia, the Late Pleistocene record of New Guinea presents some remarkable evidence for human occupation of tropical highland forests. The 50,000-year old record of the Ivane Valley provide evidence for early arboriculture or forest management practices (Summerhayes et al. 2010; 2017). The sites are found over 2000 m above sea level and show repeated burning in areas without natural fires. Archaeobotanical data indicate the exploitation of *Pandanus* nuts and yams.

Of particular relevance to the PhD research are sites dating to the MIS-2 (29,000-11,700 BP) because of the reported LGM age of one of the main study sites in the thesis (Pilanduk Cave) and the reported ages of comparative sites (Callao and Ille Caves). Some of the sites in Nusa Tenggara (Lesser Sundas) are already mentioned above, and here I enumerate a few others, with particular reference to sites from the LGM (25,000-18,000) and their subsistence data. LGM sites are relatively few in the region, compared to Terminal Pleistocene and Early Holocene sites. In the Philippines, Callao Cave of northern Luzon has a 26,000-year old layer with elongated or blade-like lithic implements (Mijares 2008). This is slightly older than the LGM, but it is the only other Philippine site (apart from Pilanduk Cave) dated around this period so far. Exploitation of forest products in Callao Cave is said to be evident from parenchymatous tissues of tubers and starch grains. The lithic tools are said to be comparable to those found in the 17,000 year old levels of Hagop Bilo rockshelter on Borneo (Bellwood 1988; O'Connor and Bulbeck 2014). Nonetheless, with the announcement of *H. luzonensis*, there is uncertainty with regards to the ascription of which human species resided in the Callao Complex during this period due to the absence of human remains in this layer.

In Java, Braholo Cave contains well-preserved LGM faunal assemblages, which show the prevalence of animals adapted to an open environment in the LGM (Amano et al. 2015; Simanjuntak 2004). This is said to contrast with the subsequent predominance of arboreal and semi-arboreal species during the onset of the Holocene. In Sulawesi, Leang Sakapao and Leang Burung 2 show occupation levels between 30,000-25,000 years ago, but appear to have been abandoned at the height of the LGM (Bulbeck et al. 2004). Freshwater shells are said to be predominant over vertebrate faunal remains in the sites.

Terminal Pleistocene and Early Holocene sites across the region (after *ca*. 16,000 BP) show increase in intensity of occupation and in the abundance of tropical rainforest taxa. These are evident for example in the Niah Caves of Borneo (Barker et al. 2007; Piper and Rabett 2016), Hang Boi in northern Vietnam (Rabett et al. 2009), Song Terus in Java (Semah et al. 2004) and Ille Cave in Palawan Island (Lewis et al. 2008). Bone technologies appear from ca. 45,000 years ago, but it was not until after the LGM that they become a more widespread component of forager toolkits (Rabett 2005, 2012). These changes occur against the backdrop of sea-level and environmental changes described above. It is at this point when tropical rainforests expand at the end of the Pleistocene that a subsistence shift to a broad-spectrum diet appears across the region (O'Connor and Bulbeck 2014).

2.3.3 Tropical Rainforest Foraging

As a subset of the Palaeolithic record, there is now growing evidence for tropical rainforest foraging and its importance in the evolution of our species (Mercader 2002; Roberts et al. 2015). Prior to this, such ecosystems where variously negatively perceived as 'green deserts' and barriers to human expansion (e.g. Bird et al. 2005; Boivin et al. 2013). This perceived marginality promoted a concurrent peripheral treatment of such environments in archaeological and palaeoanthropological investigations of human and hominin adaptations.

In Asia, a notable portion of these environments also covered areas east of the Movius Line, which were previously considered as prehistoric backwaters in lithic studies.

The ‘green desert’ debate refers to an old discourse and question raised by Headland and Bailey (1991) in a journal issue of *Human Ecology* dedicated to the question of whether hunter-gatherers have ever lived in tropical rain forests independent of agriculture. Bailey et al. (1989) explored this hypothesis by arguing that despite high biomass in tropical rainforests, edible plants, carbohydrate sources and calorie-rich fatty foods are all highly dispersed and more seasonal than generally acknowledged. Headland (1987) posed the question in terms of a starch scarcity hypothesis – also labelled as the ‘wild yam question’ – arguing that the critical limiting factor for human subsistence in rainforests was wild starch foods. Both authors came to the conclusion that at that time, there was no sufficient evidence and unequivocal cases in the ethnographic and archaeological literature of peoples living in tropical rainforests without access to cultivated foods.

The hypothesis stimulated research on tropical foraging, as well as a lot of critique. In the same volume itself, several authors present evidence contrary to Headland and Bailey’s null hypothesis. Brosius (1991) posed strong challenges to the conceptual assumptions of the hypothesis. This included the notion of ‘pure foraging,’ the dichotomy between agriculture and foraging, and the variability and ecotones in tropical forest ecosystems. Many of these objections relate to the working definition of foragers and hunter-gatherers. Brosius (1991:145) presents the case of the Western Penan in the 1980s as that of a foraging mode of subsistence “without recourse to agricultural supplements in areas mostly undisturbed by previous clearance.” Within the stewardship concept of *molong*, the Penan actively manage sago (*Eugeissona*) as their main starch source, and preferably hunt the bearded pig as a source of protein and fat.

Mercader (2002) provided critiques of these negative perceptions on tropical rainforests and instigated further studies on rainforest archaeology. This was particularly in the context of the African continent, where he suggested that *Homo sapiens* could have utilised these habitats as early as *ca*. 200,000 years ago. At this point, it was clear from other sources that as populations expanded outside of Africa, *Homo sapiens* successfully colonised and occupied such environments in Asia and into the islands of the Indo-Pacific. Over a decade on, Barton et al. (2012) and Roberts (2017) present several examples of long-term research on human-rainforest interactions, with vital papers coming from Southeast Asia and Melanesia. Indeed, despite the ‘green desert’ debates of their time, even Bailey et al. (1989) recognized that Southeast Asia presented a promising venue for exploring this question. The evidence for rainforest foraging across the Indo-Pacific region now definitively extends back into the Late

Pleistocene, with sites from South Asia (Roberts et al. 2015), Borneo (Barker et al. 2007, 2016; Bulbeck 2003), Sumatra (Westaway et al. 2017) and New Guinea (Summerhayes et al. 2010; 2017).

2.4 Indigenous Ecological Knowledge

The palaeoecological and zooarchaeological data generated in this research is also framed within the concept of indigenous ecological knowledge (IEK). This concept is often synonymously used with the term traditional environmental/ecological knowledge (TEK). TEK or IEK refers to "a cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes et al. 2000: 1252). IEK and TEK fall under the broader rubric of 'indigenous knowledge' or IK. The latter is often juxtaposed against conventional 'western knowledge' or 'Western science'. However, the epistemological distinction between indigenous knowledge and other forms of knowledge – such as western, scientific, etc. – has been rightly critiqued and collapsed (Agrawal 1995; Ellen 2004; Sillitoe 1998). It is recognized that there are substantial methodological and substantive overlaps among these knowledge systems, and all are themselves culture-bound (Ellen and Harris 2005). Nonetheless, the use of the concept persists, particularly in the literature of development studies and conservation to refer broadly to technologies and practices developed in local niches, and which may or may not be unique to a particular community or culture (Stump 2015: 2).

The term 'indigenous' is highly contentious in archaeological and anthropological discussions. The term indigenous is typically laden with political and moral significance, and is often used as an identifying marker to protect rights and interests of particular groups. Arguably, it is in these struggles over rights and territories that IK and IEK can be located and where it takes on relevance and meaning (Li 2005). It has been observed that it appears impossible to use 'indigenous' in a morally neutral or apolitical way (Ellen and Harris 2005). Conceptually, the term can force an oppositional logic of 'us and them' and more particularly, a 'hegemonic opposition' of a privileged (non-indigenous) *us* to a subordinate *them* (Ellen and Harris 2005: 2). This form of 'othering' is part and parcel of the history of archaeological and anthropological practice – and simmering underneath the notion of indigeneity are the disciplines' colonial origins. In her manifesto of 'indigenous archaeology as decolonizing practice', Atalay (2006: 284-85) explains several levels on which this manner of 'othering' operates. Through colonial contact, European and American 'westerners' initially gained the power to study not only people distant from themselves temporally (distanced by time) but also the pasts of others who were distant from themselves culturally and geographically. As the discipline developed during the 20th century, archaeologists have utilised western epistemologies to study the lifeways of others. This research has been carried out by scholars using western methodologies and generated in western-dominated forms of discourse and practice. Such epistemologies and methodologies have then been transferred to and engaged by local archaeologists, who can often find themselves reproducing works based on these dominant archaeological paradigms.

Beyond the confines of archaeology and anthropology, the notion of indigeneity also carries much ambiguity and conflicting ethical weight. The label of IEK and IK entails belonging and ownership to indigenous peoples. The most widely cited 'working definition' of indigenous peoples was devised by Special Rapporteur José Martinez Cobo (1986-1987) in the landmark United Nations study of the Problem of Discrimination against Indigenous Populations:

> "Indigenous communities, peoples and nations are those which, having a historical continuity with pre-invasion and pre-colonial societies that developed on their territories, consider themselves distinct from other sectors of the societies now prevailing in those territories, or parts of them. They form at present non-dominant sectors of society and are determined to preserve, develop and transmit to future generations their ancestral territories, and their ethnic identity, as the basis of their continued existence as peoples, in accordance with their own cultural patterns, social institutions and legal systems." (Martinez Cobo 1987: paragraph 379)

Under Philippine Law, the definition of indigenous cultural communities or indigenous peoples (ICCs or IPs) is defined under the Indigenous Peoples Rights Act (IPRA) of 1997:

> "ICCs and IPs - refer to a group of people or homogenous societies identified by selfascription and ascription by others, who have continuously lived as organized community on communally bounded and defined territory, and who have, under claims of ownership since time immemorial, occupied, possessed and utilized such territories, sharing common bonds of language, customs, traditions and other distinctive cultural traits, or who have, through resistance to political, social and cultural inroads of colonization, non-indigenous religions and cultures, became historically differentiated from the majority of Filipinos." (Republic Act No. 8371, Chapter 2, Section 3)

The notion of historical continuity is contingent to these definitions. In the case of the Philippines, pre-colonial historical connections (i.e. before the 16th century) of IPs help characterise indigeneity. Evidence for this part of the Philippine past is largely in the remit of archaeology, particularly in prehistoric archaeology. This is due to the fact that historical narratives of the Philippines overwhelmingly dwell on 'colonial periods' of the last few centuries, and gloss over the deeper past. Given this problematic state of Philippine historiography, archaeology has the potential to uncover 'precolonial' past(s) and reveal indigenous lifeways prior to Spanish and American colonisation. Such acts of reclaiming one's past (or multiplicities of the past) are essential to the project of decolonisation.

Archaeological attempts to characterise and redefine indigenous pasts coalesce in the praxis of indigenous archaeology. This encompasses active engagements and collaborations of archaeologists and local communities in the practice and interpretations of archaeological research. Nicholas (1997:85) defined indigenous archaeology as "archaeology done with, for, and by indigenous people". Smith and Wobst (2005) have also advocated for an archaeology shaped by indigenous knowledges such that it helps to decolonise the discipline. This practice of archaeology is growing today because indigenous peoples are actively creating "counter-discourses that speak back to the power of colonialist and imperialist interpretations of the past" (Atalay 2006: 294). It is further argued that indigenous archaeology need not only be done by Indigenous or Aboriginal persons. Instead, as part of decolonising methodologies, the research agenda of indigenous archaeology encompass critiques of power imbalances in mainstream archaeological practice that marginalise indigenous views and approaches that seek to make archaeology more relevant to indigenous peoples. To this end, Nicholas (2010) has called for 'the end of indigenous archaeology', i.e. to de-centre it from the margins and incorporate it into the mainstream of the discipline.

De-centering indigenous contributions and promoting multivocality in interpretations of the past are also critical elements of a postcolonialist agenda (e.g. Damm 2005; Deloria 1997; Lane 2006, 2011; Smith 2013). It has been argued that despite the colonial origins of the discipline, archaeology can be a form of anti-colonial practice through its attempts to recover unwritten pasts of former colonial subjects and challenge the denigration and dismissal of the history of indigenous groups (Lane 2011:11). The usage of the IK concept is situated within this broader agenda of decolonisation and active engagements and partnerships of archaeologists and local communities in archaeological research and practice. The privileging of normative and universalized forms of archaeological and scientific knowledge has historically led to the marginalisation of IK forms. The languages (dominantly English or other European language) and methodologies used are intrinsically tied to knowledge production.

In the process, these acts of extractive documentation and translation of archaeological data can have the effect of *dislocating* these forms of knowledge and separating them from an audience that equally deserves recognition – the local and indigenous communities living in the landscapes and places where archaeological sites are situated.

Indigenous knowledge forms have also been used in other spheres of archaeology. Stump (2013: 268) identifies three key areas in the literature wherein applied archaeology and indigenous knowledge interact. The first involves conflicts and confluences between archaeological and local interpretations. The second point deals with the question of local ownership of land, technologies, and archaeological materials. The third area covers the interests within development, conservation, and ecology in the potential efficacy and sustainability of local resource-use strategies. The field study that I conducted in the Philippines and the broader context in which the archaeological research occurs involves all three aspects. However, in the analyses and interpretations offered in later chapters, the thesis will largely deal with the third area regarding ecology and conservation. To a lesser degree, this work will also touch upon the first area involving archaeological and local interpretations of the past.

2.5 Conclusion

This chapter has provided a broad review of the palaeoecological and archaeological context of the thesis. This review lays down the conceptual setting for the ecological framework that shall be discussed in Chapter 3. The biogeographic and palaeoenvironmental data reviewed set the stage for the palaeozoological aims of the thesis and underscore the research links to modern biodiversity studies. As shall be seen in succeeding chapters, the combination of data from palaeobiology and neobiology have specific implications for biodiversity conservation issues. The archaeological record for ISEA and the overview on IEK frame the human palaeoecological components of the thesis. I set out the theoretical parameters of the thesis within the framework described in the succeeding chapter.

Chapter 3 Research Approach and Methods

3.1 Research Framework and Rationale: Ecological Approaches to Archaeological Faunas

This PhD thesis is an ecological study that employs the concept of *ecology* in a number of ways. As common in many archaeological endeavours, the project draws from the intellectual fields of biology and anthropology. The first use of the ecology concept is informed by zooarchaeology's niche in palaeoecology. Archaeozoology and palaeozoology (*vis à vis* zooarchaeology) are typical terms used by archaeologists who study faunal remains and focus on biological and ecological questions (Bobrowsky 1982; Legge 1978; Reitz and Wing 1999). The roster of quantitative methods in palaeozoology largely overlaps with zooarchaeology (Lyman 2008), although many morphological and morphometric approaches are borrowed and developed from the life sciences. One main thrust of the thesis is in describing and characterising past biodiversity as observable in the time scale of the archaeological record. This is fundamental, since, as described in previous chapters, the Philippine archipelago harbours remarkable mega-biodiversity. These islands also have a rather impoverished Quaternary palaeoecological record, and this hampers our understanding of long-term biological processes shaping faunal communities. Because we, as archaeologists, are interested in periods and time scales involving humans, another research aim covers the interactions of humans and their environments – particularly the impacts of environmental changes on human societies and the impacts of human activities on ecological habitats.

This brings us to the second element of this approach, which deals with ecological conservation. The term *ecological* typically has the connotation of conservationism in biology, anthropology and development studies. It is often connected with the notion of sustainability and the ability to persist in the same environment over long durations (Harkin and Lewis 2007). It is also a politicized concept entangled in power and identity struggles in present-day states and communities over access to natural resources. In the archaeological record, we can obtain evidence to disentangle and substantiate this perceived immemoriality of time and the persistence of traditions. It is also particularly valuable for investigating how human activities have affected environments across time.

With respect to the discourse on environmentalism, palaeozoology has long had the agenda of addressing and aiding present-day conservation efforts (Dietl and Flessa 2009;

Lyman 1996; 2006; 2015; Wolverton and Lyman 2012). The long-term data that palaeozoologists generate have much potential to contribute to major concerns in conservation biology, such as wildlife management and restoration ecology. Although some neobiologists have previously expressed reservations about the utility of palaeobiological data (e.g. Hofreiter and Barnes 2010; Houston and Schreiner 1995), palaeobiological knowledge has been increasingly appreciated and applied for conservation issues. The fossil record is still the most direct physical source of evidence for ecological and biogeographic histories of taxa and communities. Any nuanced understanding of present-day communities and forecasting of future change is contingent on the complex record of the past. For instance, Williams and Jackson (2007) observe that 'no-analog' communities (i.e. ecological communities that are compositionally unlike modern communities and hence have no modern analogues) are pervasive in the Quaternary palaeobiological record. In the case of island communities, van der Geer and colleagues' (2017) study of palaeo-island mammalian communities has shown that prevailing models of biogeography can prove inadequate if based solely on extant biotas. Different biogeographic patterns arise when long-term evolutionary processes and the impacts of humans on island faunas are accounted for in these models. These palaeobiological studies allow for more accurate models and accounts of biodiversity changes and biogeographic patterns observed at the present. These, in turn, can inform present-day conservation decisions and forecasting of ecological responses to future environmental changes. One example of how palaeozoological data have been given a high profile in conservation biology is in the controversial conservation approach of re-wilding (Donlan et al. 2006; Fernández et al. 2017; Lyman 2015). In the Asia-Pacific region, Louys et al. (2014) provide case studies for nine species to make a case for rewilding the tropics.

For the Philippine archipelago and much of Wallacea, there remains the basic task of describing and accounting for the highly biodiverse island biotas. There is increasing documentation that extant island communities are remnants of heavily impacted assemblages, many of which were transformed by humans (Ellis 2011; Steadman 2006; Zalasiewicz et al. 2011). Studies are needed to ascertain how further back in time from the Anthropocene such transformations occurred (see Waters et al. 2016). Animal translocation is a known phenomenon across Wallacea (Heinsohn 2003), but further work is needed for the Philippines in identifying invasive taxa. Furthermore, the timing and impacts of these translocation events remain largely undocumented in the region. Another critical issue pertains to defaunation, which refers to the loss of wildlife species and populations (Dirzo et al. 2014). Once again, this historical process remains understudied in a region of such extraordinary biodiversity. These fundamental records are necessary to provide more accurate ecological baselines or benchmarks for current biodiversity and conservation studies, and this is a major aim of the palaeoecological component of the PhD thesis.

The third element for an ecological approach relates to human ecology. In this sense, the term *ecological* pertains to having recurring, structural relations with the natural world (Harkin and Lewis 2007). One of the foundations of zooarchaeological methodologies and hunter-gatherer studies lies in human behavioural ecology (HBE). A principal assumption of HBE is that foragers are proficient and skilled, and this assumption is applied through the reductionist methodology of constrained optimisation (Winterhalder 2001; Winterhalder and Smith 2000). Another assumption is that people's behaviour is aimed at maximizing reproductive success (Kelly 2007, 2013). These models largely derive from optimal foraging theory (OFT), which ecologists originally developed for various animal taxa (Charnov 1976; MacArthur and Pianka 1966; Stephens and Krebs 1986), and was subsequently picked up by anthropologists for its potential in human foraging studies. The methodological and explanatory utility of HBE and OFT has been questioned on various fronts (e.g. Ingold 2000; Zeder 2012). Nonetheless, HBE is still widely used for its methodological tools for inquiry into human subsistence choices. In fact, as Gifford-Gonzalez (2018) notes, some HBE studies have provided some of the most rigorously supported cases for people violating HBE predictions, leading researchers to find other explanations beyond fitness and return rates. This reveals a powerful aspect of the application of HBE models when cases are exposed where people do not behave like 'optimal foragers' (Gifford-Gonzalez 2018). Put another way, HBE presents a set of null hypotheses, and deviations from such patterns can provide novel insights into human behaviour and sociality.

In this light, familiar methods in the zooarchaeological toolkit used to test HBE and other processualist hypotheses have also been applied to questions of social relations. The latter forms the explicit agenda of social zooarchaeology (Marciniak 2005; Orton 2012; Russell 2011). With the availability of contextual information, zooarchaeological data can shed further insights into various scales of social interactions. Intra-site analysis of faunal assemblages from spatially discrete units can potentially provide insights on food sharing, feasting and household relations. Inter-site comparisons can possibly shed light on questions on social inequality, identity, trade and exchange.

HBE and social zooarchaeology data can bear on the fourth element of these *ecological* perspectives: indigenous ecological knowledge (IEK). This fourth element informs the objective of analysing subsistence data and human behaviours. The theoretical domain of indigenous knowledge (IK) closely allies with that of social zooarchaeology. The ethnographic literature is replete with examples of how hunting and foraging practices provide fundamental sources of metaphors that structure relations between foragers, animals and the living world (Alves 2012; Anderson 2011; Brightman et al. 2012; Fernández-Llamazares et al. 2017; Medin et al. 1999; Sulkin 2005). Nonetheless, IK is also recognised as holistic and integrative, such that separating categories of technical/non-technical, rational/non-rational or economic/non-economic would be problematic and simplistic (Ellen and Harris 2005; Scoones and Thompson 1994). Given this, IK and IEK systems also incorporate practical, economic and functional strategies, along with symbolic and social aspects of human knowledge. Through archaeology, there is the potential to historicize IK: demonstrating its rootedness to place and exploring long perspectives on indigenous pasts. Sliding the scale from a regional archaeological perspective, I highlight here the idea that IK is *local*, i.e., "it is rooted to a particular place and set of experiences, and generated by people living in those places" (Ellen and Harris 2005). I further underscore the aspect of 'rootedness': that knowledge is contextualised within particular places and milieus and embedded within experiential spheres of human-environment interactions. In the author's first language, Filipino, indigenous translates to *katutubo*, where the root word (tubo) connotes 'to be rooted in' and 'to grow'. This characteristic underscores the spatio-temporal context of both archaeological knowledge and IK, and serves as a fundamental (and obvious) reference point for the usage of IK in archaeological discourse.

3.1.1 *Kaninong Kasaysayan*? (Whose history?)

Why use the concept of 'indigenous' and indigenous knowledge in a zooarchaeological project? One simple answer is to emphasise the fact that part of what we try to uncover in archaeology are histories of indigenous populations who live in particular locales. These ancient populations may or may not have direct descendants among present-day indigenous peoples, but an important link is the locale or environment on which lifeways are anchored. There is a firm need to locate and place IK and IEK, whether contemporary or of the past. An important goal of the research is to provide 'long perspectives' with regards to histories of human-environment interactions. The emphasis on diachronicity stems not only from attempts to understand the evolution and adaptation of cultures but also to highlight the historicity, specificity and temporal depth of indigenous knowledge systems. In Filipino, history translates into *kasaysayan* – in its essence, it does not distinguish between history and 'prehistory' (Paz 2003). It derives from the root word "saysay", referring to 'sense' or 'meaning'. The utility of archaeological knowledge for *kasaysayan* has been increasingly recognised (Salazar 1998; 2004). One definition of k*asaysayan* is *"salaysay na may saysay"*, i.e. history as 'meaningful narrative' (Navarro 2000). In this light, forms of archaeological knowledge can help us make sense of and give meaning to the past. This long perspective is something archaeology provides and the zooarchaeological record can offer added insights about ways of knowing about the past.

It is also pertinent to ask the question whose history: *kaninong kasaysayan*? On one level, we can look at Philippine nationalist discourses as forms of counter-discourses to prevailing colonialist historical narratives (see Paz 2014, 2017). At another level, these long-term historical (in the sense of *kasaysayan*) records can also be connected to the histories and knowledge systems of indigenous groups of Luzon and Palawan. In brief, I specify particular groups that are indigenous to the location of archaeological sites covered in this study and that maintain certain aspects of foraging lifeways.

In Luzon, of particular interest are the Agta and Aeta populations. They are known for their salient phenotype of small stature, dark skin and curly hair. This phenotype is shared with a few other Philippine groups such as the Ati of Negros and Panay, Batak of Palawan, and Mamanwa of Mindanao. The Agta of northern Luzon are well-known hunter-gatherers. Their genetic ancestry is not fully understood; however, they are hypothesised to be descendants of early/initial population expansions of *Homo sapiens* in the region and have significant admixture with other Philippine ethnic groups (Bulbeck 2013; Delfin et al. 2011, 2015; Jinam et al. 2017; Scholes et al. 2011; Thangaraj et al. 2003). Agta groups today combine subsistence practices of foraging and food production. On one hand, some groups show extensive foraging, small size, high mobility and few belongings, while other groups have larger size, more sedentization, more food production, and many belongings (Griffin 1984; 2013; Page et al. 2016: 4695; Peterson 1990). The Itawes and Ibanag are also local to the study area of Cagayan, northeastern Luzon. They are both lowland Christian ethnic groups that predominantly rely on sedentary agriculture.

On Palawan Island, the three main indigenous groups are the Batak, Pala'wan, and Tagbanua. The Batak share a similar phenotype with the Agta of Luzon. The Batak currently occupy the central part of Palawan, and its population has been in significant decline in the past several decades (Eder 1987, 1990; Novellino 2007). The Pala'wan and Tagbanua are perceived to originate from Austronesian-speaking populations. The Pala'wan mainly occupy southern portions of the island. They perceive themselves as divided into two groups: the upland (Pala'wan at bukid) and the lowland (Pala'wan at napan) groups (Novellino 2001). The Tagbanua mainly occupy the central and northern portions of Palawan Island. All three indigenous groups in Palawan have a heterogenous mode of subsistence that is mainly centred on swidden cultivation, combined with hunting and commercial foraging (Novellino 1998; 2001).

To summarise, it is with the four perspectives enumerated above – palaeoecological reconstruction, ecological conservation, human paleoecology and indigenous ecological knowledge – that the notion of 'ecological' is employed and explored in this thesis. A larger portion of the research involves studies on the biodiversity and conservationist aspects. Nevertheless, an exploration of human-environment interactions and ecological knowledge is also attempted using familiar methods in the zooarchaeological repertoire.

3.2 The Zooarchaeology Toolkit

An attempt to operationalise these modes of ecological inquiry using archaeofaunal assemblages requires the use of various methods in the zooarchaeological toolkit. Lyman (1994) still provides the authoritative compendium of methods in vertebrate taphonomy, but one must carefully choose among the myriad techniques depending on research questions and applicability. More recently, Gifford-Gonzalez (2018) has provided an updated overview of such methods that combines a critical assessment of their application to behavioural, ecological and social zooarchaeology questions.

Amid the multitude of zooarchaeological techniques, several authors have explicitly developed frameworks that advocate sequential implementation of taphonomic methods. Bar-Oz and Munro (2004) have proposed a 'multivariate taphonomic approach' that aims to determine the significant agents of assemblage formation and to disentangle the problems of equifinality. The framework prescribes three analytical stages (Bar-Oz and Munro 2004:203):

i) a descriptive stage that summarizes the representation of key taphonomic variables of each assemblage;

ii) an analytical stage that investigates the completeness and fragmentation of skeletal parts; and

iii) a comparative stage that evaluates taphonomic variation amongst subgroups within a zooarchaeological assemblage.

Marciniak (2005) also proposed a methodological framework that explicitly addresses the aims of interpretive social zooarchaeology. He emphasizes that the most efficient analytical strategy for investigating social dimensions of human-animal relationships is the interpretation of the horizontal distribution of skeletal parts across a settlement (Marciniak 2005: 103). To implement this strategy, a series of zooarchaeological methods must be conducted, namely: 1) taphonomy; 2) analysis of bone density and body part representation; 3) analysis of food utility indices and body part representation; 4) quantification of body part representation; 5) anatomical body part distribution; and 6) species composition. With these data in hand, the final step of a contextual analysis of the horizontal distribution of faunal remains can be conducted. The latter requires connecting the faunal data with archaeological features where they were deposited and other categories of archaeological data to ascertain their spatial and chronological associations.

The multivariate taphonomic framework of Bar-Oz and Munro (2004) is comprehensive in its scope of methods and is geared towards determining the most significant agents of assemblage formation. Marciniak's (2005) methodology may not be as comprehensive, although it is clearly geared towards investigating social relations. Expanding on these two models, Orton (2012) also proposed an analytical framework for social zooarchaeology. This framework's strengths lie in its methodological rigour and its principal aim of isolating archaeologically relevant patterns of human behaviour. The methodology proposed has five stages, working 'backwards' towards the death assemblage (taphoconoese):

Stage 1	Evidence for density-mediated attrition
Stage 2	Evidence for peri-depositional damage
Stage 3	Breakage and fragmentation
Stage 4	Visible human modification
Stage 5	Assessment of element representation

The taphonomic framework that is used in this thesis combines the work of Bar-Oz and Munro (2004) and Orton (2012). The main variation between the two frameworks lies in the sequencing of analytical tasks. This has to do with the methodological aim of both frameworks. Whereas Bar-Oz and Munro (2004) aim to characterize the significant agents of bone assembly and formation, Orton's (2012) approach aims to isolate archaeologically interesting patterns from more mechanistic taphonomic variables. However, the recommended analytical techniques for each of the stages in both frameworks are largely similar. These techniques are not themselves novel; instead they are well-known methods in the zooarchaeological toolkit (Gifford-Gonzalez 2018; Lyman 1994; Reitz and Wing 1999). What is important, nonetheless, is the critical assembly of such techniques and the analytical structure by which they are employed such that they target certain research problems. Sample size permitting, such methods are recommended for use so that some of the problems of equifinality are addressed and sound inferences about human behaviour and activities are drawn. The 'taphonomic workflow' of choice used in this thesis is further described in Section 3.5.

3.3 Sites and Materials

3.3.1 Selection of Sites

The main rationale for selecting archaeological sites was driven by the aim of comparing two island archaeofaunas that cover the temporal span of the Late Pleistocene to the Late Holocene. I identified the temporal and fossil gaps that exist within this time span and aimed to fill in certain gaps. To this end, three cave assemblages were chosen: Pilanduk Cave in Palawan Island and Minori and Musang Caves in Luzon Island (Figure 3.1).

Across the archipelago, there is a paucity of faunal studies that go back in time beyond the Holocene. In Palawan Island, existing zooarchaeological studies are nearly all from the Holocene. Only Ille Cave provided a faunal assemblage securely dated to the Terminal Pleistocene (Lewis et al. 2008). It was thus imperative to find and analyse a Late Pleistocene assemblage that ideally pushed back beyond the Terminal Pleistocene. Among all sites reported in the literature, Pilanduk Cave was the best candidate for this. I considered the site to have great potential due to its reported LGM age and the fact that Kress' 1970 excavation yielded a well-preserved faunal assemblage stored in the National Museum of the Philippines (NMP). Kress (2000) previously published dates for Pilanduk Cave that range from 25,000-18,000 BP. These dates were processed and obtained in the 1970s. The only other known archaeological site on Palawan that has Late Pleistocene levels is Tabon Cave (Fox 1970). However, the vertebrate remains from the 1960s excavations of the site have not been preserved in museum storage and many of them appear to have been misplaced during the intervening decades.

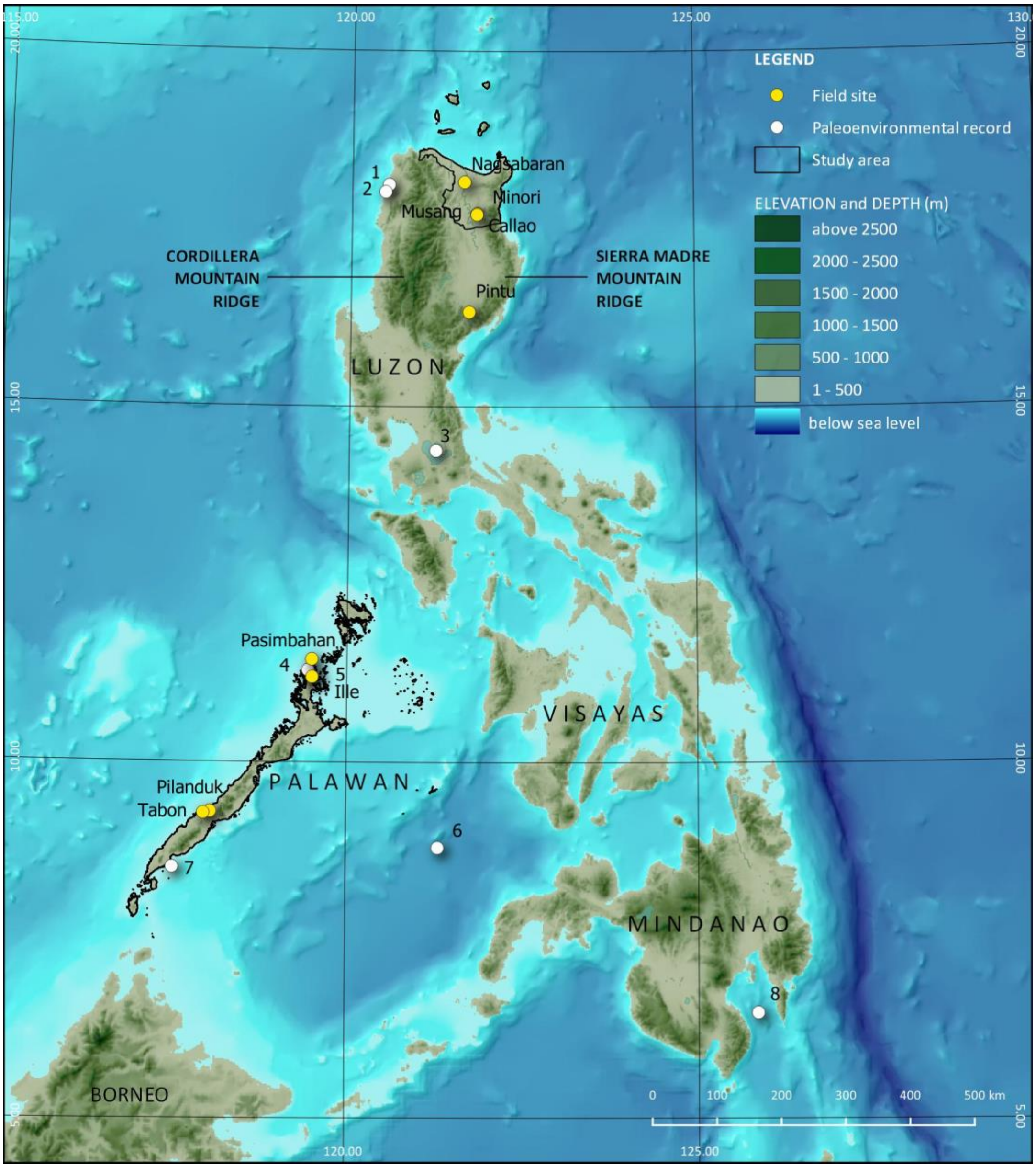


Figure 3.1 Map of the Philippines showing location of archaeological sites used in the study, along with Philippine palaeoenvironmental records described in Chapter 2: 1) Paoay Lake, 2) Currimao Coast, 3) Laguna de Bay, 4) Makinit site, 5) Makangit Cave, 6) Sulu Sea, 7) Gangub Cave, 8) Davao Gulf. Drawn by J. Villasper.

On Luzon Island, the Late Pleistocene site of Callao Cave has the oldest dated evidence of human presence in the Philippine archipelago at 67,000 years ago (Mijares et al. 2010), which has been recently ascribed to *Homo luzonensis* (Detroit et al. 2019). Callao is also the only site that has a Late Pleistocene faunal record. What the Luzon record further lacked is a continuous and well-dated Holocene faunal sequence. Published zooarchaeological work includes only two Late Holocene sites, namely, Nagsabaran open site and Pintu Rockshelter. The oldest levels for both sites are at 4500-4000 years ago. To fill the gap for a Holocene sequence, I investigated whether other known and previously excavated cave sites in Luzon had vertebrate assemblages. The NMP have long-standing projects in the Cagayan region, particularly within the Callao limestone formation where seven caves were excavated between 1977 and 1982. These were the caves sites of Rabel, Laurente, Arku, Lattu-lattuc, Callao, Minori and Musang Caves. I selected two of the sites that had the largest and better-preserved samples for the vertebrate fauna. These were Minori and Musang Caves. The Callao Cave sequence also has a Holocene component, but due to various reasons, I chose the two other sites. The analysis of materials from Callao Cave was covered by another research project and there were other specialists involved in the study of these materials. Given the time and resource constraints of the PhD project, I chose to focus on Minori and Musang Caves.

3.3.2 Excavation and Dating of Pilanduk Cave

Another key aspect of the research involves establishing a robust Late Pleistocene chronology and faunal sequence for Palawan through the re-excavation of Pilanduk Cave. Archaeological sites that date to the LGM or older are relatively rare in Southeast Asia (O'Connor and Bulbeck 2014), and hence clarifying the age and chronology of the Pilanduk record stands to be an important contribution. Kress (1977, 2000) published three radiocarbon dates for the site that range in age from 25,000 to 18,000 BP (see Chapter 4). All dates were taken from shell remains of unpublished taxonomic designation processed during the 1970s. Due to the known limitations of radiocarbon dating technology during this period particularly in relation to the calibration of shell dates, there was reasonable scepticism over the dates. Despite the limitations, the site has the largest (potential) LGM faunal and lithic assemblage known in the archipelago, based on the materials excavated by Jonathan Kress and the NMP in 1970. Re-excavation was therefore necessary in order to re-date the site using more advanced radiometric dating techniques and to provide a more robust chrono-stratigraphic anchor to the existing fossil and lithic assemblage.

The excavation was conducted during October 2016 under the directorship of Dr. Ame Garong of the NMP. Permission to excavate in the site was also given by the local government of Quezon Municipality and Barangay Maasin. The excavation team was composed of participants from the NMP, the local community of Maasin, Quezon, and the University of the Philippines (UP). Fieldwork funding was provided by the University of Cambridge Fieldwork Funds, the Evans Fund and the Anthony Wilkins Fund. Due to the logistical and resource constraints of the project, there were only eleven digging days for the project. During this short period, the team aimed to find *in situ* deposits within the site. We also aimed to uncover a spatially delimited, yet continuous, archaeological sequence that potentially covered the temporal succession previously reported by Kress (2000).

The excavation method employed was a contextual excavation approach. Deposited sediments were removed and excavated, guided by the approach of single context excavation and recording. In this approach, all features, structures, and layers are given individual context numbers. These numbers are referred to as ‘context #’ in the rest of this text. A modified version of the context recording form of the UP Archaeological Studies Program was used during the excavation. All elevation values (Z) are based on one reference point, the Datum Point of the site. To increase the resolution of archaeological recovery, dry-sieving with 2mm-mesh wires was used. Selected contexts were also targeted for wet-sieving and flotation, particularly for the recovery of archaeobotanical and microvertebrate remains. Recovered artefacts were bagged and recorded according to square, quadrant, context and depth. The archaeological finds were accessioned following the inventory protocols of the NMP. At the end of the excavation, the site was also completely backfilled following NMP protocols.

Charcoal, bone and teeth samples from the 2016 excavation were submitted to the Oxford Radiocarbon Accelerator Unit. Bone and teeth samples did not yield sufficient collagen and so all radiocarbon dates for Pilanduk Cave come from charcoal samples. Mollusc preservation was also poor and so molluscs were not selected for dating. Identification of wood charcoal samples was conducted by Jane Carlos (UP), who is also analysing macrobotanical remains from the site. Pre-treatment of samples and radiocarbon determination methods follow the protocols of ORAU. Radiocarbon dates were calibrated using OxCal v4.3.2 (Ramsey 2017) and IntCal 13 (Reimer et al. 2013).

3.3.3 Within-Site Sampling

The sampling strategy aimed to cover the entire temporal sequence documented in each site. The main study sites all have archival fossil material excavated during 1970-1983. In addition to this, new material deriving from the re-excavation of Pilanduk Cave was incorporated in the analysis. I chose material from trenches/squares with the most abundant finds that cover as much of the reported archaeological sequence and that have supporting archaeological records such as publications, inventory and excavation records. The NMP provides the repository for the archaeological records. A common problem in old collections is the loss of archaeological records and the loss of specimens. The loss of records was a significant problem for Minori Cave. Loss of records and specimens were both a problem for Musang Cave (See Chapter 4). To reconstruct provenance, specimen labels were checked against artefact inventory records (in the case of Minori and Pilanduk) and publication and excavation records (Musang), whenever available. However, it was not possible to reconstruct the original sample size retrieved during the excavations of Minori and Musang Caves because inventory records from both sites are incomplete. Further information on the available archival and published archaeological data for each site are presented in Chapter 4.

For Pilanduk Cave, I analysed a small portion of the materials excavated by Kress and the NMP, focusing on material that still retained specimen labels. The materials were stored in the site branch of the NMP in Quezon, Palawan. During the analysis in spring 2016, I unfortunately found that only a small portion of the assemblage in museum storage still retained labels and that existing site records were also insufficient to reconstruct provenance of finds. This also gave further impetus to re-excavate the site. The successful excavation of 2016 yielded sizeable assemblages from two excavation units, Trench 3 and 4 (see Chapter 4). I focused my analysis on Trench 3, which provided the longest sequence out of four excavation units opened. The Trench 4 excavation only reached up to Layer II of the site, whereas Trench 3 reached Layer IV.

For Minori Cave, I selected the two trenches that had the greatest number of remains found in storage. These two units – Squares 37 and 27 – also represent each of the two main chambers of the site, Chamber A and Chamber D, respectively. The remains from Square 37 were stored in the museum site branch in Peñablanca, Cagayan. The remains from Square 27 were found stored in the main branch of the NMP in Manila.

In the case of Musang Cave, the chosen and analysed bone assemblage come from squares G4 and G5 from the 1976 excavation of Barbara Thiel. A subsequent excavation in 1977 was conducted by the NMP. However, the excavation methodologies employed by these two teams were different. The 1977 excavation was done solely by arbitrary spits and gave no further information about archaeological layers. Only a short descriptive report was produced by the 1977 excavation and stratigraphic information was not available. In contrast, Thiel's team excavated by natural layers and 10-cm spits within the layers. Thiel's excavated material from 1976 had sufficient stratigraphic information that could be reconstructed, primarily based on her 1990 publication. The publication included a site plan, stratigraphic profile, artefact descriptions and faunal counts. The information on each bone specimen analysed primarily comes from its original bag label, which indicates the layer it came from. The information on the layers were then checked in Thiel's (1990) publication and in the excavation recording plans from the NMP archives. There was no surviving artefact inventory record, however, to verify artefact labels and reconstruct provenance.

3.4 Faunal Analysis: Identification and Quantification

The zooarchaeological recording system used in this study follows a modification of categories and attributes in the York System (Harland et al. 2003) and Bonecode (Meadow 1978). Recording of element portions follows the zonation method by Dobney and Reilly (1988). All identifications are recorded in an excel file format from which pivot tables are derived. Identifications form the core of taxonomic work, and in turn, taxonomy underpins biodiversity studies and species discovery. In this thesis, the taxonomic studies are particularly crucial due to the discovery of novel species and rare fossil evidence for extinct large mammals.

Taxonomic and osteological identifiability can have relative levels of confidence from low to high (Gifford-Gonzalez 2018). In this study, specimens that are osteologically identifiable to element (or portion of element) and that had low levels of taxonomic identifiability (e.g. large mammal, fish or avian) were included as separate categories within tallies of NISP counts. Some typical examples coming from this study are identifications of 'large mammal diaphysis (shaft)' or 'medium mammal vertebra fragment'. The cut-off used here for identifiability is when specimens could not be identified to element portion and nor could be assigned to a traditional vertebrate class of mammal, reptile, bird or fish. Such indeterminate fragments were sorted by size into categories of microvertebrate or macrovertebrate specimens. Within the mammal class, three main categories were used: large, intermediate (=medium) and small. The use of these categories is dependent on the nature of the endemic fauna of the archipelago. In most Philippine islands, the largest extant native species would be deer or pig, which are typically smaller (or dwarfed) forms compared to continental forms of the same taxa. Large mammals were further subdivided into two. Those in the size of deer and pig were tallied as 'large mammal I', and this is the most commonly observed mammal category in the assemblages. Mammals bigger than deer such as a cattle-sized bovid or tiger were tallied as 'large mammal II'. Intermediate or medium- sized mammals were those in the size range of canids, macaques and small carnivores such as civet cats and otter. Small mammals typically contain murids and bats. However, due to the phenomenon of island gigantism, giant murid species are known in the oceanic Philippines. These animals can overlap in the size range of small carnivores, such that these giant rodents were classified under medium mammal.

Taxonomic identifications were aided by morphometric analysis. For large and medium mammals, standards for measurement and nomenclature followed von den Driesch (1976) unless otherwise stated. Standards and nomenclature for murid rodents typically followed Musser and Heaney (1992) and Heaney et al. (2011). Based on previous work, the author has a database of biometric measurements of teeth and postcranial material for pigs, deer and several other native mammal taxa of Palawan. Additional data, though, were necessary for pantherines and for the native murid rodents of Luzon Island. Reference measurements were gathered from museum comparative collections of the University of Cambridge Museum of Zoology and Zooarchaeology Laboratory, Oxford University Museum of Natural History, Natural History Museum (London), and the Field Museum of Natural History (Chicago).

The main unit of quantification used in the study is the NISP or number of identified specimens. The NISP is the most basic counting unit used by zooarchaeologists and employing it allows for comparison of faunal counts across sites. Following Grayson (1984: 16), a specimen is a bone or tooth or fragment thereof. A skeletal element is a complete discrete anatomical unit such as bone or tooth (Lyman 2008:5). The NISP includes specimens identified to both element (or portion of element) and taxon. It is generally used as an estimate of relative frequencies of taxa in a faunal assemblage (Reitz and Wing 1999).

Another counting unit that will be encountered in this study is the TNF or total number of fragments, following usage by O'Connor (2008). This unit is equivalent to the NSP, or number of specimens. In this study, the TNF is mainly used for taphonomic analyses, wherein counts of identified specimens (NISP) are combined with counts of indeterminate fragments. The TNF is usually aggregated per context, temporal unit or spatial unit within an assemblage.

For various reasons, many specimens cannot be identified to either element or taxon and are considered indeterminate. Lyman (1994) notes that fragmentation has the initial effect of increasing NISP values, but as specimens are progressively broken, this leads to a reduction of NISP counts. Subsequently, fragmentation can produce an analytical absence of skeletal parts (Lyman 1994: 282). Nonetheless, what are considered indeterminate specimens retain useful taphonomic information, such as for carcass processing (Outram 2001).

As a raw counting unit, the NISP may appear to behave as a continuous, interval scale variable that has increments of one between each value (Gifford-Gonzalez 2018: 396). However, the NISP actually cannot guarantee specimen independence, since it can count more than one specimen for a fragmented element, and can also count more than one element per individual (Grayson 1984). This is the problem of *interdependence*, and accordingly, Lyman (1994) cautions that the NISP must be treated as an ordinal scale variable in statistical analyses. Based on this and other statistical criteria, non-parametric statistical tests can be more appropriate for zooarchaeological counting units.

To address the problem of interdependence, the MNI (minimum number of individuals) and MNE (minimum number of elements) are also used. The MNI is derived by identifying the most abundant element for each taxon. The MNE is an estimate of the lowest number of individual elements of a particular taxon. In this respect, the MNI estimate is based on the MNE (Lyman 2008; Marean et al. 2001). In the literature, there are a number of ways by which authors have computed the MNE (Marean et al. 2001). In this study, the MNE is calculated based on counting specimens with portions of an element that do not overlap with other specimens. The overlaps are primarily estimated based on the zonation system used. Factors such as siding, age, fusion and individual size are also taken into account when possible. Both MNI and MNE counts derive from the NISP and require a secondary calculation based on the primary quantitative data. In the case of the MNI, Lyman (2008: 70) notes that it is redundant with the NISP and that the information on taxonomic abundances within the MNI is found in the NISP. The strong linear relationship between these two units means that the MNI values can be closely predicted from NISP values. Both MNI and MNE suffer from the problem of aggregation, i.e. that different ways of aggregating or grouping specimens can produce different values. The MNE lends its main utility to the analysis of skeletal element representation and patterns of fragmentation. It is also used here to compute for another counting unit, the MAU or minimal animal unit. Following Lyman (2008:133), the MAU is derived by dividing MNE values for each anatomical part or portion by the number of times that element occurs in one complete skeleton. From the MAU, another counting unit is derived, the %MAU. Lyman (1994:255) observes that %MAU is equivalent to the value of

%survivorship that Brain (1969) originally calculated. This measure is computed by dividing all MAU values by the greatest observed MAU value in the assemblage and multiplying the results by 100. The MAU and %MAU are units that are used for the analysis of skeletal part frequencies.

3.4.1 Measures of Taxonomic Diversity and Structure

Another set of quantification units involves measurement of taxonomic diversity. Zooarchaeologists have typically used alpha diversity measures derived from ecology and applied them to archaeological assemblages. Alpha diversity measures diversity at spatially defined units, often at the level of ecological communities (Magurran 1988, 2004). In archaeology, it is commonly applied to an assemblage or series of assemblages from particular geographic regions. Archaeologists deal with a subset of the death assemblage (taphoconoese), yet we are also interested in what this can tell us about the living biotic communities (biocoenose) from which they derived. Measures of taxonomic diversity allow the assessment of assemblage structure and faunal community structure, as well as inform patterns of human subsistence.

One of the most basic measures of diversity is taxonomic richness. In the ecological literature, this is also called numerical species richness or *S,* defined as the number of species per specified number of individuals (Magurran 2004: 75). In zooarchaeology, it is often referred to as the number of identified taxa or NTAXA (Lyman 2008). NTAXA or *S* is a nominal scale measure that is also used as an archaeological measure of ecological resources utilized by human groups, wherein the variation can be measured per geographic location and per temporal period.

Another important estimate looks at how abundant each of the identified taxa are within an assemblage. This is taxonomic evenness or equitability (Magurran 1988). I use Simpson's index (D) and its reciprocal (1/D) as a measure of evenness. Faunas are said to be taxonomically even if each has the same number of individuals (Lyman 2008). The Simpson's index provides a good estimate of diversity at relatively small sample sizes (Magurran 2004). The reciprocal of Simpson's index (1/D) is attributed to be less sensitive to effects of taxonomic richness and more sensitive to dominance of the assemblage by one taxon (Lyman 2008). Low values of 1/D indicate that an assemblage is dominated by one taxon and consequently have less evenly distributed frequencies of taxa than those with higher values. Another measure, taxonomic heterogeneity, summarizes relative abundances of taxa and is a function of both richness and evenness. The conventional measure used is the Shannon-Weiner index (H). From the Shannon-Weiner index, the Shannon index of evenness (*e*) can also be derived, following the equation $e = H/\ln S$. The values of this index fall between 0 and 1, and the lower the value of *e*, the less even the assemblage. Diversity indices (Section 3.4.1) were calculated in PAST version 3.19 (Hammer et al. 2001), following (Harper 1999).

3.5 Faunal Analysis: Vertebrate Taphonomy

The taphonomic workflow (Table 3.1) employed in this research combines recommendations of the frameworks devised by Bar-Oz and Munro (2004) and Orton (2012). The main goal of the taphonomic analysis is to identify and characterise human-induced modifications in the assemblages. This involves distinguishing human and non-human agents involved in the accumulation of the assemblage and describing the effects of these agents. Stage 1 is a summary descriptive stage, as suggested by Bar-Oz and Munro (2004). A summary of taphonomic modifications is provided in tabular form in order to present an initial quantitative picture of the relevant taphonomic variables in an assemblage. Macroscopic bone surface modifications were the focus of the analysis. The bone modifications are grouped into two general categories: abiotic factors and biotic factors. Abiotic factors include mechanical and physical processes caused by water action, wind, sunlight, etc. Biotic factors include modifications produced by living organisms, including humans. Significant patterns observed in the summary of taphonomic data can be further investigated, particularly as they relate to the main agents of assemblage formation. The next three stages involve the analyses of density-mediated attrition, anatomical representation and fragmentation. Further focus is then given to patterns of anthropic modifications when available, particularly in the form of burning, fracturing and butchery marks. The details of the methods chosen for each analytical stage are further explained in Chapter 8.

Statistical analyses for morphological and taphonomic data were conducted using PAST version 3.19 (Hammer et al. 2001) and R Studio version 3.4.4 (R Core Team 2018). The R package ggplot2 (Wickham 2016) was used to analyse and visualise quantitative taphonomic data.

Table 3.1 Taphonomic workflow employed in the analysis, with references to equivalent stages in the frameworks devised by Bar-Oz and Munro (2004) and Orton (2012).

Stage	Description	Stage under Bar-Oz and Munro (2004)	Stage under Orton (2012)
1	Summary of taphonomic variables	1	2, 4
2	Density-mediated attrition	2.2	1
3	Anatomical representation	2.3, 2.4	5
4	Fragmentation	2.3	3
5	Human modifications	1	4

3.6 Conclusion

This chapter has outlined the research approach and the rationale behind the ecological framework proposed in this thesis. As outlined above, the usage of the *ecological* concept follows four perspectives: palaeoecological reconstruction, ecological conservation, human paleoecology and indigenous ecological knowledge. I have also described the faunal assemblages and the zooarchaeological methods selected for this research. These methods are implemented in the succeeding data analyses in Chapters Four to Eight.

Chapter 4 The Archaeology of Luzon and Palawan

4.1 Introduction

This chapter presents the archaeological background of the Philippines, with particular focus on the islands of Luzon and Palawan. The chapter also presents the first set of results of the thesis involving the re-excavation and re-dating of Pilanduk Cave on Palawan Island. Out of more than 7000 islands across the archipelago, Luzon and Palawan are the foci of the study since they hold the longest archaeological sequences in the Philippines. Most of the data used for the periodisation of Philippine archaeology derive from sites in these two islands (Fox 1970; Paz 2017). These are based on several decades of sustained archaeological investigations in these two islands since the 1960s. The Late Pleistocene evidence from the Philippines is an integral part of the archaeological record of tropical forest foraging, since the archipelago holds very early records of human presence both in continental (Palawan) and oceanic (Luzon) islands. These records help us understand the complexities and antiquity of such behaviours and adaptations, which lie at the centre of discussions on human modernity and diversity.

The main study sites and comparative sites are described per island. The exception is for Pilanduk Cave, which was purposely re-excavated for this thesis project and hence has its own section that provides original data regarding the results of the excavation (Section 4.4). Although the oldest study site (Pilanduk Cave) is of LGM age, the temporal backdrop of this study begins with the 67,000-year old levels of Callao Cave in Luzon, which to date hold the oldest direct evidence for human fossils in the archipelago. In Palawan Island, the oldest known archaeological site is Tabon Cave (*ca*. 50,000-30,000 years ago). Because this project will combine the zooarchaeological analysis with existing faunal records, I also present the background for Terminal Pleistocene and Holocene comparative sites in both islands and the faunal data from them. For Luzon, the main study sites are Musang and Minori Caves (Section 4.2). The comparative sites are Callao Cave, Nagsabaran site and Pintu Rockshelter (Section 4.2). In Palawan, the main comparative sites are Ille, Pasimbahan and Tarung-tarung Caves (Section 4.3). From here, I present the new archaeological data for Pilanduk Cave in a separate section (Section 4.4).

4.2 Luzon Island Archaeology

Luzon is the largest island in the archipelago and holds the oldest archaeological records in the Philippines. The archaeology of Luzon is largely anchored on the sites in Cagayan province and the Cagayan Valley (Figure 4.1). The valley is surrounded by three major mountain ranges: the Sierra Madre to the east, the Cordilleras to the west and the Caraballo to the south. It is an interarc basin that is 250 km long and 80 km wide, containing extensive Plio-Pleistocene fluvial and pyroclastic deposits (Mathisen and Vondra 1983). These deposits are divided into the Awidon Mesa and Ilagan formations.

The Cagayan Valley is long known for fossil finds of Pleistocene megafauna (Beyer 1947; Koenigswald 1958). The fossil fauna was tentatively associated with a 'pebble culture' for which von Koenigswald (1958) proposed the name 'Cabalwanian'. Following these earlier reports, Fox (1971) initiated the Cagayan Valley Archaeological Project as part of the quest of the NMP for 'Early Man' in the archipelago. During these explorations, 54 localities were identified in the valley that contained stone tools and fossils of Pleistocene mammals (Fox 1971). Many of these localities are found in the town of Solana (Cagayan province) and the adjacent town of Rizal (Kalinga province), within the Awidon Mesa formation. The fossil sites contain possible Middle Pleistocene megafauna including *Elephas*, *Stegodon*, *Rhinoceros*, and *Geochelone* (de Vos and Bautista 2001). The lithic tools found in the area were composed of unretouched flakes, choppers and other unifacially retouched pebble tools (Dizon and Pawlik 2010). However, the chronostratigraphic associations of both fossils and stone tools have not been clearly established because of alluvial transport and secondary deposition in old riverbeds (see Chapter 6 Section 2).

The cave sites that are part of this study belong to the Callao Limestone formation of Peñablanca town within the Cagayan province (Table 4.1, Figure 4.1). This limestone formation is situated in a physiographic transition zone between the Cagayan Valley to the east and the Sierra Madre to the west. The Spanish place name 'Peñablanca' ('white rock') was historically ascribed to the town due to this geological feature. The Cagayan Valley is drained by the Cagayan River. One of its tributaries, the Pinacanauan de Tuguegarao River, drains into the Peñablanca area and bisects the Callao formation into north and south sections.

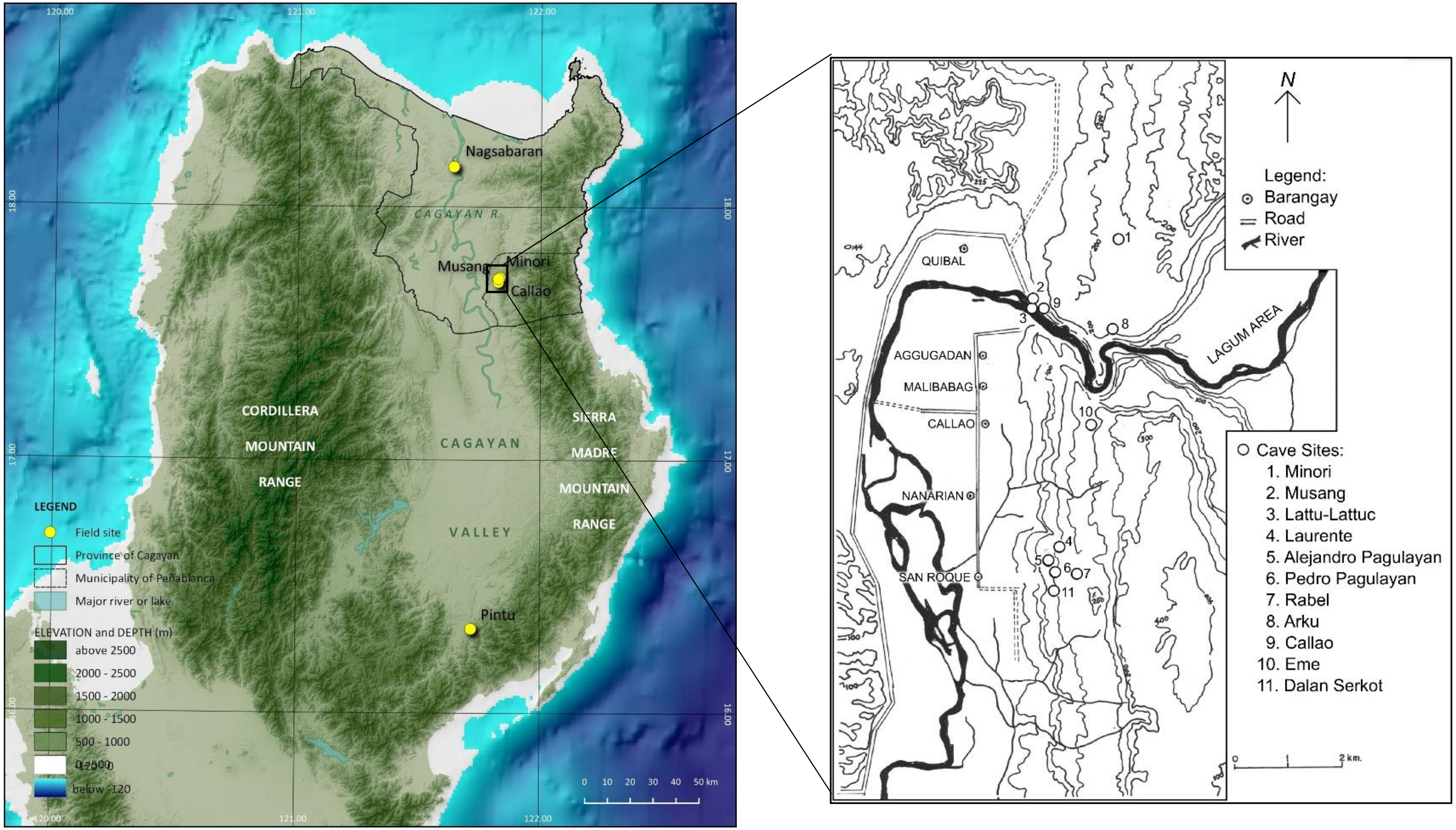


Figure 4.1 Map of northern Luzon (L) and the Peñablanca area (R) showing the location of Minori (1), Musang (2) and Callao (9) Caves and other sites. Peñablanca map (R) is modified after Mijares (2005: Figure 2). Barangay refers to local political village units. Luzon map drawn by J. Villasper.

A series of explorations were also undertaken by the NMP in the Callao formation between 1976 and 1977 (Ronquillo and Santiago 1977; Figure 4.1). At that time, 43 caves and rockshelters were identified that contained archaeological material. Following these discoveries, excavations were conducted in several cave sites between 1977 and 1982. Among the sites excavated are those included in this study: Musang and Minori Caves.

As synthesised by Mijares (2001, 2005, 2008), the Peñablanca excavations revealed two major cultural levels in the Holocene. The older horizon is from the Mid to Early Holocene with flake assemblages of andesite and chert, faunal remains mostly consisting of deer, pig, and freshwater gastropods. These older deposits were found in Musang, Minori, Callao, Eme and Dalan Serkot Caves (Mijares 2005, 2008). A younger cultural horizon of Late Holocene age is identified in most of the cave sites, and it contains similar archaeological finds, but is mainly distinguished from the older layer by the presence of earthenware pottery. Mijares reports the oldest date for the introduction of pottery in the Peñablanca area at 1950–1740 cal BC (3900–3690 cal BP) from Dalan Serkot Cave (Mijares 2005).

More than 30 open-air shell midden sites of Late Holocene age were also discovered in the Cagayan Valley since the 1970s (Amano 2011). One of these was first reported as Alaguia shell midden site, which was subsequently re-named Nagsabaran. This site is important for its relatively well-dated Neolithic and Metal Period sequence and for its well-preserved animal remains (Hung 2009; Hung et al. 2011; see Section 4.2.4). Another important shell midden site worth mentioning here is the Andarayan site, where a red-slipped pottery fragment with a rice husk inclusion has been dated to 3400 ± 125 BP (4000–3400 cal BP) (Snow et al. 1986). This, to date, is the earliest evidence of rice in the Philippines.

In the following sections, I provide the archaeological background for the study sites. However, I begin the archaeological descriptions with the oldest known site included in this study, Callao Cave. I also describe two Late Holocene sites that have vertebrate faunal records: Nagsabaran open-air site and Pintu Rockshelter. The radiometric dates quoted in the site descriptions are those reported by the authors. I have also calibrated the radiocarbon dates and the age ranges at 95% probability are shown in Table 4.1.

Table 4.1 Reported radiometric dates for study sites (boldface) and other relevant sites in Luzon Island. Radiocarbon dates are the default unless indicated by **for uranium series and ***for electron spin resonance dates. Calibration was done using OxCal 4.3 (Bronk Ramsey 2017) and ranges shown are at 95.4% probability. Dates for Nagsabaran are not exhaustive (see original source for all dates).

Site	Location	Age	Reported Radiometric Dates (BP)	Calibrated Age Range (BP)	Source
Callao	Cagayan, Luzon	Late Pleistocene to Late Holocene	66,700 ±1000**		Mijares et al. 2011
			54,300 ± 1900***		
			52,000 ±1400***		
			25,968 ±373	30,929–29,369	
MINORI	Cagayan, Luzon	Early Holocene to Late Holocene	4590 ±50	5465–5052	Mijares 2001
MUSANG	Cagayan, Luzon	Early Holocene to Late Holocene	11,450 ±170	13,708–12,991	Thiel 1988
			10,750 ±150	13,035–12,239	
			9670 ±220; 9390 ±280	11,804–10,401; 11,600–9795	
			4980 ±150; 4110 ±130	6173–5326; 4960–4244	
Nagasabaran	Cagayan, Luzon	Late Holocene	3940±40; 3390±130	4517–4248; 3980–3362	Hung et al. 2011
			3050±70; 2670±40	3442–3040; 2850–2745	
			2240±270; 1820±40	2918–1613; 1865–1625	
Pintu	Nueva Vizcaya, Luzon	Late Holocene	3881 ±240	4960–3643	Peterson 1974
			3291 ±230	4150–2950	
			2261 ±150	2719–1947	
			1401 ±100	1530–1084	

4.2.1 Callao Cave

Callao is a five-chambered cave and is the largest cave in the Callao limestone formation. The mouth of the cave is nearly 20 meters wide, and the height of the first chamber reaches up to 50 meters. All archaeological excavations were conducted in the first chamber. The second chamber has been turned into a local chapel, and it was reported that certain sections of the cave were dug for this purpose. 'Callao' or '*kalaw*' is the local name of the hornbill, which previously inhabited the cave complex.

The site was first excavated in 1979-80 under the direction of Maharlika Cuevas (1980). Subsequent excavations were then conducted by a team led by Armand Mijares in 2003, 2007, 2010 and 2015. The archaeological and stratigraphic data presented here are from Mijares (2005) and Mijares et al. (2011). An initial aim for re-excavating Callao Cave was to document the foraging-farming transition during the Mid-Late Holocene. Mijares (2008) further observed that out of 11 cave sites in the cave complex, eight were not excavated to the bedrock and have Holocene-age radiocarbon dates. This observation, along with the announcement of the enigmatic *Homo floresisensis* (Brown et al. 2004) in Flores Island, stimulated succeeding attempts to re-excavate Callao Cave.

A total of ten stratigraphic layers were reported from the 2003 excavation of the site (Mijares 2007). Of relevance to the foraging-farming transition are Layers 3 and 4. Layer 3 is a late Neolithic deposit with shell ornaments, earthenware, flake tools, human remains, bat bones and riverine gastropods. Layer 4 is also a Neolithic deposit with pottery but has no shell ornaments.

The 2003 Callao excavation also produced an age of 25,968 ±373 BP for one cultural layer: Layer 8 (Table 4.1 Luzon dates). This is notable because Callao is one of only four sites in the archipelago that have cultural layers dating to MIS-2 (*ca*. 30,000 – 12,000 BP). Two other sites are in Palawan Island (Tabon and Pilanduk Caves) and another in Mindoro Island (Bubog Cave). Layer 8 contained a relatively sparse record: a hearth deposit, chert and quartz flake tools and a few fragmentary burnt bones. Layer 9 and 10 were devoid of artefacts.

Work resumed in 2007 and in 2010, wherein four additional cultural layers are reported (Mijares et al. 2010). The oldest cultural layer in Callao described so far is from a breccia deposit, Layer 14 (270-295 cm below surface), containing animal bones and a human third metatarsal

(Mijares et al. 2010). The latter represents the oldest known human fossil in the archipelago. The human fossil was dated by uranium series and electron spin resonance to 67,000 ± 1000 BP. The small size and other morphological features of this hominin bone raise the question of whether it may be another dwarfed endemic hominin similar to *Homo floresiensis*. The singular toe bone was provisionally assigned to *Homo sapiens*. However, additional human fossils were recovered in subsequent fieldwork, and these new fossils (now totaling 13 hominin specimens) have been ascribed to the novel species *Homo luzonensis* (Detroit et al. 2019).

The Late Pleistocene assemblage used for comparison in this PhD study comes from these four layers from the 2007 excavation. A total of 807 bone fragments were recovered and analysed (Mijares et al. 2010; Piper and Mijares 2007). Two-thirds of the vertebrate remains were found in Layer 14, including the human third metatarsal. There are no other known bone accumulators in the faunal community of northern Luzon, and along with three cut marks found on a distal tibia fragment, indicating that the assemblage comes from human activity (Piper and Mijares 2007). The native Philippine brown deer (*Rusa marianna*) dominates the assemblage, constituting over 90% of identifiable bone. The Luzon warty pig (*Sus philippensis*) is also present, along with a large bovid evidenced by two tooth fragments. The first fossil rodents in Luzon are also reported in the Late Pleistocene levels of Callao (Heaney et al. 2011). Two murid species were described: the extant *Apomys microdon* and a fossil member of the genus *Batomys*. In total, five mammal species were identified in these levels.

4.2.2 Musang Cave

Musang Cave is a site located within the Callao formation, with an elevation of 65 masl (meters above sea level). The entrance faces south and the cave is about 37 meters long. The front section of the cave chamber is well-lit and its ceiling reaches up to 4 meters (Figure 4.2). The back portion of the chamber is poorly lit and has a higher ceiling of over 20 m. Most of the excavation units were in the front portion of the cave.

A team led by Barbara Thiel was the first to excavate in Musang Cave during 1976-77. She published a site report from which I draw much of the Musang Cave archaeological background (Thiel 1990). Within the NMP archives, a few recording plans, letters and short reports pertaining to the excavation are also stored, and most of these were written by Thiel.

Figure 4.2 Musang Cave showing (L-R): the cave mouth (viewed from the south), the narrow path leading to the cave mouth and platform, and view from inside the cave (viewed from the north). Photographs: J. Ochoa.

The mapping of the cave floor divided the surface into 2-meter grid squares (Figure 4.3). Seven excavation units were opened during 1976-77, consisting of 2 x 2 m and 1 x 1 m squares. These are: G4, G5, F6, G7, F3, D2 and D12. The NMP also conducted a re-excavation of the site during 1978-79, in order to investigate the archaeological findings of Thiel. However, only short reports of the excavation were produced by the NM team and there were no other excavation records or site report for the 1978-79 investigations. Hence, the data for Musang Cave derive mainly from the published analysis of Thiel (1990).

Thiel used three main stratigraphic components for describing the archaeology of the site: soil layers, excavation levels ('spits') and cultural layers. She identified five soil layers (1-5) and two major cultural layers (I and II) (Figure 4.4). The older cultural layer (Layer I) is found mainly within soil layer 3, which is described as a hard, dark yellowish brown clay with many inclusions of small pieces of limestone. This layer contains flake tools, gastropod shells and animal bones. The younger cultural layer (Layer II) is mainly found within soil layer 2, a dark brown sandy clay loam. Similar lithic and faunal materials are found in this layer, but with the addition of pottery, an iron fragment, a brass needle, glass beads, clay earrings and shell ornaments. Most of the excavated material came from squares G4 and G5.

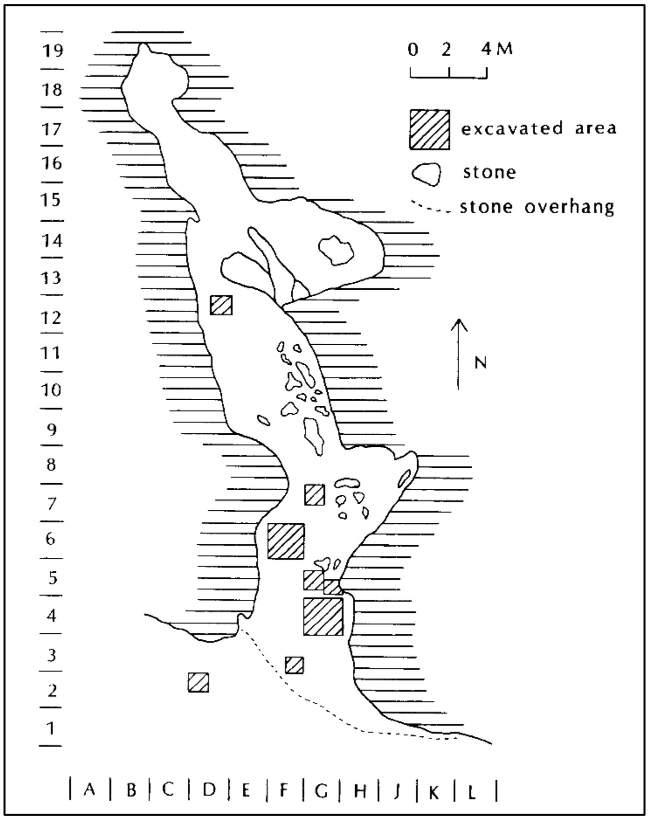


Figure 4.3 Musang cave floor plan, from Thiel (1990: Figure 2).

Thiel (1990) reports radiocarbon dates taken from shell remains of unknown taxonomic designation (Table 4.1). I quote here the calibrated age ranges at 95% probability. Cultural Level I has four dates ranging in age from 10,650 to 6930 cal BC. Cultural Level II has two reported dates ranging in age from 4095 to 2320 cal BC. Based on the dates for this younger level, Thiel (1990) posited early dates for pottery at 3740 cal BC. For the brass needle, Thiel reported the associated age of 2680 cal BC. However, the author advised caution with this early dating because the needle was separated from the dated shell sample by 2 m horizontally (Thiel 1990:77).

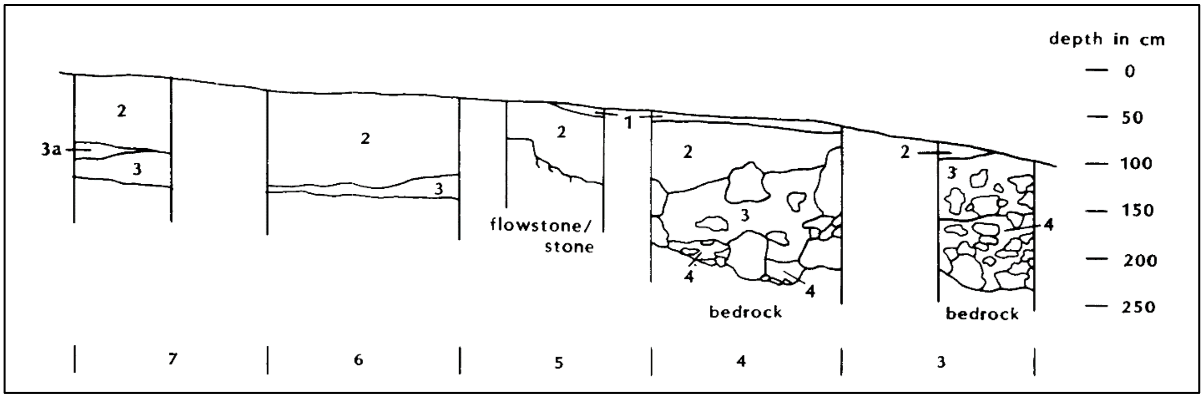


Figure 4.4 Stratigraphic profile of excavated areas F and G of Musang Cave. Legend: 1. Dark brown very hard sandy clay loam with pottery, animal bone, shell and flake tools. 2. Dark brown hard sandy clay loam with pottery, animal bone, shell and flake tools. 3. Dark yellowish brown hard clay with many small limestones and with animal bone, shell and flake tools (no sherds). 3a Dark yellowish brown soft, sandy clay with many small pieces of limestone and a few sherds and shells. 4. Very dark grayish brown, very stony hard clay with no cultural remains. After Thiel (1990: Figure 4).

Thiel used soil composition and presence of pottery as a distinguishing trait in separating cultural layers and excavation levels. Three main earthenware pottery types were found on site: plain brown, black and red-slipped. Cultural Layer I is designated as aceramic and occurs in excavation levels 4 to 12. Cultural Layer II is ceramic-bearing and occurs in levels 1-7. There is an apparent overlap in levels 4 to 7. The author separated excavation levels 4 to 7 into pottery-bearing (4a, 5a, 6a and 7a) and non-pottery bearing sections (4, 5, 6, and 7). Thiel's excavation plans and records show that in Square G4, the northeast quadrant of the square contained pottery until level 7, while the rest of the quadrants did not have ceramics.

I maintain some reservation with regards to the segregation of Levels 4 to 7 and finds based on observations from the faunal remains. The bones from Levels 1 to 7 have varying states of preservation and carbonate concretions (see Chapter 8), indicating that there has been some post-depositional mixing of remains in these levels. Although Thiel states that ceramics are only present in the northeast section of G4, there is no means to check the provenance of ceramic finds or bone fragments because specimen labels only indicate the soil layer and/or level and not the 3-dimensional coordinates. There was no existing inventory of finds in the NMP archives. Furthermore, there are faunal remains of presumed non-native taxa that occur across Levels 4 to 7, and these may also be indicators that faunal remains were also mixed into *in situ* remains.

Thiel (1990: Table 1) provides a preliminary description of the bone assemblage and raw counts of pig, deer, and human remains. Pig bones supposedly comprise about 98% of the assemblage. A quick re-study of the bones, however, reveal that some human bone fragments were misidentified and labelled as pig bones. The human bones also had a different state of preservation from the fauna, indicating that they were intrusive. Some bones with low identifiability (e.g. long bone shaft fragment or ribs) have been designated as pig remains even though there is no sufficient morphological information on the bones for specific taxonomic designation. For these reasons, I do not use the bone counts from Thiel for comparative purposes and rely on my own re-analysis of the materials.

In terms of the fauna, Thiel (1990) reports that there were nearly three times as much animal bone in Cultural Layer II compared to Cultural Level I. Drastic reduction of shell remains is also observed in Cultural Layer II, which only has about 5% percent of the amount in shell in Cultural Level I. In the older level, it appears then that the cave was primarily used as a campsite for shellfish gathering, whereas hunting was more intensive in the Layer II. Thiel also argued for probable resource intensification in the use of shellfish based on the diminishing sizes of shell taxa across the sequence.

The zooarchaeological analysis focuses only on the collection from Thiel's excavation because it has proper documentation. The subsequent NMP excavation has no information about stratigraphy or excavation records. I also focus on two main squares, G4 and G5, because these squares have the longest sequences, the greatest number of remains excavated, and the most number of remains preserved in museum storage. Post-excavation assemblage loss is apparent in that the numbers of bones in Thiel's counts (1990: Table 1) for the large mammals (pig, deer and human) do not match NISP and TNF per square in the current analysis. It is not certain if some of the finds were brought into a different storage place of the NMP or if they were brought by Thiel to the United States. Regardless, G4 and G5 still retain a relatively good assemblage size compared to the original excavated assemblage.

4.2.3 Minori Cave

Minori Cave is a four-chambered cave that was first excavated by the NMP in 1981 under the former chief of the Archaeology Division, Wilfredo Ronquillo (1981) (Figure 4.5). It is situated further north in the Callao formation and is found at 240 masl. There are two cave openings, a northeast- and a west-facing entrance. The west chamber is labelled as Chamber D (Site accession code: II-1977- J11A) and the northeast chamber is Chamber A (Site accession code: II-1977- J11B). Chamber D was excavated in 1981 while Chamber A was excavated in 1982. There is no published record of the 1981-82 excavations and the data that I cite here are from unpublished manuscripts in the NMP (Orogo 1982; Ronquillo 1981). The excavation procedure followed observed natural layers and used 5-cm spits. All artefacts were plotted in three dimensions and sediments were sieved using 4-mm screens. Two soil layers were identified in these excavations. A topsoil layer of dark brown clay (Layer I) and a stony, slightly loose and yellowish brown clay (Layer II). In Chamber A, Orogo (1982) reports that Layer I contained lithic tools, bone and shell remains, earthenware sherds and modern (*ca*. 20th century) artefacts. Layer II contained similar lithic tools and faunal remains but did not have modern materials and had a smaller number of earthenware sherds. Layer II was only exposed in Squares 30 and 37 of Chamber A. Logbook records for Chamber D indicate a similar description of finds, but there is no official report on the excavation of the chamber. In the absence of detailed stratigraphic records, I have mainly used the Minori Cave artefact inventory forms and excavation logbook to reconstruct the stratigraphic associations of materials excavated during 1981-82 excavations.

A re-excavation of Chamber D was conducted in 1999 by a team led by Armand Mijares (2001, 2002). Two major cultural levels were uncovered: an Early Holocene level with lithics and faunal remains and a mid to late Holocene level with similar lithics and fauna, but with the addition of earthenware ceramics. The stratigraphic plan from the 1999 excavation is the only existing stratigraphic profile for Minori Cave, and it shows the two cultural layers (labelled as spits) reflected in the profile of Square 45 (Figure 4.6). The lithic artefacts are predominantly made from andesite, and a few were from chert. A single radiocarbon determination of 4590 ± 50 B.P. was obtained for the younger cultural layer that contained lithic tools and ceramics. This pattern in the Callao formation – wherein two Holocene cultural layers are found with similar lithic and faunal material and the younger layer is differentiated by ceramic finds – is replicated in Musang, Eme, and Dalan Serkot Caves (Mijares 2005; Thiel 1990).

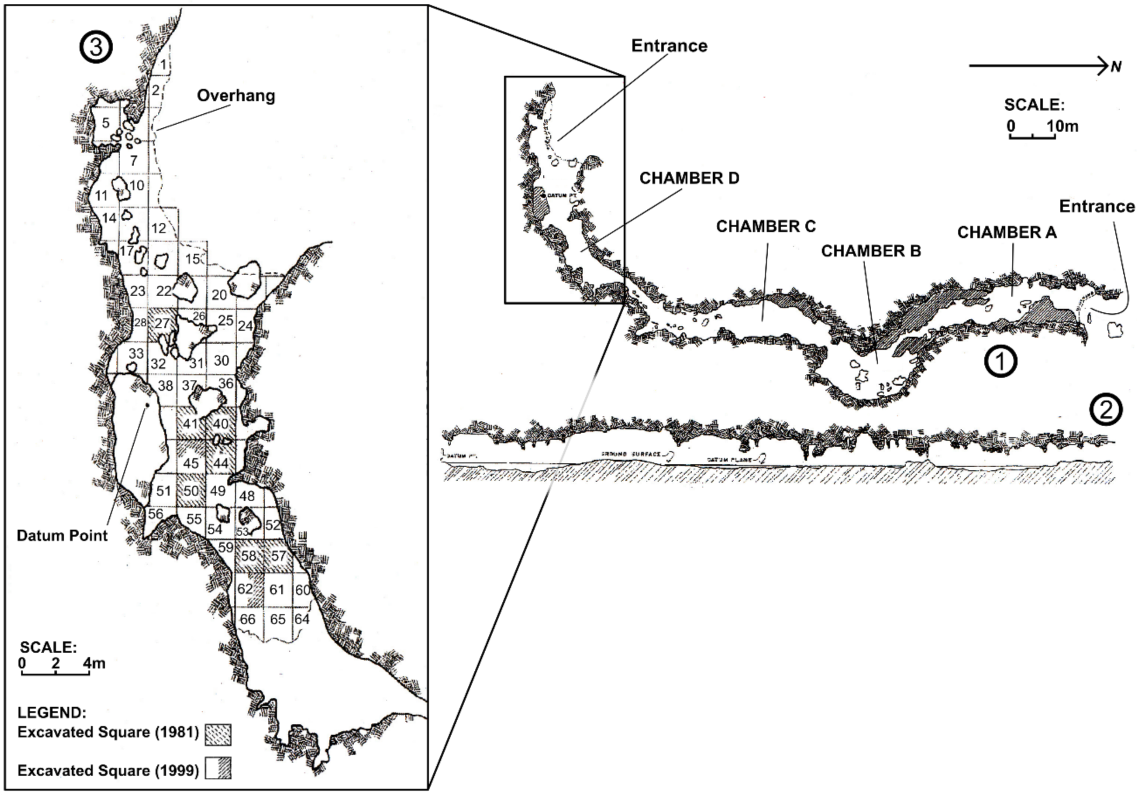


Figure 4.5 Minori Cave plan showing 1) cave floor and designated chambers, 2) Longitudinal cross-section of cave, 3) Grid plan of Chamber D and excavated squares. Modified from Figures 2 and 3 of Mijares (2002).

Mijares (2001, 2002) has argued for the presence of an expedient lithic technology in Minori Cave. Coarse- and fine-grained lithic tools are hypothesised to have been used on hard contact materials such as bamboo and rattan. It is argued that the lithics were expediently utilised to maintain such organic tools. A more formal lithic technology did not need to be developed, and this is deemed an appropriate cultural adaptation in a specific environmental setting (Mijares 2001:150). This was based on the analysis of a sample of Minori andesite flakes. The flakes did not possess features of retouch, but the microwear analysis showed that nearly all were utilised. A portion of these were used on hard contact materials.

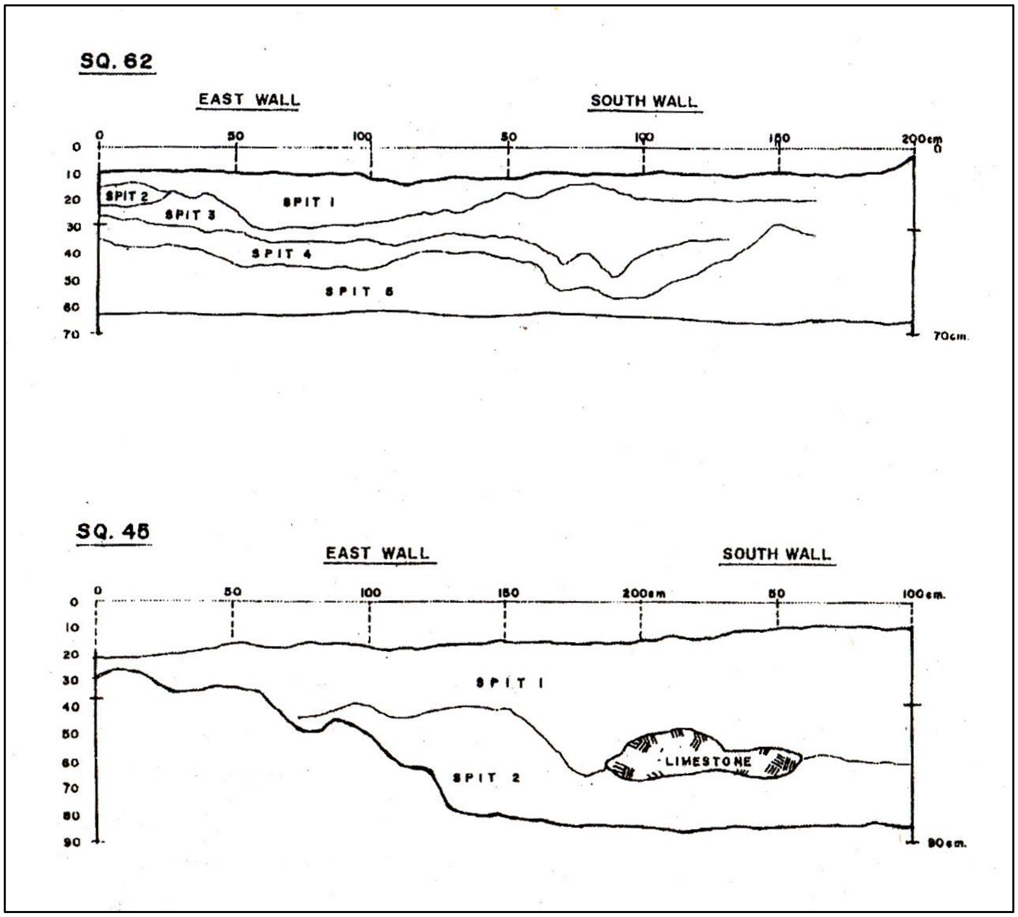


Figure 4.6 Stratigraphic profile for Squares 62 and 45 of Minori Cave Chamber D that were excavated in 1999. After Mijares (2002: Figure 4).

De Vera-Alba (1990) provides a preliminary study of the vertebrate fauna from the 1981 excavation of Chamber D. Deer is the dominant taxon, followed by wild pig. Numerous rodent remains were listed, but were not further identified. Macaques and carnivores are also reported, although the carnivores were also not further identified. I present De Vera's identifications in Chapter 6 for comparison with my own analysis.

One of the main interests of the thesis is to look at the question of animal translocation, as it relates to both biodiversity changes and human impacts on local environments. In this regard, I submitted two macaque (*M. fascicularis*) tooth specimens from Minori Cave for radiocarbon dating to the Oxford Radiocarbon Accelerator Unit and the results are shown in Table 4.2. The museum specimens are from Square 37 in Chamber A and were excavated in 1982. Only two specimens were submitted due to limited funds (which were mostly allocated for Pilanduk Cave) and due to the relative rarity of macaque remains. Square 37 had the greatest number of macaque remains (n=14) among all excavation squares (see Chapter 7). The chosen specimens were recovered from Layer II, which contains earthenware ceramics. They were found at a similar depth but have dissimilar ages. The recorded depths are -226 and -227 cm, which are only about ~10 cm below the surface. Surface depth from the local datum point of Square 37 is -215 to -219 cm. Macaque remains are only found in the uppermost levels of Minori Cave, and the macaque specimen with the lowest depth is recorded at -229cm. Because of the relative shallowness of levels in which macaque remains were found, it is very likely that there has been mixing of remains in the uppermost levels. This is the main reason why direct dates on targeted taxa were taken. One of the specimens (Minori-2409) yielded a recent age of AD 1645-1927. Another specimen (Minori-2402) yielded an older age of 1860–1706 cal BP. All quoted age ranges are at 95.4% probability. To date, these are the only directly dated macaque specimens in the archipelago. Effectively, the age of Minori-2402 represents the minimum age for the presence of macaques on Luzon (see Chapter 7 discussion on translocation). There are currently no older records for macaques on Luzon, and they are not represented in the Pleistocene levels of Callao Cave.

Table 4.2 Radiocarbon dates for macaque tooth specimens from Chamber A of Minori Cave. Calibration was conducted using OxCal 4.3.2 (Bronk Ramsey 2017). Calibrated age ranges are at 95.4% shown in BP and CE. LDP = local datum point.

Accession Code	OxA No.	Layer	Depth from LDP (cm)	Radiocarbon age (BP)	Calibration age range (cal BP)	Calibration age range (cal CE)
2402	36333	Layer II	227	1833 ± 25	1860–1706	90–244
2409	36334	Layer II	226	217 ± 24	305–14	1645–1927

4.2.4 Nagsabaran Site

Nagsabaran is an extensive shell midden site located in the northern Cagayan town of Lal-lo. The 4.2-hectare open-air site lies on the south bank of Zabaran Creek, a small tributary of the Cagayan River. There are two major depositional periods: an early Neolithic phase (beginning at *ca.* 4500–4000 cal BP) consisting of lower alluvial silts and a Late Neolithic/Metal Period shell midden phase (*ca.* 2500 cal BP to AD 400) (Hung 2009; Hung et al. 2011; Oxenham et al. 2015). Nagsabaran site provides secure dates for the introduction of ceramics in Luzon in its early Neolithic levels. The earlier phase contains red-slipped pottery, trapezoidal-sectioned stone adzes, baked clay penannular earrings and jade ornaments. The Late Neolithic/Metal Period layers contain black and red pottery, iron tools, bronze bells, glass beads and human burials.

The faunal remains from Nagsabaran were analysed by Amano (2011) and Piper et al. (2009). The assemblage is dominated by wild fauna, particularly deer and wild pig. There is said to be no apparent shift from hunting to a reliance on domestic animals for food even in the later periods of site occupation, as might be expected in a 'Neolithic transition'. Several domesticates are recorded, nonetheless. The site has the oldest record of introduced domestic pigs (*S. scrofa*) in the archipelago, with several associated dates on charcoal and one specimen holding a direct date of 3940 ± 40 BP or 4517-4248 cal BP (Hung et al. 2011; Piper et al. 2009). Nagsabaran also has Late Neolithic/Metal Period records for domestic water buffalo (*Bubalus bubalis*) and domestic dogs (*Canis lupus familiaris*) (Amano et al. 2013). These identifications are important because there are very few well-studied archaeofaunal assemblages on Luzon and few well-dated records of introduced domesticates in the region.

4.2.4 Pintu Rockshelter

Pintu/Busibus Rockshelter is in Nueva Vizcaya province, which is located south of the Cagayan Valley. It also lies on the eastern side of the Sierra Madre and on the banks of the Ngilinan River, a tributary of the Cagayan River. It was excavated in 1968-1969 by a team led by Warren Peterson (1974). Eleven soil layers were uncovered up to a depth of 1.75m. Eight of the layers had cultural material. Layer 10 shows the deepest evidence of occupation, with a pig mandible fragment and a few lithic tools. Significant quantities of lithics and bone appear in Layers 7 to 1. Pottery first appears in Level 6 with one vessel; thereafter, earthenware is present in small numbers from Layers 5 to 1. There are no metal, stoneware or porcelain artefacts, but two beads are recorded in Layers 4 and 5. Peterson (1974) reports four radiocarbon dates derived from charcoal samples (Table 4.1). The samples were from Layers 4, 5, 6 and 10. The author states that the probable time span of occupation of these layers is from 4120 to 2110 cal BP. The dating for Layer 6, where pottery appears, is 3520-3060 cal BP.

The faunal material from Pintu was studied by Mudar (1997). A total of 1029 fragments were analysed, 296 of which were identified to taxon. Eighty-five percent of the sample came from Layers 3 and 4, which post-date 2100 uncal. BP. Deer is the most common taxa (n=157), followed by wild pig (n=123). Four specimens are also attributed to the domestic water buffalo in Layers 2, 4 and 5. Macaque remains are also reported (n=7) in Layers 3, 4 and 5. Based on the faunal evidence, Mudar (1997) states that the cave was used as a base camp intermittently occupied for both extended and limited periods. This is supported by the skeletal representation of pig and deer, where both high and low meat-bearing elements are present. The narrow range of species represented, absence of fish, and the focus on hunting terrestrial game are said to be indicative of occupation during the rainy season.

4.3 Palawan Island Archaeology

Palawan is the fifth largest island in the archipelago. The archaeology of Palawan, and arguably a large part of Philippine palaeohistory, is anchored on the Tabon Cave Complex. Tabon Cave is located in a limestone formation in Lipuun Point, Quezon municipality (Figure 4.7) in southern Palawan. The complex consists of over 200 caves that were first explored by the NMP during the 1960s (Fox 1970), hence the collective name Tabon Cave Complex. Over 30 caves have been assessed that have archaeological deposits. Fox' 1962-66 excavations in Tabon yielded human fossils and cultural assemblages that documented the Late Pleistocene human occupation of Palawan. The cave is named after a local species of megapode (*Megapodius cumingii*) called *tabon*, which nested and dug holes in the cave to lay its eggs.

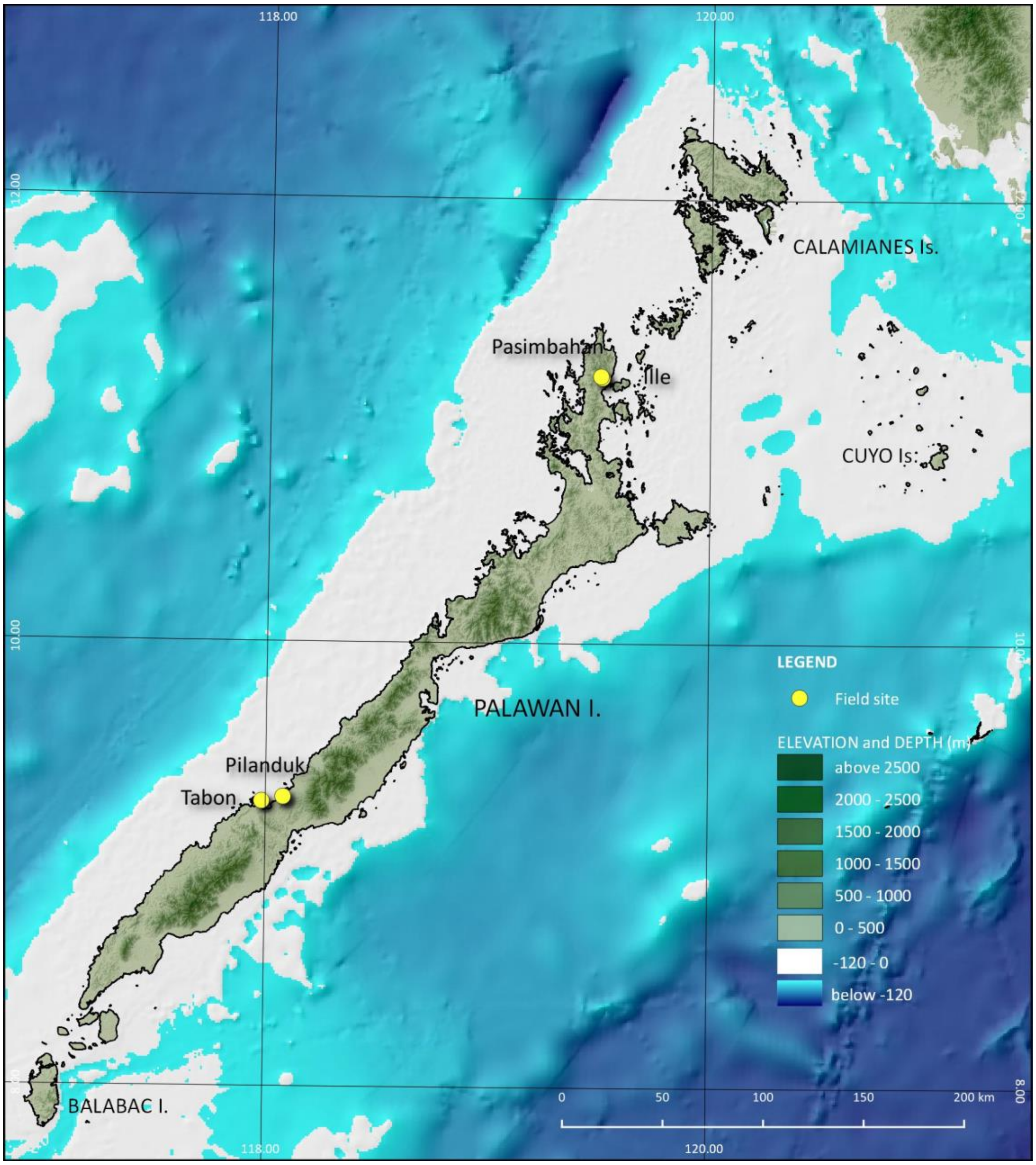


Figure 4.7 Map of Palawan Island showing present-day coastlines and the location of archaeological sites. The maximum extent of the island group (or 'Greater Palawan') during the Last Glacial Maximum is approximated by the -120 m isobath. Note that the Calamianes, Balabac and Cuyo Islands would have been connected to the main island in this reconstruction. Map drawn by J. Villasper.

Prior to the 2010 discovery of the Callao human, 'Tabon man' represented the earliest human in the archipelago. The Tabon Cave human fossils are ascribed to *Homo sapiens* (Fox 1970, Dizon 2002). The inventory of Pleistocene *H. sapiens* fossils totals to 13, which includes a frontal bone (the 'Tabon skull cap'), a right mandible fragment from Fox' 1962 excavation, and eleven fossils from a 2000 re-excavation of the site (Détroit et al. 2004). The fossils were found in association with lithic assemblages, which Fox categorised as Flake Assemblages I-IV. Fox associated the human fossils with Flake Assemblage III, which has a ^{14}C date of 23,000 ±1000 BP (Table 4.3). Subsequent direct dating of the frontal bone yielded a date of 16,500 ± 2000 years cal BP (Dizon et al. 2002). Détroit and colleagues (2004) published direct U-series dates on two more human fossils, yielding dates of 31,000 ± 8000 BP and 47,000 ± 11,000 BP. The dates confirm Fox's earlier dates and estimates on the Late Pleistocene age of Tabon, but the maximum age of the fossils must be taken with caution. Lewis et al. (2007) also conducted preliminary dating of a speleothem formation underlying Flake Assemblage II through uranium-series methods, and provided an age range of 20,200 to 19,400 BP. As mentioned in Chapter 2, Choa (2018) has provided new dates for Tabon Cave, particularly in reference to Flake Assemblages II and III, which were previously dated by Fox and Lewis to MIS-2 (*ca*. 23,000–20,000 BP). The new dates push back the age range of these layers to MIS-3, at 39,000–33,000 cal BP.

Tabon Cave, along with several other caves in Lipuun Point, were characteristically used as burial sites in later periods. This is a phenomenon that is observed across the archipelago and in many other Southeast Asian sites. Fox (1970) describes a jar burial complex for Palawan, including that of Manunggul Cave. In Philippine chronology, periods labelled as 'Late Neolithic', and 'Metal Period' were initially based on the material culture and chronology of the Tabon Cave Complex.

Fox also investigated nearby cave systems in Quezon, including those in the Iwaig River area. An important discovery was Duyong Cave, which is named after the dugong (*Dugong dugon*). Numerous bones of this large marine mammal were found scattered on the surface and subsurface of the site. A single flexed Neolithic human burial is described by Fox (1970:60) that has associated *Tridacna* adzes and *Conus* ornaments. One of Fox's junior colleagues, Jonathan Kress, further explored cave systems around the Iwaig (=Iwahig) River. Two important cave sites were excavated – the Late Pleistocene site of Pilanduk Cave and the Holocene-age Sa'gung Rockshelter. Subsequent investigations by Reis and Garong (2001) also revealed additional sites in southern Palawan, such as Tarung-tarung Cave, which contained vertebrate assemblages.

To the north of Palawan, cave sites in the El Nido area have produced an equally rich archaeological record. The area was already recognized as an important area from early investigations of Carl Guthe (1927) and the University of Michigan Expedition. It was subsequently explored and studied by the NMP (Fox 1970). Our current knowledge of the archaeology of northern Palawan is anchored on Ille Cave, which has produced well-stratified and well-preserved cultural remains spanning the last 14,000 years (Lewis et al. 2008). The current research is undertaken by the Palawan Island Palaeohistoric Research Project (PIPRP). Another cave site investigated by the PIPRP is Pasimbahan-Magsanib Cave, which also contains a sizeable vertebrate assemblage.

4.3.1 Ille Cave

Ille Cave is located in the Dewil Valley of El Nido town in northern Palawan (Figure 4.7). The earliest layers of the site date back to the Terminal Pleistocene and continue up to the near-present. Two major mouths at the base of the tower – the East and West mouths – serve as the main access to the cave system. The two main excavation trenches were placed in these openings.

The data reviewed here for the archaeology and dating of Ille Cave come from Lewis et al. (2008). The deepest cultural levels consist of several steeply sloping sedimentary layers of clay and gravels. They are of Terminal Pleistocene age, based on a radiocarbon date on charcoal from context 866 of 14,116–13,820 cal BP (Table 4.3). Immediately below context 866 is context 1306, a sedimentary horizon that produced a sizeable animal bone assemblage mixed with chert flakes, obsidian flakes and charred nut fragments. Overlying these clay and gravel layers is a cultural horizon with several human cremation burials and hearth features. These are dated between 9,000 to 11,000 cal BP. The human remains are of considerable significance, because they are the oldest known human cremations in Island Southeast Asia.

By the mid-Holocene, an extensive shell and bone midden is observed across the site. This layer has radiocarbon dates spanning 5500-6500 cal BP (Lewis et al. 2008; Szabo et al. 2004). The shell midden deposits are dominated by marine and mangrove molluscs. Human burials with associated ground and polished shell and stone burial goods were also found. The uppermost deposits contain more midden remains and an extensive human burial layer. These layers have pottery, and based on artefact typology, they range in age from the Metal Period up to later historic times.

Table 4.3 Reported radiometric dates for Pilanduk Cave and other sites in Palawan Island. Radiocarbon dates are the default unless indicated by **for uranium series dates. Calibration was done using OxCal 4.3 (Bronk Ramsey 2017) and ranges shown are at 95.4% probability. Calibrated dates in boldface are as originally reported by the source. Dates for Ille Cave are not exhaustive (see source for all dates).

Site	**Location**	**Age**	**Reported Radiometric Dates (BP)**	**Calibrated Age Range (BP)**	**Source**
	Palawan Island				
Tabon	Quezon, Palawan	Late Pleistocene to Late Holocene	47,000 + 11,000/–10,000** 31,000 + 8000/–7000** 30,100 ± 1100 23,200 ± 1000 16,500 ± 2000** 9250 ± 250	 36,876–31617 29,791–25,653 11,193–9777	Detroit et al. 2004 Dizon et al. 2002 Fox 1970
PILANDUK	Quezon, Palawan	Early Holocene to Late Holocene	25,470±1000 18,340±370 18,260±650	31,530–27,725 23,066–21,260 23,712–20,556	Kress 1980, 2000
RS 2	Quezon, Palawan	Holocene	11,130±50	13,095–12,836	Reis and Garong 2001
Ille	El Nido, Palawan	Terminal Pleistocene to Late Holocene	12,120±60 9740±75; 9215±45 9400±45; 9340±46 8920±45; 8799±40 8155±50; 8315±50 5804± 38; 5769±37	**14,116–13,820** **10,974–10,786; 10,501–10,252** **10,733–10,515; 10,473–10,419** **10,198–9905; 9951–9663** **9260–9006;9425–9280** **6677–6494; 6662–6481**	Lewis et al. 2008
Pasimbahan–Magsanib	El Nido, Palawan	Early Holocene to Late Holocene	9442±46 7793±24; 7590±25 4697±25; 4333±25 3401±26	**10,790–10,559** **8630 – 8538; 8421 – 8370** **5225–4645; 4970–4845** **3704–3573**	Ochoa et al. 2014

The vertebrate faunal data of Ille Cave are derived from my Master's thesis (Ochoa 2009) and subsequent publications (Ochoa and Piper 2017; Piper et al. 2011b). The Terminal Pleistocene and Early Holocene layers (ca. 14,000–9,000 cal BP) are dominated by deer remains. Two species were identified based on the notable size distinction of teeth and post-crania. The larger species is attributed to the genus *Rusa,* while the smaller species is ascribed to the extant *Axis calamianensis,* or the Calamian hog deer. The hog deer is known as a native inhabitant of the smaller islands of the Calamianes that are immediately north of Palawan. Deer are now extinct on Palawan Island itself, and they are not known from historical accounts about the natural history of the island. Also represented in the oldest layers of the site, but absent from the Middle Holocene onwards (*ca*. 7000 cal. BP) are the tiger (*Panthera tigris*) and a canid (*Canis/Cuon*). Both are also extinct. A few other extant mammals are represented in the Terminal Pleistocene such as the wild pig (*Sus ahoenobarbus*), the long-tailed macaque (*Macaca fascicularis*), and the Palawan porcupine (*Hystrix pumila*). Macaque remains increase beginning in the Early Holocene and are then fairly common throughout the rest of the sequence. Most of the extant small carnivore species are also represented across the Holocene sequence such as the common palm civet (*Paradoxurus hermaphroditus*), binturong (*Arctictis binturong*) and the endemic stink badger (*Mydaus marchei*). These Terminal Pleistocene and Early Holocene records of the extant taxa are important evidence of their natural distribution on Palawan. By the Middle Holocene to the Late Holocene, the wild pig becomes the dominant mammal prey. Deer remains are extremely rare, and only the smaller deer species has been identified. The different timing of extinctions of large mammals on Palawan is likely indicative of different trajectories to extinction (Ochoa and Piper 2017). I revisit the data on mammalian extinctions in Chapter 7.

4.3.2 Pasimbahan Cave

Pasimbahan-Magsanib Cave is another site in the karstic Dewil Valley, about two kilometres away from Ille Cave. The term 'Pasimbahan' roughly translates to place of worship, and there are some caves in the El Nido area that locals refer to as *pasimbahan*. These places are imbued with sacred meaning and ritual significance by the local Cuyonon and Tagbanua (Paz 2012). The cave is in the southwest face of the Istar karst formation and is about 6 km away from the present-day coastline.

The archaeology of Pasimbahan Cave is described by Paz (2012) and Ochoa et al. (2014). It was first excavated in 2007 under the direction of Dr. Victor Paz. Six major excavation units were opened, namely Trenches A, B, C, D, E and J. The deepest and oldest layers of the site are located in the adjacent trenches A and B. Three radiocarbon dates were obtained in these levels, ranging in age from 8000 to 10,500 cal BP (Ochoa et al. 2014) (Table 4.3). The Early Holocene layers consist mainly of hearth features, burnt limestone rocks, shell deposits, chert flakes and animal bones. The shell remains are dominated by terrestrial and freshwater species, but individual *Tridacna* (giant clam) valves and modified *Melo* bailer shells were also found. Overlying these deposits is an extensive shell and bone midden layer found across five trenches. The midden is characterised by numerous mangrove and marine taxa, burnt limestone rocks, wild pig bones and various other medium vertebrates. Two ^{14}C dates ranging from 5200 to 4600 cal BP place these deposits in the Middle Holocene. The abundance of wild pig remains, marine and mangrove mollusc taxa, and associated radiocarbon dates agree with the Ille Cave sequence and biostratigraphy. In the northern Palawan record, it is evident that deer is the dominant taxon up until the Early Holocene, after which the wild pig becomes dominant during the Middle and Late Holocene.

The youngest levels of the site also contain shell midden deposits and numerous commingled human remains. A radiocarbon date was obtained from one of these midden deposits. The dated material is from a wild pig maxilla fragment and produced an age of 3704–3573 cal BP. This pig bone fragment was found in an archaeological context (context 71) where a hog deer (*Axis*) tibia fragment was identified, but the latter specimen failed to produce enough collagen for radiocarbon dating. Hence, the associated age of another bone from the same context is used as a temporal marker of deer presence.

Analysis of the Pasimbahan Cave bone assemblage reveal the presence of many of Palawan's extant mammal fauna, including many of those described from Ille Cave (Ochoa et al. 2014). It also documents the Late Holocene presence of one locally extinct species, the Calamian hog deer. The latest occurrence of deer in the site is recorded from three late Holocene midden contexts. One of these is a shell midden deposit (context 403) in Trench J where Indo-Pacific glass beads and tradeware were in the same levels as a few deer remains. This may indicate deer presence in a temporal context within the last millennium. However, redeposition also characterizes the upper layers (i.e., due to hydrological activity and interment of human remains) and hence the dating from context 71 is retained as a more secure chronological marker for the Late Holocene presence of the hog deer. Whether this represents a marker for its last occurrence deserves further investigation.

4.3.3 Tarung-Tarung Cave

Further explorations in Lipuun Point and Kalatagbak area of Quezon province in southern Palawan also yielded additional records of Holocene-age vertebrate assemblages. Reis and Garong (2001) conducted test pit excavations in four locations: RS1 and RS2 in Lipuun Point and Tarung-tarung and Merasuen Caves in Kalatagbak. A single radiocarbon date was retrieved from RS 2, yielding an age of 11,130 ±50 BP (13,095–12,836 cal BP). The four excavations yielded a relatively small faunal sample (n=753), with Tarung-Tarung Cave having the largest sample size (n=354). The authors identified 31 genera and 28 species of terrestrial vertebrates, including three previously unrecorded taxa: an owl *Otus* sp., the swiftlet *Collocalia salangana*, and a small shrew *Crocidura* sp. The study highlighted both the insular and continental affinities of the Palawan fauna.

4.4 The Archaeology of Pilanduk Cave

Pilanduk Cave is located in Magmisi (also Nəgmisi) Peak in Quezon municipality of southern Palawan, with the geographic coordinates 9° 17.998' N and 118°4.698' E. In geographic maps, the hill is also labelled as Devel Peak. It is part of a wider carbonate formation called the Alfonso XIII formation that is of Late Middle Miocene age (Rehm 2006) and that coevals with the Tabon limestone (Aurelio and Pena 2010). Magmisi Peak is about 20 km away from Lipuun Point and the Tabon Cave complex. “Misi” means smile in the Pala’wan language, and it pertains to a wide notch on the north face near its peak, which from a distance appears like a smile or a grin. The formation is less than a kilometre away from the present-day coast.

The cave is well-lit and measures about 40 m long at the overhang and about 20 m wide in the broadest central section (Figure 4.8). It is approximately 165 m above sea level. Iwahig is the local name of the area and of the major river system that currently cuts through surrounding agricultural fields, secondary lowland forests and mangrove forests. The Iwahig River finally empties into the West Philippine/South China Sea. The name *pilandok/pilanduk* is the vernacular term for the Philippine mouse-deer (*Tragulus nigricans*), which is an endemic of the small island of Balabac off the south coast of Palawan. This animal is not known to have a natural distribution on Palawan itself, but it is reported to have been translocated into southern Palawan in present times. Pilanduk is also a term used for the Calamian hog deer.

Figure 4.8 Magmisi Peak (top) facing west and as visible from the village road; and panoramic photographs of Pilanduk Cave showing the cave interior (middle, viewed from the northeast) and the cave mouth (bottom, viewed from inside the cave/from the west). Photographs: J. Ochoa.

4.4.1 Archaeological Background and Fieldwork Objectives

Pilanduk cave is an important Philippine site that contains a large and well-preserved faunal and lithic assemblage of Late Pleistocene antiquity. The site is particularly crucial to the thesis because it is the only site of reportedly Last Glacial Maximum (LGM) age in the whole archipelago that contains a sizeable faunal assemblage. Callao Cave in northern Luzon has a layer with a direct date that place it into the Last Glacial Period (*ca*. 26,000 BP), but the archaeological remains from this layer are minimal. On Palawan itself, Tabon Cave is the only other site with direct dates that place it well into the Pleistocene, but Fox's excavations and more recent investigations have not yielded a big faunal assemblage. Ille Cave in northern Palawan, on the other hand, reveals cultural layers that date up to the Terminal Pleistocene only.

The first archaeological exploration of Pilanduk Cave was in 1962 under the auspices of the NMP. The first archaeological excavation was conducted in 1969-70 by a team led by Jonathan Kress. Kress (1980:60) reports that at the beginning of the excavation, the surface of the cave was partially covered by underbrush and that much of the centre had been disturbed by the activities of the *tabon* bird. Three radiocarbon dates taken from shell were reported by Kress (1980, 2000) that range from 25,000 to 18,000 uncal. BP (Table 4.4). Kress (2000) reports four Palaeolithic cultural layers from the excavations and corresponding ages for three of them. The deepest layer, Layer IV, was dated at 25,470 ±1000 BP. The youngest layers, Layers II and I, yielded dates at 18,340± 370 BP and 18,260 ±650 BP, respectively. During the time of Late Pleistocene occupation, the site would have been further inland because of the MIS-2 sea-level lowstand. GIS reconstructions place this at about 40 km distance from the coast (Robles et al. 2015). Kress (1980) reports that after the Late Pleistocene occupation, the site was rarely utilised until around 3000 years ago (or later) when it was used as a jar burial site.

Table 4.4 Pilandok Cave cultural chronology from Kress (1977, 2000). Radiocarbon dates are uncalibrated and were taken from shell taxa with unreported taxonomic designations. Layer III is said to be more similar in composition to Layers I and II. Calibrated ages are shown in Table 4.3.

Layer	Age/Dates*	Dating sample number and material
Jar burial layer	Metal Period	n/a
Layer I	18,260 ±650 BP	I-5488 on shell
Layer II	18,340 ±370 BP	I-5492 on shell
Layer III	n/a	n/a
Layer IV	25,470 ±1000 BP	I-5490 on shell

The archaeological materials recovered in the excavation are described by Kress in three separate publications: the lithics and vertebrate fauna (Kress 1977), the ceramics (Kress 1980) and the mollusc assemblage (Kress 2000). Regarding the vertebrate fauna, there are no published faunal counts. Kress (1977) provides a very brief description, observing that bones of deer predominate in all four layers. Some wild pig, monkey, monitor lizard, porcupine and tortoise remains were also identified. The author interprets the abundance of deer as representing an economy with a relatively narrow subsistence base and specialised hunting.

Kress (1977:39) describes the lithic assemblage in Layer IV as a flake industry manufactured largely from flint. The flakes vary greatly in size and proportion and retouching was not observed. The lithic assemblage from Layers III, II and I is also a flake industry largely made from flint. Nonetheless, it differs from the Layer IV industry in that there is a much greater uniformity in flake morphology and extensive retouch is also apparent. Kress describes this industry as ‘specialized’, wherein knapping techniques appear more standardised and tools were manufactured with specific characteristics for specialised tasks (Kress 1977:42).

Kress (2000) also reports on the mollusc assemblage. Thirty-one species were identified in the assemblage, with 90% coming from freshwater and terrestrial taxa. This pattern is said to confirm the inland environment of the Palaeolithic levels of the sequence, which contrasts with the current coastal environment of the area. The author further notes that there is an increasing trend in abundance of total volume of molluscs. There is a 68% increase of material from the Layer III to Layer II and an 81% increase from Layer II to Layer I. Kress (2000:319) interprets this as evidence for the intensification of the use of the cave during this period.

The ceramic assemblage from Pilanduk Cave derives from the uppermost levels attributed to the Late Neolithic/Metal Period jar burial phase. Kress (1980) reports that a total of 570 sherds were collected. These were categorised into two groups, ceremonial and utilitarian. The large burial jars are attributed to the ceremonial ceramics. The author also reports the presence of three shell ornaments associated with the ceramics: a *Meretrix* shell bead, an *Arca* shell pendant and a worked oyster fragment.

The radiocarbon dates from the Palaeolithic layers were taken on shell remains of unreported taxonomic designation. Due to the known limitations of radiocarbon dating technology during the 1970s, particularly as it was applied on shell, these dates are not well accepted in the literature. Stratigraphic details were also not published. The uncertainty in the dates and in the site records provide a tentative sequence for Pilanduk. Despite these limitations, the site has yielded an archaeological sequence that is important due to its attributed antiquity and the large volume of faunal and lithic material. In view of the existing archaeological data deriving from the work of Kress, the new work aimed to:

1. Provide a robust stratigraphic anchor to the existing faunal and lithic assemblage;
2. Recover archaeological remains from *in situ* deposits, especially in light of the constant threat of treasure-hunting in the area; and
3. Re-date the archaeological sequence of the cave.

4.4.2 Excavation and Recording

The excavation was conducted in October 2016 with a team consisting of members from the NMP, the local barangay of Maasin and the University of the Philippines. Actual digging days consisted of eleven days out of a projected three weeks of fieldwork.

The entire cave was mapped at the beginning of the excavation to produce a cave floor plan (Figure 4.9). A datum point was established on a limestone block near the entrance of the cave, and from here a datum plane was established. An arbitrary 2 x 2 m grid map was constructed, and this was the basis for mapping and labelling the trenches. Natural and archaeological features were then plotted on the floor plan. In the absence of a full cave floor plan from the 1970 excavation, re-mapping enabled the team to trace the original location of the excavation trenches opened by Kress (2000). In total, four excavation units were opened: Trench 1 (N4W4) in the north area, Trench 2 (S4W2) in the outh area, and Trenches 3 (S1W3) and 4 (S2W4) in the middle area where portions of the original central cave floor remained intact.

A large portion of the cave has been disturbed by treasure hunting activity, especially the central cave floor (Figure 4.9). A visit was conducted in July 2015 to survey the site. A relatively new treasure hunter's pit was observed in the north section of the cave. It also revealed a vertical section of intact archaeological deposits in this area, and this was the basis for opening Trench 1. In late 2016, another pit was found in the southwest portion of the cave, attesting to the continuing threat of treasure hunting. In 2016, the middle portion of the cave was largely covered with backfill from various diggings. These activities have largely spoiled and/or buried *in situ* deposits, and hence it was a challenge to locate such deposits. Re-mapping the site enabled the team to reconstruct the extent and level of the original cave floor. Based on this reconstruction, Trenches 3 and 4 were opened. Trench 2 was opened to investigate *in situ* deposits in the south end of the cave.

Excavation followed natural layers and features using trowels and hand-collection. Within thick deposits or layers, arbitrary 10-cm spits were also used. All sediments from trowelling and hand-collection were dry-sieved through 2-mm screens. In addition, 5-litre bulk samples were taken from recorded layers and features for flotation and wet-sieving. As mentioned in Chapter 3, a 'single context' recording system was used in the excavation. Soil layers and archaeological features were each given individual context numbers. This unique number is the main reference number for all materials associated with the layer or feature. A running inventory of contexts was logged in a 'context inventory form'. Individual contexts have their own 'single context recording form' and all three-dimensional spatial data are recorded on this form. Horizontal plans and vertical profiles were recorded on the context recording forms. At the end of the excavation, stratigraphic profiles were drawn for all excavation units. All trenches were then backfilled following the protocols of the NMP. The archaeological materials recovered were all cleaned, bagged and accessioned using the inventory system of the NMP.

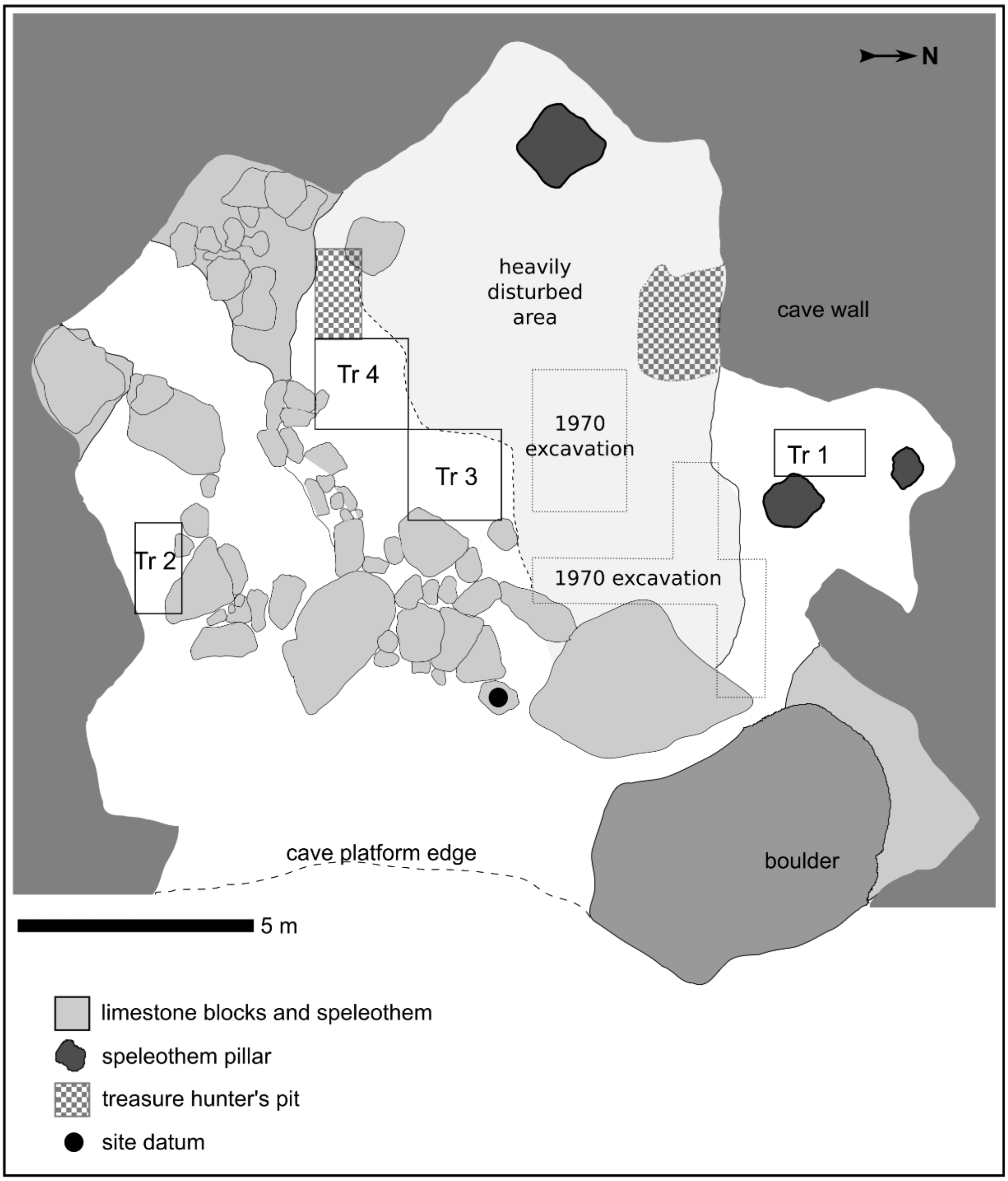


Figure 4.9 Pilanduk Cave floor plan showing location of Trenches (Tr) 1 to 4 and the estimated location of the trenches excavated in 1970 by Kress (2000). The central cave floor has been heavily disturbed by treasure-hunting activities. Mapping by M. Lara and A. Peñalosa. Digitised by M. Lara and J. Ochoa.

4.4.3 Stratigraphy and Chronology

The stratigraphic sequence for Pilanduk Cave is best represented by the Trench 3 sequence, which shows six major layers (Table 4.5, Figure 4.10). Due to the limited time available, it was only in Trench 3 that the excavation went relatively deep (over 1m), and only in its southwest quadrant (1x1 m). The first three layers in Trench 3 are equivalent to and contemporaneous with several contexts uncovered in adjacent Trench 4. In the peripheral Trenches 1 and 2 only three layers are replicated.

Layer I consists of loose silt deposits, backfill from treasure hunter pits and modern materials. The layer is observed in Trenches 3 and 4. Earthenware pottery is also found. Layer II consists of dark greyish brown clayey silt deposits with numerous lithics and animal remains. Evidence of burning across this layer is evident from the sediment, ash inclusions and burnt animal bones. Earthenware pottery is also observed, including large jar fragments. Isolated human bones were also found, which have a different preservation state from the animal remains. The animal remains have a dark brown to black colour (due to burning), whereas the human bones do not show this discolouration and retain the natural colour of bone. The human bones are also more heavily weathered than the animal remains. These differences in preservation states indicate that the human remains are not part of the midden deposition and derive from a different deposition event. Kress (1980, 2000) previously observed that the site was used as a jar burial site as evident from four large jar vessels found in 1970. In the 2016 excavation, a minimum of at least five large vessels was recovered, along with eight small vessels (De Leon 2017). The large vessels cut into the postulated Palaeolithic midden deposits and earthenware sherds are found in the upper levels of Layer II. These upper levels of Layer II correspond to context 111 in Trench 3 and contexts 122, 123 and 126 in Trench 4. The lower portion of Layer II has no earthenware sherds. This is represented by context 112 in Trench 3 and contexts 124, 125, 127, 128 and 129 in Trench 4. These contexts were grouped together into Layer II because of the similar sediment and artefact composition. The main difference would be the absence of sherds in the lower levels. In comparing contexts 111 and 112, there appears to be more ash concentration and hearth remains in context 112 compared to context 111, and hence the distinction among the contexts is also useful for segregating an upper and lower section of Layer II.

Table 4.5 Description of archaeological layers and associated contexts in Pilanduk Cave. A tentative correspondence with Kress's (1977, 2000) chronology is proposed.

Layer	**Description based on Trench 3 and 4 Sequence**	**Associated Contexts**				**Kress's chronology**
		Trench 3	**Trench 4**	**Trench 1**	**Trench 2**	
I	Topmost sediment of loose silt with modern materials, treasure hunter's back dirt of varying sediment composition, and earthenware pottery.	110, 114, 115	121	1, 2, 3, 4, 5, 6	100, 101	Jar burial layer
II	Mid to dark greyish brown silty clay and clayey silt layers with numerous burnt bones and lithics. Earthenware pottery is also present, associated with some human remains (possible jar burials); pottery is intrusive and cuts into midden remains.	111	122, 123, 126			Layer I
II	Mid to dark greyish brown clayey silt layers with ash concentrations/hearth remains, numerous burnt bones and lithics; pottery is absent from hereon.	112	124, 125, 127, 128, 129, 130	absent	102	Layer II
III	Mid greyish brown silt with less ash concentrations, numerous burnt bones and lithics.	116, 117	not reached	absent	absent	Layer III
IV	Mid yellowish brown silt with limestone slabs, lesser animal bones and lithics.	118	not reached	absent	absent	Layer IV
V	Mid yellowish brown clayey silt with small limestone fragments and no artefacts.	119	not reached	absent	absent	n/a
VI	Limestone bedrock	not reached	not reached	8	103	not known

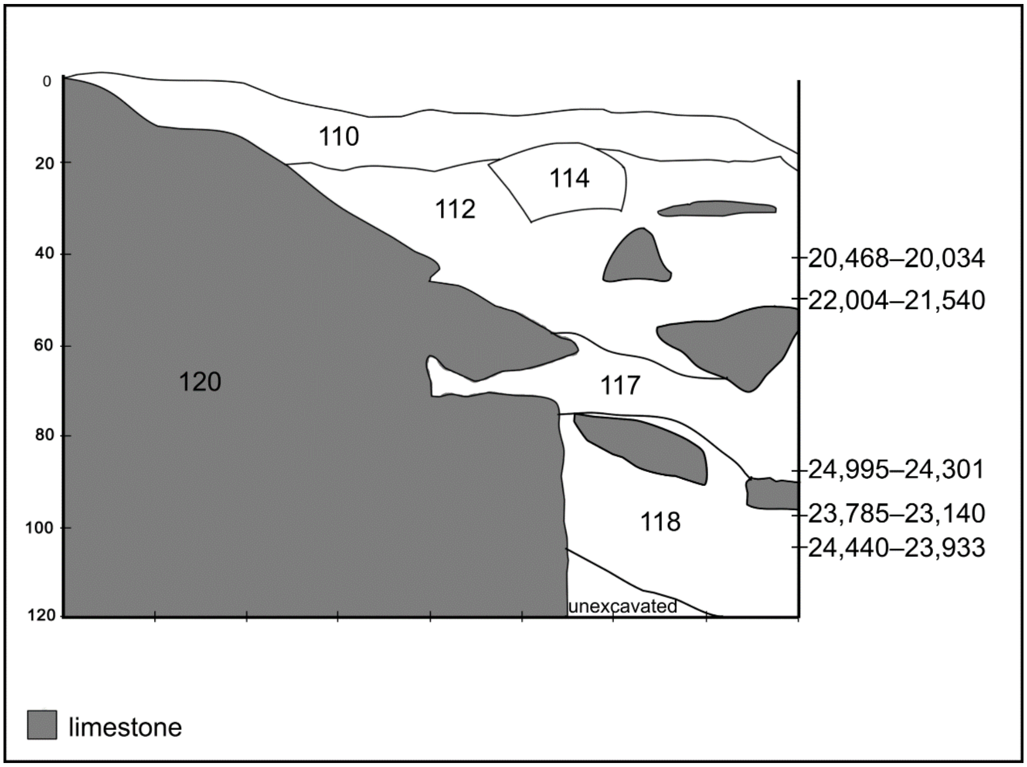


Figure 4.10 Stratigraphic profile of the south wall of Trench 3 of Pilanduk Cave, which shows the entire excavated sequence. Numbers in the layers refer to archaeological contexts (see Table 4.5 for descriptions). Context 114 is a large earthenware fragment representing a jar burial context that intrudes into context 111. Dates shown are calibrated age ranges at 95% probability (see Table 4.6).

In Kress's (1977, 2000) chronology, only the Palaeolithic deposits were numbered. Kress (1980:60) notes that the cave was inhabited by Upper Palaeolithic hunter-gatherers, and after 16,000 BC, it was visited rarely until the burial jars and offerings were deposited. He also notes that the ceramic assemblages were found at or near the surface of the site. In our 2016 investigations, the surface of the cave was extensively disturbed such that a new layer of sediment has covered Kress' Layer I. It was still observable, nonetheless, that the burial and ceremonial jars were in this topmost layer, and in the upper levels of Layer II. In the current chronology, Kress's Layers I and II possibly correspond with the upper and lower levels of Layer II (Table 4.5). Further stratigraphic data (e.g. stratigraphic profile or soil descriptions) from the 1969-70 excavations are unavailable and so direct comparison is not possible. Kress (2000) only published a site plan and the radiocarbon dates. I base the correspondence of layers mainly on the description of finds that Kress (1977, 1980, 2000) provided. Kress reports that there are "three thick and rich Pilanduk

Cave components" (1977: 42) that contain several hearths and numerous animal bones and lithics. These "components" appear to correspond to Layers II to III (Table 4.5).

Layer III consists of a mid-greyish brown silt with fewer ash concentrations, but still with numerous burnt bones and similar lithics. It is represented by contexts 116 and 117 in Trench 3. Layer III, and others below it, are only observed in Trench 3. Trench 4 only reached Layer II. In Trenches 1 and 2, the sequences were much shallower; only Layer II was observed, after which bedrock was already uncovered.

Layer IV consists of a mid-yellowish brown silt with numerous limestone slabs. There is considerably less evidence of burning in this layer compared to the upper layers. There is also a lesser quantity of animal bones and lithics. Layer V is comprised of mid-yellowish brown clayey silt with small limestone fragments (versus the large limestone slabs in Layer IV). In the 1x1 m section in Trench 3, there were no artefacts found in Layer V. Layer VI is designated as the limestone bedrock. It was reached in Trenches 1 and 2 but not in Trenches 3 and 4.

Table 4.6 Radiocarbon dates for Pilanduk Cave. Samples are all from Trench 3. Ages were calibrated using OxCal 4.3 and IntCal 13 and are shown at 95.4% probability (Bronk Ramsey 2017). LDP = local datum point. All samples are from wood charcoal.

Accession No.	OxA No.	Species	Context	Depth from LDP (cm)	Radiocarbon age (BP)	Calibration age range (cal BP)
5397	37182	*Michelia* sp.	112	46	16,785 ± 65	20,468–20,034
5587	36553	*Wrightia* sp.	112	52	17,980 ± 70	22,004–21,540
6210	36332	*Pinus* sp.	117	90	20,460 ± 90	24,995–24,301
6255	37180	*Kibatalia* sp.	118	98	19,500 ± 90	23,785–23,140
6255	37181	*Kibatalia* sp.	118	98	19,570 ± 80	23,875–23,295
6257	36331	*Syzygium* sp.	118	103	20,120 ±90	24,440–23,933

New radiocarbon dates were obtained for Pilanduk Cave (Table 4.6). All samples are from charcoal. Macrobotanical identifications were conducted by the project archaeobotanist, Jane Carlos. Submitted bone and teeth dating samples did not yield sufficient collagen. All samples are from the Trench 3 sequence. Three contexts were dated: contexts 112, 117 and 118. Two ages are reported for specimen 6255, one of which is a control sample (OxA-37181). The age produced agrees with OxA-37180. Ages shown in Table 4.5 follow a sequence from highest to lowest depth. Note that specimen 6210 (OxA-36332) has a slightly older age range than specimens 6255 and 6257. Nonetheless, the calibrated age range for specimen 6210 overlaps with specimen 6257. Specimen 6210 was taken from the base of context 117 (Layer III), where there might have been mixing of sediments and movement of charcoal remains in the interface between contexts 117 and 118 (Figure 4.10). This date may likely represent an age for context 118 (Layer IV).

Table 4.7 Trench 3 specimen counts for animal bones, lithics and shells per context from the 2016 excavation of Pilanduk Cave.

Finds	**Context 110**	**Context 111**	**Context 112**	**Context 117**	**Context 118**
Bones	710	3017	7458	3055	671
Lithics	57	173	364	132	49
Shells	62	304	483	406	209

The ages retrieved from the samples indicate two general phases of Late Pleistocene occupation. The ages for context 112 represent an LGM occupation at *ca*. 21,000-20,000 cal BP. The calibrated age ranges for context 112 overlap with calibrated ages of two dates published by Kress (2000; see Tables 4.3 and 4.4) for his Layers I and II. The second phase of occupation is represented by context 118 (Layer IV). The calibrated ages for context 118 (ca. 25,000–23,000 cal BP) are close to the uncalibrated age (*ca*. 25,000 BP) for one sample published by Kress (2000) for his Layer IV. The high quantity of faunal remains and lithics in contexts 111, 112 and 117 compared to context 118 indicates a more intensive occupation period in the younger phase. This is reflected in the raw counts of archaeological finds per context in Trench 3 (Table 4.7). This agrees with Kress's (2000) description of site intensification based on his analysis of the mollusc remains.

4.5 Conclusion

This chapter has presented the archaeological background for the three main study sites of the thesis, along with comparative sites that have published zooarchaeological analyses. Two new radiocarbon dates have also been presented for Minori Cave. These are direct dates on macaque teeth, which have implications for the age and distribution of this species on Luzon. The chapter has also presented new archaeological evidence for Pilanduk Cave based on the 2016 re-excavation of the site. The results clarify the chronology and stratigraphy of the site and confirm its MIS-2 age. Two main occupation phases are represented in the Late Pleistocene deposits: an intensive occupation phase during the LGM (21,000–20,000 cal BP), and an older phase at 24,000–23,000 cal BP. The new dates and stratigraphic evidence are in agreement with Kress' (1977, 2000) previous descriptions of the Palaeolithic deposits. These results demonstrate that Pilanduk Cave presents the largest LGM archaeological assemblage in the archipelago, which has significant potential for understanding the LGM human occupation of Palawan and the Philippines. The thesis will investigate this further through the succeeding zooarchaeological analyses.

Chapter 5 Late Pleistocene Fossil Vertebrates of Pilanduk Cave

5.1 Introduction

In this chapter, I present the analysis of the terrestrial vertebrate record of Pilanduk Cave in Palawan Island. The archaeological analysis presented in Chapter 4 and the faunal analysis in this chapter serve to provide a Late Pleistocene faunal record for Palawan that extends beyond the oldest archaeological levels of Ille Cave at 14,000 cal BP. As described in the previous chapter, the Pilanduk Cave assemblage currently represents the most substantial archaeological and vertebrate fossil record of the Last Glacial Maximum in the Philippines, dating from 25,000 to 20,000 cal BP. Cultural layers dating between 30,000 and 18,000 BP (MIS-2) have also been recorded in Callao Cave in Luzon Island and Bubog Rockshelter in Mindoro Island. However, the archaeological remains found in these other sites that date to this period are relatively sparse. The archaeological visibility of the LGM across the Philippine archipelago is affected by sea-level fluctuation. Many coastal areas across the islands, including Palawan, that were exposed during the LGM are presently underwater. This is identified as one of the reasons for the rarity of LGM sites on Palawan (Robles et al. 2015), and hence the confirmation of LGM dates and re-excavation of Pilanduk are significant. The site is currently less than a kilometre from the coast, but it would have been 40 km inland during the periods of LGM occupation.

The main body of the chapter presents the accounts of species for Pilanduk, along with data on systematics, ecology and previous fossil records. The focus of the analyses is on the extirpated taxa because confirmation of the Late Pleistocene presence of extinct species is crucial for our understanding of Philippine faunas. Biological data for the extant species are primarily derived from synopses of Philippine and Palawan mammals (Esselstyn et al. 2004; Heaney et al. 2010). To provide the context for the Pilanduk vertebrate assemblage, an overview of the island fossil record follows.

5.2 Palawan Island Vertebrate Fossil Record

The current oldest known vertebrate fossil record for Palawan comes from Tabon Cave, primarily represented by Pleistocene *Homo sapiens* remains that range in age from 47,000 to 16,000 BP (Détroit et al. 2004; Dizon et al. 2002). Fox (1970) reported on the presence of other vertebrate taxa in Tabon such as deer and pig; however, the remains were never properly described. Only a few of the Tabon vertebrate remains are currently found in the museum collections, indicating that they may have been discarded or not curated in the intervening decades (Corny 2008). Within the same karst complex, Fox (1970:47) also reported on the presence of wild pig and deer remains from nearby Guri Cave, which date to *ca.* 4000 BP. A re-excavation of Guri Cave by Heng (1988) showed that deer was common in the assemblage but, curiously, wild pig remains were reportedly absent in the sequence, contrary to the report of Fox (1970).

Reis and Garong (2004) presented a Holocene faunal sequence from four cave sites in southern Palawan, two of which are in the Tabon Cave complex, and another two in the Kalatagbak area close to where Pilanduk Cave is located. They identified 28 vertebrate species, including two new records for bird taxa (*Otus* sp. and *Collocalia salangana*), and a new record for a shrew species (*Crocidura* sp.) The only large mammal recorded was the Palawan bearded pig (*Sus ahoenobarbus)*. According to the authors, their data highlight the more insular affinities of Palawan (largely because of the absence of large mammals with low dispersal capabilities) in comparison with Borneo. The low abundance of hunted taxa and the predominance of microvertebrates appear to indicate that these sites were not intensively occupied by humans.

Presently, the most sizeable fossil vertebrate record for the island comes from the Dewil Valley of El Nido in northern Palawan. As described in Chapter 4, Ille Cave presents a sequence from the Terminal Pleistocene to the near present, documenting the first fossil records for several extinct and extant mammal and reptile taxa of the island (Ochoa 2009; Piper et al. 2011). Of particular interest is the first record of the tiger (*Panthera tigris*) on Palawan (Piper et al. 2008), as well as the description of two deer taxa and a canid. Nearby Pasimbahan Cave also presents a 10,000-year Holocene sequence, detailing taxa similar to those found in Ille Cave (Ochoa et al. 2014). Together, these two sites provide evidence for the changing composition of the island's mammal fauna in the last 14,000 years. Three large mammals – tiger, rusine deer, and hog deer – were extirpated in the Holocene. As a consequence of diminishing deer populations, a resource switch is evident in the subsistence record, with the Palawan bearded pig becoming the main large prey of humans from the Mid Holocenek onwards (Ochoa and Piper 2017; Piper et al. 2011).

The cultural layers of the Ille Cave sequence only reach as far back as the Terminal Pleistocene, and the Tabon vertebrate remains were never properly described. As a result, Palawan has a limited Pleistocene faunal record. The rich fossil record of Pilanduk is a significant contribution that addresses this paucity, and it provides evidence for the crucial climatic period of the Last Glacial Maximum.

5.3 Pilanduk Cave Vertebrate Fauna: An Overview

A total of 8491 specimens were analysed from Pilanduk Cave, of which 7826 were from the 2016 re-excavation of the site (Table 5.1). The remaining 665 fragments were from an attempt to analyse materials from Kress' older excavation, but very few fragments turned out to have sufficient stratigraphic information to make the exercise worthwhile. The analysis of the 2016 assemblage was focused on the Trench 3 sequence, since this unit had the longest/deepest excavated sequence among all trenches. Proportion of bone identified to taxon is at 18% for Pilanduk

A total of seven mammalian taxa were identified, together with two reptile taxa (Table 5.1). The Pilanduk Cave evidence currently represents the oldest dated fossil records of these nine identified taxa, since the Tabon vertebrate fauna was not described in detail. Bone accumulation is very dense and approximately equal across contexts 111, 112 and 117, whereas there was much less bone accumulation in context 118 (Table 5.1). Cervid remains dominate across all layers (Figure 5.1). In particular, the larger cervid (*Rusa* sp.) is the more abundant of the two species of deer (Section 5.4.7). The Palawan bearded pig is the next most abundant animal in contexts 111, 112 and 117. All other taxa occur in much smaller numbers; nonetheless, these confirm the Late Pleistocene (LGM) presence of these species on Palawan Island. This includes rare fossil finds for the tiger uncovered in contexts 111, 112 and 117 (Section 5.4.4). Records for macaques are also found in the LGM deposits and this has implications for its native status on the island (Section 5.4.1).

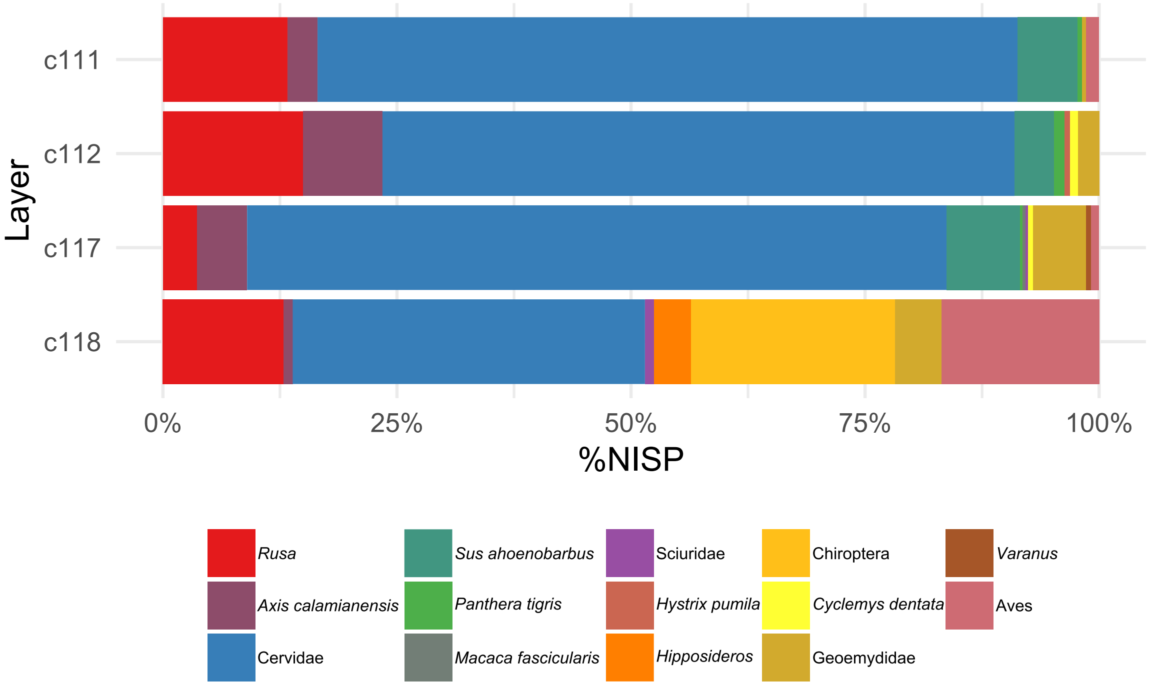


Figure 5.1 Relative taxonomic abundance (%NISP) of vertebrate taxa at Pilanduk Cave across four major archaeological layers. NISP = number of identified specimens, c = archaeological context. NISP counts are in Table 5.1.

5.4 Accounts of Species

Species accounts for each of the identified non-volant mammal taxa follows in this section. The only volant mammal identified is the diadem roundleaf bat (*Hipposideros diadema*) found in context 118 (see Ochoa 2009 for morphological description of this bat species). Detailed treatments are specifically provided for the tiger (*Panthera tigris)* and deer (*Rusa* and *Axis*). Due to the rarity and extinct status of these fossil taxa, further analyses are needed in order to clarify the taxonomy and morphology of these mammals in the Palawan record.

5.4.1 Order Primata

Family Cercopithecidae
Macaca fascicularis

The bones of long-tailed macaque are very rare in the assemblage, numbering to only four specimens. Only one fragment was found *in situ*, a left ischium fragment from context 117. The rest of the specimens consisted of a lower left canine fragment, a complete right astragalus and a right mandible fragment with no teeth. The three specimens are redeposited cranial and post-cranial elements found on the surface of the site. Comparing the specimens to the state of preservation of other specimens found *in situ*, the remains appear to originate from the LGM deposits based on their taphonomic similarities to the former, rather than from the Late Holocene burial deposits. The LGM bone accumulation primarily consisted of partially mineralised bone that were brown to dark brown in colour. They are typically only slightly weathered and have dark spots attributed to mineral staining (see Section 8.2). These attributes were observed on the three macaque surface finds. In contrast, the Late Holocene burial deposits consisted of moderate to highly weathered fragments that retained the natural colour of bone (cream/white). The macaque is relatively rare in Pilanduk; however, this taxon is a relatively common and abundant intermediate mammal in the Holocene sequence of Ille and Pasimbahan Caves.

Modern Philippine macaque populations are said to differ little from Bornean macaques (Heaney et al. 2010), and this has implications for origin and dispersal. The species is widespread in the Southeast Asian region and is also known to have been introduced to some oceanic islands of Indonesia by humans (van den Bergh et al. 2001). On Palawan, it is considered a native of the island based on biogeographic and phylogenetic grounds (Esselstyn et al. 2004; Fooden 1995; Heaney et al. 1998). Molecular phylogenetic data clearly signal a Sundaic origin, with most Philippine sequences clustering in one group (Blancher et al. 2008, 2012; Tosi and Coke 2007). Mitochondrial DNA sequence phylogeny also shows low nucleotide diversity in Philippine macaque samples, suggesting a bottleneck following initial dispersal by Indonesian stock (Blancher et al. 2008). Because the Philippine macaque population is reportedly free of introgression from the rhesus monkey as compared to mainland (Vietnamese) *M. fascicularis*, the former is posited as an isolated population that had experienced a founding effect followed by a rapid initial expansion (Blancher et al. 2012: 605-606; see Section 7.4.2). However, the status of Palawan macaque populations in this scenario is uncertain since only macaques from the oceanic Philippines appear to be represented in modern DNA studies (or in some cases, the island provenance of Philippine samples are unstated). In this light, the Pilanduk and other Palawan fossil records provide evidence in support of the native status of *M. fascicularis* on this island, documenting its relatively continuous LGM to Late Holocene presence (Ochoa et al. 2014; Piper et al. 2011; Reis and Garong 2001). It goes by several local names, including *bakes* and *amu*.

Table 5.1 Number of identified specimens (NISP) by layer from Pilanduk Cave excavated by NMP and JO during the 2016 field season and in 1970 by J. Kress. Trench 3 Layers refer to context numbers. *Locally extinct species. ** Two additional specimens of tiger were retrieved from Trench 4.

Taxon		**Trench 3 Layers**				**2016**	**Kress' Excavation**					**1970**		
	surface	**111**	**112**	**117**	**118**	**Total**	**Layer 1**	**Layer 2**	**Layer 3**	**Layer 4**	**No Layer**	**Total**	**Total**	**% NISP**
Axis calamianensis	19	7	30	19	1	76	1				8	9	85	1.0
Rusa sp.	80	29	53	13	13	188	10	6		7	40	63	251	3.0
Cervid	128	163	239	266	38	834	39	8	37	5	106	195	1029	12.1
Sus ahoenobarbus	5	14	15	28	0	62	8	3	7		11	29	91	1.1
Panthera tigris	1	1	4	1		9**							9	0.1
large mammal	28	979	1004	1718	266	3992	65	8	163	8	59	303	4295	50.6
Macaca fascicularis	1			1		2					2	2	4	0.05
Sciuridae				1	1	2							2	0.02
Hystrix pumila			2			2							2	0.02
intermediate mammal		3	1	5	3	12	1		1			2	14	0.2
Hipposideros diadema					4	4							4	0.05
Chiroptera					22	22							22	0.3
Varanus cf. *palawanensis*				2		2							2	0.02
Geoemydid		1	8	20	5	34			2		1	3	37	0.4
Cyclemys dentata			3	2		5							5	0.1
bird		3		3	17	23							23	0.3
macrovertebrate		971	962	483	106	2522	3		55		1	59	2581	30.4
microvertebrate		2			30	32							32	0.4
	261	2173	2321	2562	506	7825	127	25	265	20	228	665	8490	100.0

5.4.2 Order Rodentia

Family Sciuridae
Sundasciurus/Hylopetes

The squirrel is represented by only 2 fragments, one each from context 117 and context 118. The identified specimens – consisting of a proximal femur fragment and mandibular fragment with no teeth – preclude differentiation between *Sundasciurus* (tree squirrel) and *Hylopetes* (flying squirrel). The presence of these obligate canopy dwellers, along with the macaque, indicates tree cover in the vicinity of Mt. Magngisi. Locally, squirrels are known as *bising* and flying squirrels as *bia'tat* and *tapilak*.

5.4.3 Family Hystricidae
Hystrix pumila

The Palawan porcupine is represented by a mandibular fragment and an isolated molar fragment from context 112, representing a single individual. The porcupine is recorded from four other archaeological sites on the island from the Terminal Pleistocene to the Holocene: RS1 and Tarung-Tarung Cave in southern Palawan (Reis and Garong 2004) and Ille and Pasimbahan Caves in northern Palawan (Ochoa and Piper 2017). Porcupines occur in lowland primary forest, as well as heavily disturbed secondary forest/grassland mosaic (Heaney et al. 2010). It is a nocturnal species, foraging primarily on the ground and feeding on plant material. It is locally known as *durian* or *landak*.

5.4.4 Order Carnivora

Family Felidae
Panthera tigris

Nine specimens belonging to a large and robust pantherine were recovered from Pilanduk Cave (Figure 5.2). Measurements of all specimens are presented in Table 5.2. The size of the fossils points to the largest pantherines – *Panthera tigris* and *Panthera leo* (Tables 5.3 and 5.4). From the Late Pleistocene to the present-day, the only recorded pantherines in Southeast Asia are the tiger (*P. tigris)* and the leopard *(P. pardus).* There is no modern or fossil record of the lion (*P. leo*) in the region. The current tiger taxonomy recognizes six living subspecies: Bengal tiger *P. t. tigris*, Amur tiger *P. t. altaica*, South China tiger *P. t. amoyensis*, Sumatran tiger *P. t. sumatrae*, Indochinese tiger *P. t. corbetti*, and Malayan tiger *P. t. jacksoni* (Goodrich et al. 2014; Luo et al. 2004, 2010). Based on historical and archaeological evidence, the tiger had a broader distribution in Island Southeast Asia in the past. The historic distribution of the tiger included Java and Bali; however, they both became extinct in the 20th century. The only living tiger population in the Sundaic Islands is the Sumatran tiger. The fossil record of Borneo has also produced some rare tiger material, particularly from Niah and Madai Caves (Harrison 1998; Piper et al. 2007).

Molecular genetic data have provided numerous insights on the demographic and evolutionary history of modern tigers. The time to the most recent common ancestor for modern tigers has been estimated at 72,000-108,000 years ago (Luo et al. 2004). The phylogenetic placement of the South China tiger (*P. t. amoyensis)* is considered basal in phylogeographic reconstructions, and a once widespread tiger population was present from China to the Sunda Shelf (Driscoll et al. 2009; Luo et al. 2004; Xue et al. 2015). Subsequently, this population became isolated, likely due to rising sea levels during interglacial periods. A second wave of tiger expansion and divergence is said to have replaced much of the range of the Amur tiger on mainland Asia and evolved into the current recognized subspecies (Kitchener and Yamaguchi 2010). In the case of the Island SEA tigers, the genetic ancestry of the Bali and Java tiger indicates that they form a strongly supported monophyletic clade with the Sumatran tiger that is distinct from other modern mainland subspecies (Xue et al. 2015). Tiger fossils have been found in paleontological deposits in Java dated to as old as 1.2 million years ago (van den Bergh et al. 2001). However, because coalescence time of modern tiger lineages is within the last 100,000 years, the modern

Sundaic tigers are likely not derived from these older tiger populations on Java (Kitchener and Yamaguchi 2010). Instead, tigers from the islands of Sumatra, Bali, and Java appear to be descended from a more recent population expansion during the Late Pleistocene, particularly when the islands were connected intermittently during periods of glacial cycles (Xue et al. 2015).

The presence of the tiger on Palawan Island has been previously reported in Ille Cave, represented by only three specimens: two fragments from a Terminal Pleistocene layer and one from an Early Holocene layer (Ochoa and Piper 2017; Piper et al. 2008). Some scepticism was previously expressed by van der Geer and colleagues (2010) regarding the native presence of the tiger on Palawan, when the two fossils were first described from the Terminal Pleistocene levels (14,000 cal BP) of Ille Cave. To help clarify the issue, a detailed treatment of the fossil tiger identifications is provided below. The Pilanduk Cave record considerably adds to the fossil inventory of the tiger on Palawan and extends its spatio-temporal distribution into the LGM. Out of nine specimens, two complete elements were found: a refitted third metacarpal and a sub-terminal phalanx. The other seven specimens are fragments of metapodia and phalanges. The metapodia are more clearly distinguishable based on the proximal articulation, and in this case, two specimens with proximal ends (specimens 9274 and 7365) are more easily identifiable. Nonetheless, upon careful examination and measurement, distal heads of the metapodia can also be differentiated to digit and side, based on the outline and shape of the heads and epicondyles. What follows is the individual description of each pantherine specimen. In the text and figures, MC refers to metacarpal and MT refers to metatarsal.

Table 5.2 Inventory and measurements (in mm) of pantherine specimens from Pilanduk Cave. *Asterisk indicates that ascription to *P. tigris* is provisional due to the fragmented state of specimens and/or lack of measurable landmarks. GL= greatest length (for complete specimens only), MD=maximum diameter, Bp= proximal breadth (medio-lateral), Dp= proximal depth (antero-posterior), Bd = distal breadth, Dd = distal depth, Sd = smallest transverse diameter of diaphysis. Bd for metapodials is taken at the epicondyles.

Bone ID	Trench/Grid	Context	Side	Portion	Element	GL	MD	BP	Dp	Bd	Dd	Sd
9274	surface	surface	L	complete	third metacarpal	105.56		25.1	20.42	24.48	19.3	14.8
5393	3	112	R	complete	sub-terminal phalanx	35.25		16.15	14.08	14.63	9.96	10.5
7365	4	127	R	proximal	third metacarpal		25.1	25.02	22.15			
7366	4	127	R	distal	third metacarpal		35.83			19.3	18.12	
8803	S2W5	surface	R	distal	fourth metacarpal		35.43			18.52	17.52	
5811	3	112	R	distal	fifth metatarsal		23.76			14.81	15.31	
5247*	3	111	\	distal	proximal phalanx		14.65			12.42	8.77	
5812*	3	112	\	proximal	distal phalanx		24.2					
5394*	3	112	\	proximal	distal phalanx		27.38					

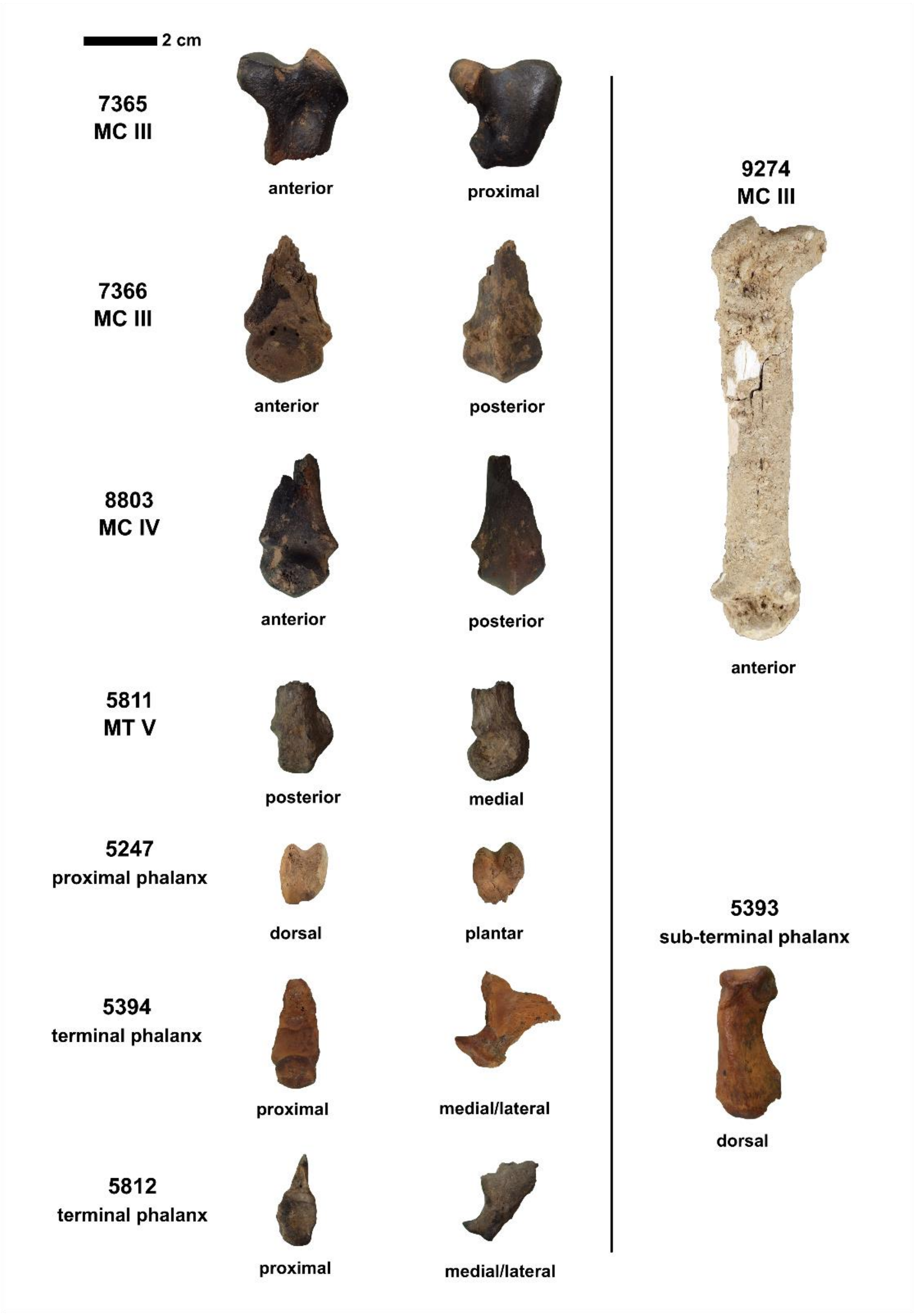


Figure 5.2 Nine fossil metapodial and phalanx specimens from Pilanduk Cave referred to *Panthera tigris*. Complete specimens are shown on the right in anterior/dorsal views. Fragmented specimens are shown on left-hand rows in two aspects. MC = metacarpal, MT = metatarsal. All images shown at 2 cm scale.

5.4.4.1 Pantherine Metapodials

Pilanduk-9274. This specimen is a left third metacarpal from a large and robust pantherine (Figure 5.3). The specimen was found amongst surface finds from treasure hunters' back dirt to the east of Trench 1/Grid N4W4. The specimen is composed of two fragments that were refitted during sorting of surface finds from this area of the cave. The breakage was relatively fresh, and presumably the damage occurred during prior treasure-hunting activities in the site. The specimen is wholly covered in thin calcareous concretion, and the cervid bones found alongside it were also covered in concretion. Comparing this state of preservation to all the bones recovered *in situ* across the site, this taphonomic condition was observed on specimens found in grid N4W4 and N3W4 in the northern section of the cave. In Trench 1 (which has the grid number N4W4) in particular, bones with calcareous concretion were found in contexts 5 and 6, which correspond to Layer I and II of the site. It is possible, then, that this specimen comes from similar levels in and around grid N3W4, where deep treasure hunter pits were observed (refer to Figure 4.11).

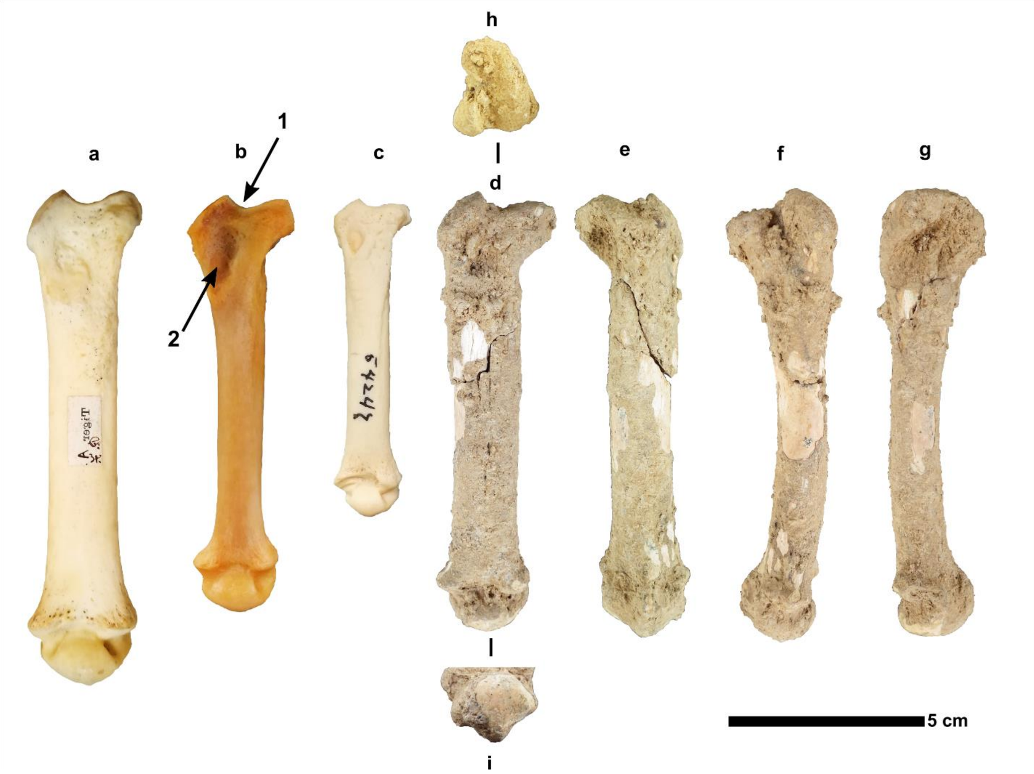


Figure 5.3 Fossil left third metacarpal (Pilanduk-9274) referred to *Panthera tigris* in anterior (d), posterior (e), medial (f), lateral (g), proximal (h) and antero-distal (i) views. Comparisons are with the third metacarpals of modern Bengal tiger (a, OUMNH 3756, mirror view of R side), captive Sumatran tiger (b, FMNH 165401) and captive leopard (c, FMNH 54247). Refer to text for labels 1 and 2.

The specimen's overall size and outline of the distal head indicates that it belongs to a middle-digit metapodial, while the proximal articulation clearly distinguishes it as the third metacarpal (MC III). Biometric comparisons with modern pantherines (Figure 5.4, Tables 5.3 and 5.4) show that the specimen distinctly falls in the range of the tiger and is much larger than leopard comparatives. The specimen falls in the lower size range of tiger, indicating that it belongs to a smaller-sized individual compared to larger continental tigers. The largest museum reference individuals are Bengal and Siberian tigers, while the smallest ones are zoo specimens from Sumatra and Peninsular Malaysia. Pilanduk-9274 is moderately longer and has a more robust diaphysis compared to the Sumatran and Malaysian tiger reference. This more pronounced robusticity likely has to do with the individual being from the wild, as compared to the Sumatran and Malaysian comparatives, which are known captive individuals.

Table 5.3 Summary of metapodial measurements (in mm) of Pilanduk Cave fossil and modern pantherines. N = number of samples of modern individuals, MC = metacarpal, MT = metatarsal, Bp = proximal breadth, Dp = proximal depth, Bd = distal breadth, Dd= distal depth. Breadth measurement is medio-lateral and depth is antero-posterior. Measurements for modern pantherines are given as ranges. *underestimated value due to slight damage on 5811.

Element	Taxon	N	Bp	Dp
MC III	Pilanduk-9274		25.1	20.42
	Pilanduk-7365		25.02	22.86
	P. tigris	13	21.01-27.56	20.91-28.84
	P. pardus	4	14.51-17.21	13.48-16.41
	P. leo	2	21.6-28.12	22.41-26.37
		N	Bd	Dd
MC IV	Pilanduk-8803		18.52	17.52
	P. tigris	13	17.81-22.11	17.09-21.3
	P. pardus	4	11.01-14.06	10.9-13.64
	P. leo	2	18.85-20.37	19.65-21.74
MT V	Pilanduk-5811*		14.81*	15.31*
	P. tigris	13	15.6-20.18	16.53-20.23
	P. pardus	4	11.03-12.71	12.21-13.3
	P. leo	2	17.54-18.83	18.95-20.84

Table 5.4 Measurements (in mm) of fossil (Pilanduk) and modern pantherine metacarpal III. GL = greatest length, Bp = proximal breadth, Dp = proximal depth, Bd_Ep = distal breadth at the epicondyles, Bd_Con = distal breadth at the condyles, Dd= distal depth, MinTd= minimum transverse diameter of shaft, MinAPD = minimum antero-posterior diameter of shaft. Measurement conventions follow von den Driesch (1976) and Hemmer et al. (2011).

Museum	Number	Taxon	Locality	Side	Sex	GL	BP	Dp	Bd_Ep	Bd_Con	Dd	MinTD	MinAPD
PNM	9274	*P. tigris*	Pilanduk	L		105.56	25.1	20.42	24.48		19.3	14.8	
PNM	7365	*P. tigris*	Pilanduk	R			23.05	22.15					
PNM	7366	*P. tigris*	Pilanduk	R					19.3		18.12		
UC GCL	151	*P. tigris*	unknown	L	unknown	111.17	25.37	23.5	22.88	20.31	20.12	13.81	12.81
OUMNH	3756	*P. tigris*	India	R	male	110.58	25.46	25.82	24.34	21.22	20.56	15.08	13.25
OUMNH	14223	*P. tigris*	Perak, Malaysia	L	unknown	108.64	25.85	25.99	23.15	21.45	21.26	14.18	12.59
OUMNH	14225	*P. tigris*	unknown	L	unknown	116.47	26.66	28.84	24.36	23.21	20.48	13.25	12.24
UMZC	K. 5627	*P. tigris*	Selangor, Malaysia	L	female	99.11	21.01	21.07	20.16	18.05	17.52	11.97	10.6
FMNH	159999	*P.tigris altaica*	Zoo (Asia)	L	female	110.86	27.56	25.54	24.16	20.51	19.64	13.36	11.89
FMNH	188486	*P.tigris altaica*	Zoo	L	female	109.75	24.44	23.78	22.39	20.06	19.2	11.41	11.31
FMNH	60760	*P. tigris tigris*	Zoo - India	L	female	106.81	23.58	21.68	22.7	18.16	19.55	12.5	11.25
FMNH	165401	*P. tigris*	Zoo - Sumatra	L	male	97.91	24.17	22.73	20.1	17.44	18.18	9.95	9.67
FMNH	57172	*P. tigris*	Zoo - India	R	female	111.43	25.21	23.1	23.27	19.9	20	11.87	11.3
FMNH	134496	*P. tigris*	Zoo (Asia)	L	male	107.81	27.41	25.63	23.25	21.41	21.15	11.64	12.21
FMNH	134497	*P. tigris*	Zoo (Asia)	L	female	114.11	24.32	24.29	22.08	18.88	19.78	12.25	11.94
FMNH	134607	*P. tigris*	Zoo (Asia)	L	unknown	96.9	22.67	20.91	20.94	18.38	17.16	10.41	9.63
OUMNH	14239	*P. pardus*	unknown	L	unknown	68.56	16.64	13.48	13.15	11.28	12.41	8.27	7.01
OUMNH	14235	*P. pardus*	unknown	R	unknown	62.93	14.51	13.71	11.97	10.3	10.75	7.47	6.74
FMNH	54247	*P. pardus*	Zoo (Africa)	L	male	75.65	17.21	16.41	15.76	12.69	13.14	9.69	8.67
FMNH	196089	*P. pardus*	Zoo (Asia)	L	male	77.46	16.54	15.19	14.61	12.5	13.73	8.38	8.05
FMNH	153777	*P. pardus*	Zoo (Africa)	L	female	73.97	16.2	15	13.92	12.5	13.19	8.12	7.5
FMNH	60051	*P. pardus*	unknown	L	male	74.14	15.5	14.98	13.84	11.96	12.2	7.62	7.16
OUMNH	14200	*P. leo*	unknown	L	unknown	104.96	23.96	22.41	20.12	18.23	18.73	13.71	11.69
OUMNH	14201	*P. leo*	unknown	L	male	118.53	28.12	26.37	23.18	20.72	20.51	15.36	12.48
UCMZ	K. 5463	*P. leo*	Africa	R		119.88	24.95	24.9	22.63	20.55	21.64	15.17	12.71
UCMZ	K. 5466	*P. leo*	unknown	L	female	105.21	21.6	23.24	20.55	18.4	19.09	10.96	11.53

Although the reference sample is small, certain morphological features are noted that can possibly distinguish tigers, lions, and leopards. In terms of the morphology of the proximal articulation of the MC III, the tiger shows a more indented midline proximal articulation (#1 in Figure 5.3) seen in proximal and anterior view, and this indentation continues onto the antero-proximal surface of the diaphysis (#2 in Figure 5.3). This feature is relatively shallower in two observed lions. There is also some observable difference in the attachment site on the lateral side of the MC III, which receives the proximal end of the fourth metacarpal. In the tiger, this is usually a deeper notch/articulation compared to the lion, because the articulating facet in the MC IV is relatively more bulbous in the reference tigers versus the lions. The proximal-medial articulation of the MC III is also more elongate and narrower in tiger versus lion references. In the referred specimen 9274 (and in 7365 below), these three morphological features are aligned with tiger morphology. Nonetheless, further comparison with additional modern individuals is necessary. In comparison to a leopard specimen (OUMNH 14239), the rugosity and robusticity of the proximal articulation are similar to those of a tiger, but the leopard is considerably smaller than the tiger and Pilanduk-9274 in all dimensions. It is worth noting that the leopard comparative is likely from a captive individual, and captivity appears to impact size of individuals. From observations of a few captive leopard and tiger reference individuals included in the study, their bones appear to be smaller in size and more gracile compared to wild individuals.

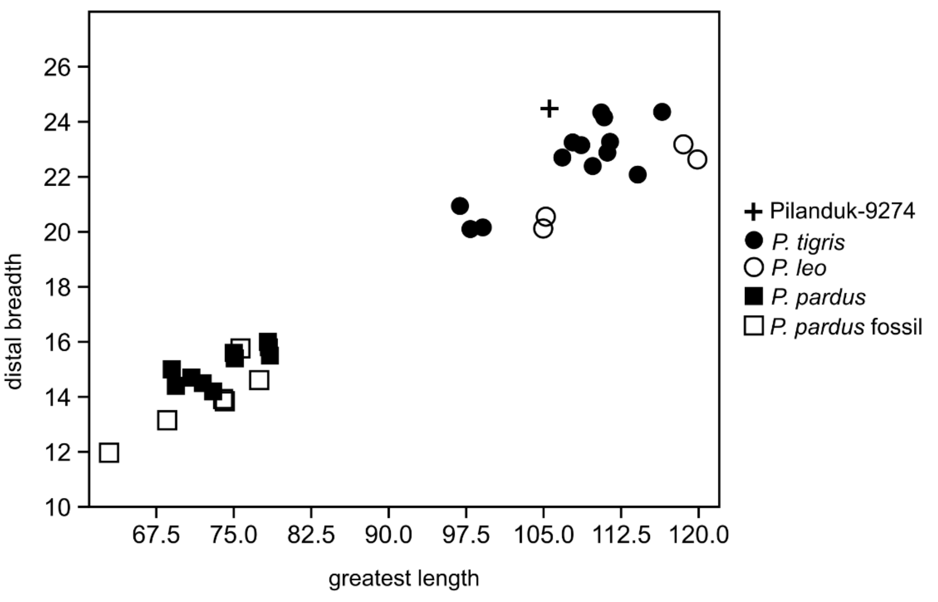


Figure 5.4 Bivariate plot of fossil and modern pantherine (*Panthera*) third metacarpal measurements (in mm). Distal breadth is measured medio-laterally at the epicondyles. Measurements of Pilanduk Cave and modern comparatives are in Table 5.4. Fossil data for *P. pardus* are from Diedrich (2013).

Pilanduk-7365. This is a proximal fragment of a right third metacarpal (Figure 5.2). It was found *in situ* within Layer II (context 127) of Trench 4. The specimen is black in colour and charred, as were many of the bones found in this layer. The specimen is of a similar size as Pilanduk-9274, a left MC III, and the two specimens may belong to the same individual (Table 5.2). Pilanduk-9274 may appear to have slightly bigger dimensions, with a 2-mm difference, but this is due to the calcareous concretion adhering to it. Pilanduk-7365 was found in the southern portion of the cave, whereas Pilanduk-9274 was in the northern section, approximately 12 meters away from Trench 4. Biometric comparison with modern pantherines place it in the size range of the tiger (Tables 5.3 and 5.4).

Pilanduk-7366. This is a distal fragment of a right third metacarpal of a large robust felid, consisting of the head, epicondyles and a small portion of the distal diaphysis (Figure 5.2). It was found in association with Pilanduk-7365 within Layer II (context 127) of Trench 4. The specimen is charred and of a similar state of preservation as Pilanduk-7365.

A note must be made on the identification of distal heads, because this is more difficult compared to the more readily identifiable proximal articulations. Based on observations on nine complete sets of modern tiger metapodia, the outlines and overall morphology of distal condyles do vary for each metapodium of the manus and pes. With careful comparison to complete sets of reference metapodia and measurement, it is possible for fragmented distal ends to be identified when the heads and epicondyles are present. Without complete sets, though, identification is not possible. The distal heads of the metapodia have a midline ('sagittal') ridge separating a medial and lateral side of the head, and the outline and skew of the head relative to this ridge are particularly useful for identifying distal heads. The first step is to compare which digit a specimen belongs to, and then compare whether it is from the metacarpus (MC) or metatarsus (MT). Middle digits (Digit III and IV) have more symmetrical heads, while peripheral digits (Digit II and V) are more asymmetrical. Digit I is excluded from description here because in pantherines, the pollex is not well-developed, while the hallux is vestigial. The morphology of the epicondyles and the grooves surrounding the head also allow further basis for identification and siding. The following traits outlined here for the fragments of distal metapodia have been checked against nine sets of reference metapodia from four museum collections.

In Pilanduk-7366, the relative symmetry of the distal head (wherein the lateral and medial outlines of the head are rounded, wide and relatively proportional) distinguishes it as a middle digit (Digit III or IV) metapodial. Digit III metapodia have broader heads than digit IV, wherein the medio-lateral breadth at the epicondyles is greater than the dorso-plantar/antero-posterior depth of the head. In comparison, Digit IV is narrower medio-laterally, wherein the breadth and depth of the distal end are nearly equal. The specimen has a relatively broad head, aligning it better to the third digit. Comparing the MT III to the MC III, the MC III and the referred specimen have a slightly more bulbous head on the dorsal aspect versus the slightly more flattened head of the MT III. The distal head of the MT III also appears more symmetrical than the MC III and the referred specimen. The morphology of the epicondyles and the overall outline of the head (as viewed distally and dorsally) of the specimen also match the MC III better than the MT III, and also allow siding to the right side.

Pilanduk-7366 is the same side as the proximal MC III specimen Pilanduk-7365, and these two fragments were found in the same level and have very similar taphonomic and preservation states. They likely belong to one individual element. Furthermore, specimen 7366 is nearly identical in morphology and very close in metrical dimensions to the distal end of 9274, except that they are of opposite sides. Because of the similar dimensions, specimens 9274 (left MC III), 7365 and 7366 (right MC III) may likely belong to the same individual, though it is notable that these two elements where found on opposite sides of the cave (9274 in the north and 7365-66 in the south). Biometric comparisons with modern pantherines (Tables 5.3 and 5.4, Figure 5.5) place specimen 7366 in the range of *P. tigris* instead of the smaller *P. pardus*.

Pilanduk-8803. The specimen is a right fourth metapodial of a large robust felid, with the head, epicondyles and the distal end of the diaphysis (Figure 5.2). The relative symmetry of the distal head indicates that it is a middle digit metapodial (Digit III or IV). Compared to third digit metapodia, Digit IV has a narrower head relative to the midline ridge, as seen on the anterior and posterior (palmar) aspects. On the anterior aspect, the head also appears slightly flattened in Digit III and more bulbous in Digit IV. The epicondyles are also less robust in Digit IV. The specimen has a narrow bulbous head and less robust epicondyles, indicating it is a fourth digit metapodial. Comparing MT IV and MC IV, the MT IV has a more curved diaphysis and broader head as viewed on the dorsal aspect, whereas a flatter diaphysis and narrower head is observed in MC IV. The shape of the distal diaphysis and the dorsal aspect of the head of the referred specimen conform better with the MC IV morphology. Biometric comparisons with MC IV specimens from modern pantherines (Table 5.3, Figure 5.5) place the specimen in the range of *P. tigris* instead of the smaller *P. pardus*.

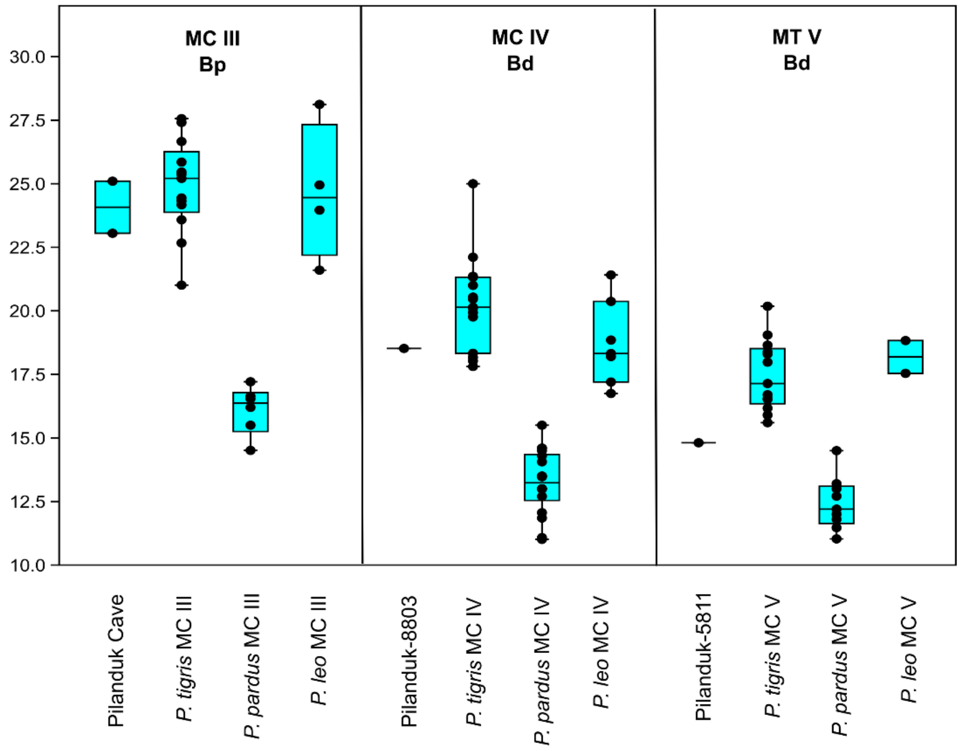


Figure 5.5 Box-and-jitter plot of pantherine (*Panthera*) metapodial measurements (in mm). MC = metacarpal, MT = metatarsal, Bp = proximal breadth, Bd = distal breadth. For Pilanduk-5811 MT V, the measurement is underestimated due to slight damage on the specimen.

Pilanduk-5811. This is a distal fragment of a right fifth metatarsal with the head and epicondyles (Figure 5.2). The asymmetry of the head indicates a peripheral metapodial (Digit II or V). Digit II metapodia are generally larger in overall dimensions than Digit V and have broader heads and larger epicondyles. In contrast, Pilanduk-5811 is relatively narrow and has smaller epicondyles, aligning it better to Digit V. Comparing MC V and MT V, the MC V is generally more robust, with a broader head, short and stout diaphysis, and the midline ridge is more skewed from the midline axis. Pilanduk-5811 conforms better to an MT V morphology, with a relatively narrower head, and a straighter midline ridge, as viewed from the distal end. This comparison of distal end proportions is observed both in large continental tigers, and in smaller tiger individuals that are closer or smaller in size compared to the referred specimen. Once again, biometric comparisons with MT V specimens from modern pantherines (Table 5.3, Figure 5.5) place the specimen in the range of *P. tigris* instead of the smaller *P. pardus*.

5.4.4.2 Pantherine Phalanges

Pilanduk-5393. This is a right-sided sub-terminal (=intermediate) phalanx of a large pantherine (Figure 5.6). The curved and asymmetrical diaphysis, as well as the diagonally slanted distal end are typical of felids, as this morphology allows for the retraction of the claws attached to the terminal phalanx. The length and curvature of the diaphysis of the specimen indicate that it belongs to a middle digit (Digit III or Digit IV). Comparison with two articulated sets of tiger phalanges points to either the third or fourth digit of the manus, or third digit of the pes. In contrasting tigers and lions, the morphology of the proximal articulation is observed to be variable, but for some lion middle digits, the proximal articulation has a more pointed triangular outline compared to the tiger. This specimen has a relatively more concave outline that is common to many tiger specimens observed.

Figure 5.6 Fossil sub-terminal phalanx (Pilanduk-5393) referred to *Panthera tigris* in dorsal (a), plantar (b), and proximal (c) views.

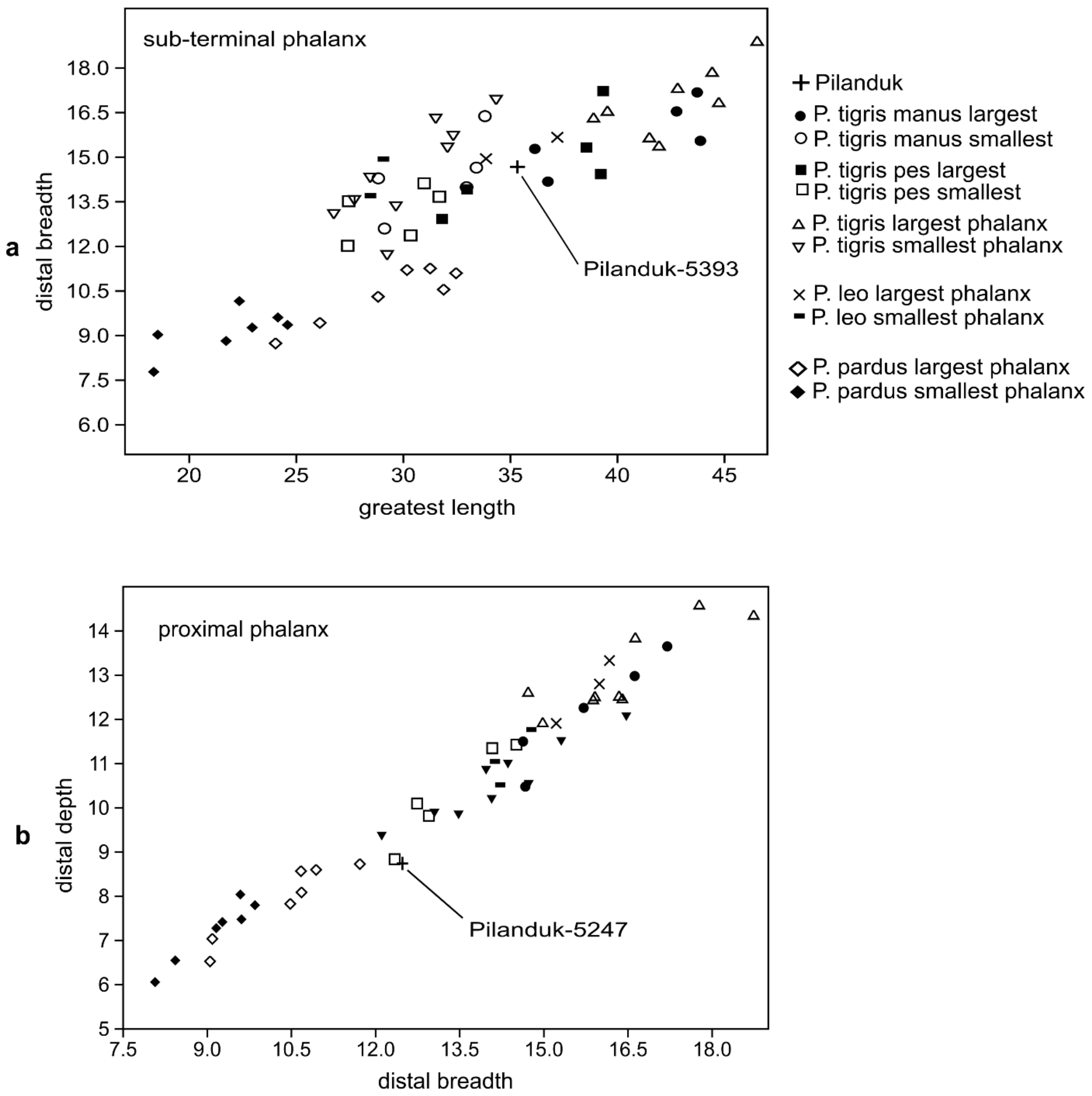


Figure 5.7 Bivariate plot of Pilanduk Cave fossil and modern pantherine phalanx measurements (in mm): a) sub-terminal phalanx, b) proximal phalanx. For each modern reference individual, the largest and smallest phalanges among available digits were measured to show the size range (greatest length). For *P. tigris*, certain elements could be distinguished between the manus and the pes based on labels, and in such cases, the largest and smallest specimens were each measured for the manus and pes. For most other individuals, differentiation was not possible because specimens were not labelled accordingly, and in such cases, the largest and smallest specimens among available digits are represented here.

Biometric comparison (Figure 5.7; Table 5.5) shows that the referred specimen falls in the range for tiger middle digit measurements and is well beyond leopard measurements. Based on two available sets of articulated hand and feet specimens of modern tigers, the largest of tiger digits is Digit III and the smallest is Digit V. Comparing the manus with the pes in individual sets, Digit III of the manus is larger than that Digit III of the pes, while Digit V of the manus is larger than Digit V of the pes.

As shown in Figure 5.7, the smallest phalanges (Digits V and II) of tiger can overlap in greatest length dimensions with the largest phalanges (middle digits) of leopard (Digits III or IV). However, the diaphyses and widths of tiger phalanges are much more robust than leopards, and so these dimensions do not overlap. Moreover, the morphology of the peripheral digits (Digits V and II) is very different from the morphology of middle digits, and so a tiger peripheral digit can be differentiated from leopard middle digits based on gross morphology. The referred specimen falls in the lower end of the size range for middle digit (=largest phalanges) measurements (Table 5.5). Based on this, we can infer that it belongs to a small- to medium-sized tiger individual. This follows a similar size pattern observed for the complete third metacarpal (Pilanduk-9274).

Pilanduk-5247. This is a distal end of a proximal phalanx of a large carnivore (Figure 5.2). The morphology fits a large pantherine, but taken in isolation, the fragmented distal portion of the tiger phalanx have some similarities to a large ursid (*Ursus*). The proximal outline is better for morphological discrimination, but it is absent on the specimen. Nonetheless, there are no known large ursids of this size in SEA; the only known ursid in the region is the sun bear, *Helarctos malayanus*, which is a much smaller carnivore compared to the tiger, and the smallest of extant bears. Comparative metrics with modern pantherines indicate that it overlaps in size with the smallest phalanges (=peripheral digits) from reference sets of tiger phalanges (Figure 5.7). The specific overlap is with a Sumatran tiger Digit V of the pes. For this specimen, ascription to *P. tigris* is provisional.

Table 5.5 Measurements (in mm) of pantherine intermediate (sub-terminal) phalanges. GL = greatest length, Bp = proximal breadth, Dp = proximal depth, Bd = distal breadth, Sd= smallest transverse diameter of diaphysis; M = manus, P = Pes. Largest and smallest specimens for manus and pes of each individual were measured whenever possible.

Museum	Number	Taxon	Locality	Digit	GL	BP	Dp	Bd	Dd	Sd
PNM	5393	*P. tigris*	Pilanduk		35.25	16.15	14.08	14.63	9.96	10.5
OUMNH	3756	*P. tigris*	unknown	Manus III	43.72	17.78	16.5	17.18	11.65	11.18
				Manus V	33.81	16.88	14.38	16.38	11.34	11.66
				Pes III	39.33	18.29	15.8	17.22	11.07	11.18
				Pes V	30.97	15.32	13.88	14.12	9.85	12.04
OUMNH	14223	*P. tigris*	Malaysia	largest	38.88	16.54	16.32	16.34	11.69	11.86
				smallest	31.51	16.23	15.42	16.29	11.67	11.61
OUMNH	14225	*P. tigris*	unknown	largest	44.42	18.98	17.94	17.88	12.92	10.32
	14225			smallest	34.33	18.51	16.64	16.92	12.47	12.14
UC GCL	151	*P. tigris*		largest	44.73	17.66	15.76	16.86	12.3	10.43
	151			smallest	32.33	16.31	14.31	15.71	10.93	10.64
UMZC	K. 5627	*P tigris*	Malaysia	\	28.45	14.17	13.38	14.3	9.98	10.48
FMNH	159999	*P. tigris altaica*	Zoo	largest	42.81	17.88	16.11	17.34	12.83	9.05
				smallest	27.71	14.71	13.53	13.55	11.17	9.43
FMNH	188486	*P. tigris altaica*	Zoo	largest	39.53	16.51	15.42	16.57	11.4	8.19
				smallest	26.75	14.69	12.51	13.08	10.64	9.2
FMNH	60760	*P. tigris tigris*	Zoo: India	largest	41.94	16.63	14.44	15.4	10.64	9.08
				smallest	29.24	13.23	11.98	11.7	9.08	9.02
FMNH	165401	*P. tigris*	Zoo: Sumatra	M largest	36.14	16.13	14.04	15.28	10.94	7.64
				M smallest	28.83	14.59	13.48	14.29	9.97	9.16
				P largest	32.98	15.54	13.34	13.92	9.88	9.46
				P smallest	27.45	13.53	12.24	13.52	9.84	9.03
FMNH	31153	*P. tigris*	India	largest	46.52	20	18.11	18.92	12.88	10.88
				smallest	32.06	15.85	14.77	15.31	11.55	11.42
FMNH	57172	*P. tigris*	Zoo: India	largest	41.49	17.07	14.42	15.68	11.17	8.63
				smallest	29.65	15.94	13.18	13.34	10.38	9.8
FMNH	134496	*P tigris*	Zoo	M largest	42.76	16.77	16.53	16.54	12.12	8.71
				M smallest	33.41	16	15.19	14.65	11.55	10.46
				P largest	38.55	17	15.87	15.33	11.21	9.39
				P smallest	31.68	14.71	13.75	13.67	9.94	9.04
FMNH	134497	*P. tigris*	Zoo	M largest	43.87	16.34	15.13	15.55	11.16	8.28
				M smallest	32.95	14.57	13.86	13.99	10.48	9.44
				P largest	39.22	16.27	14.61	14.43	9.88	8.85
				P smallest	30.34	13.41	12.24	12.37	9.61	9.69
FMNH	134607	*P. tigris*	Zoo	M largest	36.75	15.42	14.36	14.18	11.71	7.53
				M smallest	29.12	14.1	12.86	12.6	10.62	7.62
				P largest	31.81	14.59	13.48	12.92	10.68	7.65
				P smallest	27.4	13.51	12.2	12.02	10.76	7.69
OUMNH	14239	*P. pardus*	\	largest	28.82	10.59	9.54	10.31	7.81	6.1
	14239			smallest	21.72	10.17	8.92	8.82	6.77	7.73

Table 5.5 continued. Measurements (in mm) of pantherine intermediate phalanges.

Museum	Number	*Taxon*	Locality	Digit	GL	BP	Dp	Bd	Dd	Sd
	14235	*P. pardus*	\	largest	26.1	9.74	9.05	9.43	6.77	5.16
	14235			smallest	18.53	10.1	9.39	9.03	6.6	5.61
UMZC	K.5845	*P. pardus*		P largest	24.03	9.45	8.77	8.74	5.9	5.54
				P smallest	18.34	8.81	7.79	7.78	6.03	6.24
FMNH	54247	*P. pardus*	Zoo	M largest	30.17	12.2	11.88	11.21	8.71	6.91
				M smallest	23	11.3	11.29	10.02	8.12	7.11
				P largest	27.22	11.85	11.49	10.81	7.6	7.55
				P smallest	22.34	10.66	11	10.16	7.71	7.89
FMNH	196089	*P. pardus orientalis*	Zoo	largest	32.46	11.21	11.2	11.1	7.98	5.5
				smallest	24.14	10.66	10.47	9.61	7.78	6.22
FMNH	153777	*P. pardus*	Zoo: Africa	M largest	31.88	10.78	9.84	10.55	8.2	5.9
				M smallest	25.86	10.03	9.48	9.45	7.71	6.02
				P largest	29	11.01	10.03	10.47	7.87	6.35
				P smallest	24.59	9.84	9.43	9.36	7.72	6.5
FMNH	60051	*P. pardus*	Zoo	M largest	31.25	11.24	10.5	11.26	8.04	4.84
				M smallest	24.16	10.48	10.05	9.76	7.63	5.74
				P largest	28.71	11.88	10.68	11.04	7.71	6
				P smallest	22.94	10.4	9.9	9.27	7.27	6.3
OUMNH	14200	*P.leo*	\	largest	33.86	15.48	15.24	14.95	9.6	10.27
	14200			smallest	29.07	16.01	15.24	14.94	10.47	11.44
UCMZ	K. 5466	*P. leo*	Zoo	largest	37.19	15.6	14.94	15.67	10.76	9.37
	K. 5466			smallest	28.46	14.43	13.26	13.71	10.86	10.15

Pilanduk-5812 and Pilanduk-5394. Two proximal fragments of the terminal phalanx were also identified, belonging to a large pantherine (Figure 5.2). The fragments consist of the proximal articulation, but the external bone surrounding the sheath for the claw is not present. They are identifiable as belonging to a large felid and distinguishable from *Ursus*, based on the morphology of the proximal articulation. *Ursus* has a medial ridge, which is absent in *Panthera*. The placement of foramina on the proximal end are also different for both genera. The specimens are relatively large compared to *P. pardus*; however, due to the damage on the specimens, there are no measurable landmarks. Hence, the ascription of these two specimens to *P. tigris* is provisional.

Based on morphological, biometric and biogeographic data presented above, six specimens are clearly ascribable to the largest known extant pantherine in Southeast Asia, *Panthera tigris*. Three other phalanx specimens are only provisionally ascribed to the tiger, based on their fragmented state and lack of measurable landmarks. The Pilanduk pantherine specimens described here provide further evidence for the presence of the tiger on Palawan. The minimum number of individuals (MNI) is one, based on the size, preservation and provenance of the pantherine specimens. All the tiger specimens found *in situ* come from the 22,000–20,000-year old layer of the site (Layer 2). Morphometric comparisons with modern tigers indicate that the Pilanduk tiger is smaller than Bengal and Siberian tigers, but larger than two reference individuals of captive Malayan and Sumatran tigers. As will be described in Chapter 8, three of the pantherine specimens bear butchery marks. This may raise the question of whether tiger animal parts were being transported across long distances from other places in Southeast Asia. Another line of evidence in support of the living presence of the tiger on the island has to do with evidence for carnivore gnawing on-site. Although there is minimal evidence for gnawing across the assemblage, three deer specimens bear clear evidence for large carnivore gnawing. Two of these fragments – a proximal femur and a proximal tibia – bear canine punctures from a large carnivore. The size of the canine punctures indicates that these come from a large carnivore in the size range of a tiger. The taphonomic marks indicate that there were living tigers in the landscape that scavenged, albeit rarely, on human refuse in the cave.

5.4.5 Order Cetartiodactyla

Family Cervidae

Cervids represent the most abundant taxon in the Pilanduk Cave assemblage. Currently, deer are extinct on the main island of Palawan itself and the exact timing of extinction is unknown. A small population of hog deer (*Axis calamianensis*) is presently restricted to the smaller islands north of Palawan, the Calamianes. In previous work on Ille and Pasimbahan Caves in northern Palawan, we differentiated two deer taxa, distinguished primarily on size (Ochoa et al. 2014; Piper et al. 2011). In the case of the Pilanduk assemblage, a similar pattern is observed, wherein a smaller cervid is attributable to the extant hog deer (*Axis*), and a larger cervid taxon (*Rusa*) is also present. The Pilanduk cervid remains provide further evidence for the fossil deer of Palawan, both expanding the sample size and producing better-preserved skeletal remains. *Rusa* and *Axis* are also distinguishable based on antler morphology. The Pilanduk Cave assemblage allows the first antler morphological descriptions based on well-preserved antler remains, which other sites on the island have not yielded any to date.

Three cervid taxa are native to the Philippine archipelago: *Axis calamianensis* (Calamian hog deer) of the Palawan faunal region, *Rusa marianna* (Philippine brown deer) of the Luzon and Mindanao regions, and *Rusa alfredi* (Visayan spotted deer) of the Negros-Panay region (Table 5.6; Heaney et al. 2010). All three are endemic and restricted within each faunal region.

Table 5.6 Body size, distribution and habitat of extant hog deer (*Axis*) and sambar deer (*Rusa*) in the Philippines and Southeast Asia. Data come from the FMNH Synopsis of Philippine Mammals (archive.fieldmuseum.org/philippine_mammals/), Ultimate Ungulate website (ultimateungulate.com), and Animal Diversity Web (animaldiversity.org).

Species	Adult weight (kg)	Head and body length (cm)	Modern Distribution	Habitat
Axis calamianensis	23-40	100-115	Calamianes Islands only (north of Palawan Is.)	grasslands, open forest, mixed forest
Axis porcinus	30-50	125-135	India and Southeast Asia	dense forest, floodplains and wet grasslands
Axis kuhlii	50-60	140	Bawean Island only	primary and secondary forest and grassy clearings
Rusa marianna	40-96	100-170	Luzon, Mindanao, Leyte Islands	primary and secondary forest and grassy clearings
Rusa alfredi	36-59	128	Negros and Panay Islands	primary and secondary forest and grassy clearings
Rusa timorensis	50-115	142-185	Indonesian Islands	deciduous forest, forest edges, grasslands
Rusa unicolor	109-260	162-246	Inda, Pakistan, Southeast Asia, South China	primary and secondary forest, scrub forest

5.4.6 *Axis calamianensis*

Remains of a small-sized cervid are attributed to *Axis (=Hyelaphus) calamianensis*, the Calamian hog deer. It is a small brown deer with a stocky build and short legs that is found in grasslands and patches of open forest in the small islands of Culion, Busuanga and Calauit off the north coast of Palawan. It is the smallest of the three native Philippine deer and is also the smallest of extant Southeast Asian hog deer (Table 5.6). One local name is *pilanduk/pilandoc* (a general term for deer), which the cave site is named after. Together with the Bawean deer (*A. kuhlii*) and Indochinese hog deer (*A. porcinus*), the three Southeast Asian hog deer constitute a separate clade referred to as subgenus *Hyelaphus (*Meijaard and Groves 2004, Pitra et al. 2004) that is phylogenetically distinct from the chital (*Axis axis*). The first fossil description of this cervid comes from Ille Cave (Ochoa 2009; Piper et al. 2011), and subsequently from Pasimbahan Cave (Ochoa et al. 2014), primarily distinguished through size of dental remains. In Tabon Cave, Fox (1970:39) noted that the deer found in this cave was of a small form based on the antlers recovered and suggested that it was related to the Calamian deer.

Antler morphology provides a reliable way to differentiate cervid genera. At least seven antler fragments show traits that align with *Axis* (Figure 5.8). Compared to *Rusa, Axis* antlers are smoother, slenderer and have shallower gutters. The *Axis* antler is lyrate in shape with a high pedicle, and the beam of modern *Axis (=Hyelaphus)* has a particular inward curvature that contrasts with observed modern Philippine *Rusa* specimens.

Dental and post-cranial measurements of cervid remains from Pilanduk separate into two different-sized groups, the smaller of which is attributed to *Axis* (Tables 5.7 and 5.8). *Axis* and *Rusa* may be separated using tooth morphology, with *Axis* having generally higher-crowned and narrower teeth than *Rusa* relative to their size (Figure 5.9). Additional traits are outlined by Moigne et al. (2004) and Amano (2017). However, the traits listed (i.e., stylids, back fossa) were observed on both taxa from Pilanduk Cave. Size is still the main differentiating trait for the dental remains. The small-sized cervid teeth from Pilanduk Cave overlap with or are smaller in dimensions than modern *A. calamianensis* (Figure 5.10).

A similar pattern is observed for post-cranial remains. Certain post-cranial measurements (e.g., tibia and metacarpal) fall below the dimensions recorded for *A. porcinus* elements. Note that there are no available museum references for post-cranial remains for *A. calamianensis* and *R. alfredi* due to the rarity of these taxa. It is known, though, that *A. calamianensis* has a smaller body size and weight than *A. porcinus* (Table 5.6). Hence, the measurements of elements that fall in the lowest end of the biometric range and that are smaller than *A. porcinus* can be attributable to *A. calamianensis* (Table 5.8).

Figure 5.8 Comparison of *Rusa* and *Axis* antler fragments from Pilanduk Cave. Beam fragment (Pilanduk-4502U) referred to *Axis calamianensis (1),* with corresponding detail inset (2). Specimens (3) to (11) are all referred to *Rusa*: (3) to (7) are beam fragments, with corresponding detail inset (4); (8) to (11) are pedicle and coronet fragments. Modern comparatives in anterior views are: A) *Axis calamianensis* FMNH 62808, and B) *Rusa marianna* from Mindanao Island FMNH 56431. All shown at 5 cm scale except for (2) and (4).

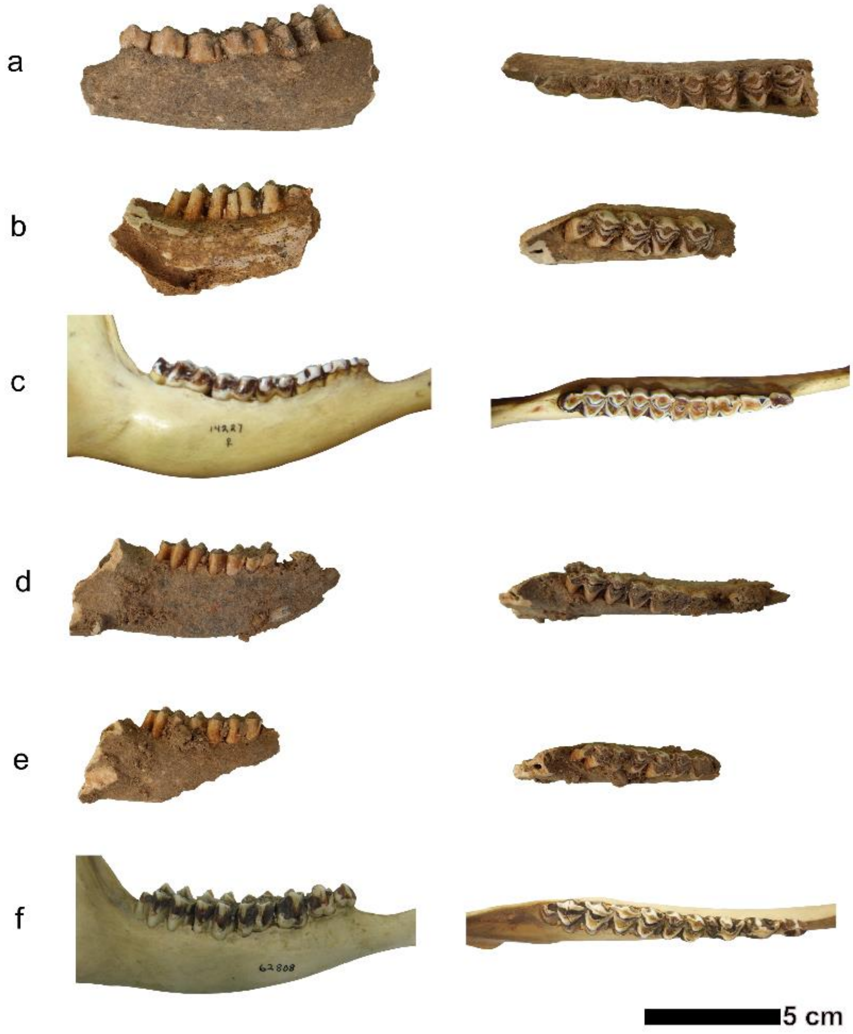


Figure 5.9 Comparison of fossil *Rusa* and *Axis* mandibular dentition from Pilanduk Cave in labial (L column) and occlusal (R column) views. a) 4500A - *Rusa*, b) 4500B - *Rusa*, c) MCZ 14227 - *R. marianna* from Luzon, d) 4500H - *Axis calamianensis*, e) 4500C - *A. calamianensis*, f) FMNH 62808 - *A. calamianensis*. All specimens are of the right side except for (a). Comparative modern specimens are (c) and (f).

Table 5.7 Maxillary and mandibular tooth measurements (in mm) of Pilanduk cervids compared with archaeological (Ille Cave) and modern *Axis* and *Rusa* comparative species. All measurements are cervical (taken above cementum/enamel junction). Anterior width = width of anterior cusp, Posterior width = width of posterior cusp. For modern reference, (N) refers to number of individuals. FMNH measurements were taken with PJ Piper.

Maxillary													
Source/ Specimen	Taxon	Locality	P4 Length	P4 Width	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width	M3 Posterior width
FMNH	*Axis calamianensis*	Calamianes	7.36 - 8.61 (3)	9.15 - 11.15 (3)	11.02 - 13.26 (6)	10.5 - 12.93 (6)	10.72 - 13.42 (6)	13.3 - 14.84 (4)	11.45 - 12.68 (4)	11.78 - 13.3 (4)	15.08- 15.12 (2)	11.54 - 12.5 (2)	10.3 - 11.32 (2)
MCZ	*Axis porcinus*	India	8.6-9.2 (3)	11.3 -12.4 (4)	10.5 - 11.5 (3)	12.8-14.5 (3)	13.7-14.9 (3)	14.1-14.9 (2)	16.2-16.8 (2)	15.6-15.9 (2)	\	\	\
FMNH	*Rusa alfredi*	Negros	9.05 - 10.7 (3)	12.36 - 12.9 (3)	11.5 - 14.38 (5)	13.3 - 14.2 (5)	13.04 - 14.26 (5)	13.5 - 17.3 (4)	15.04 - 15.72 (4)	14.1 - 15.51 (3)	15.25 - 16.37 (3)	13.98 - 15.16 (3)	14.34 - 14.66 (2)
FMNH	*Rusa marianna*	Mindanao	7.7 - 9.27 (5)	10.72 - 11.91 (5)	10.28 - 12.39 (8)	12.49 - 13.8 (8)	11.8 - 14.34 (8)	11.63 - 14.58 (7)	13.32 - 15.09 (8)	13.1 - 14.78 (7)	13.17 - 15.67 (7)	12.9 - 14.38 (7)	11.46 - 13.57 (5)
FMNH	*Rusa marianna*	Luzon	9.03 - 11.17 (6)	13.4 - 15.2 (6)	12.4 - 15.12 (10)	13.75 - 17.03 (10)	13.95 - 17.04 (9)	15.06 - 18.28 (10)	15.84 - 18.66 (9)	15.3 - 18.68 (8)	16.12 - 18.3 (7)	16.8 - 17.94 (5)	15.3 - 16.89 (5)
FMNH	*Rusa unicolor*	SEA	12.34 -13.76 (3)	15.99 - 17.56 (3)	15.59 - 17.24 (4)	19.72 - 21.42 (4)	19.62 - 21.18 (4)	19.74 - 21.13 (4)	22.56 - 23.08 (4)	22.17 - 22.8 (4)	21.2 - 22.43 (3)	20.02 - 22.49 (3)	20.57 - 21.31 (2)
FMNH	*Muntiacus muntjak*	Borneo	6.34 - 7.86 (3)	9.03 - 9.95 (3)	8.4 - 9.68 (4)	10.22 - 12.23 (4)	10.61 - 12.02 (4)	9.15 - 10.62 (3)	11.33 - 13.06 (3)	11.0 - 12.76 (3)	9.97 - 10.88 (3)	10.98 - 12.62 (3)	9.88 - 11.88 (3)
17512	*Rusa sp.*	Ille Cave									16.96	14.75	14.36
17827	*Rusa sp.*	Ille Cave									16.38	17.3	14.71
20044	*Rusa sp.*	Ille Cave						14.42	16.21	16.53			
20046	*Rusa sp.*	Ille Cave									16.18	16.4	14.23
5742	*Axis calamianensis*	Pilanduk			11.33	11.15	11.56	13.13	14.34	13.87			
9276e	*Rusa* sp.	Pilanduk	8.78	13.45	12.43								
9276n	*Rusa* sp.	Pilanduk	9.96	12.73									
4032	*Rusa* sp.	Pilanduk	10.84	13.25									
137	*Rusa* sp.	Pilanduk			11.25	15.12	14.87						
129	*Rusa sp.*	Pilanduk			13.85	\	\	17.03	18.08	16.47			
7945c	*Rusa* sp.	Pilanduk			13.74	12.17	14.7						
8004b	*Rusa* sp.	Pilanduk			14.24	14.01	\						
8004c	*Rusa* sp.	Pilanduk			13.68	14.44	13.1						
6216	*Rusa* sp.	Pilanduk						15.39	\	\			
7945b	*Rusa* sp.	Pilanduk						16.98	16.67	16.72			
8062a	*Rusa* sp.	Pilanduk						18.03	18.22	18.1			
8062b	*Rusa* sp.	Pilanduk						16.93	18.98	18.72			
7945a	*Rusa* sp.	Pilanduk									16.81	18.03	15.85
9276f	*Rusa* sp.	Pilanduk									16.48	17.72	16.86

Table 5.7 continued. Measurements (in mm) of cervid mandibular molars.

Mandibular												
Source/ Specimen No.	Taxon	Locality	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width	M3 Width of middle cusp	M3 Posterior width
FMNH	*Axis calamianensis*	Calamianes	9.82 - 11.93 (6)	7.35 - 8.02 (6)	7.15 - 8.52 (6)	14.06 - 14.76 (4)	8.04 - 9.79 (4)	7.3 - 8.88 (4)	18.26 - 19.78 (2)	8.77 - 10.6 (2)	7.7 - 10.62 (2)	3.72 (1)
MCZ	*Axis porcinus*	India	11.6-11.7 (2)	7.9-8.1 (2)	8.2-8.7 (2)	13.6 (1)	9.8 (1)	9.5 (1)	\	\	\	\
FMNH	*Rusa alfredi*	Negros	11.22 - 13. 78 (5)	8.45 - 9.5 (5)	8.77 - 10.47 (5)	14.25 - 16.48 (4)	10.14 - 11.38 (3)	10.43 - 11.32 (3)	20.49 - 20.9 (3)	9.78 - 11.04 (3)	10.17 - 11.24 (3)	5.49 - 5.88 (3)
FMNH	*Rusa marianna*	Mindanao	10.24 - 12.96 (8)	7.76 - 8.7 (8)	8.5 - 9.44 (8)	12.34 - 14.53 (8)	9 - 9.82 (8)	8.91 - 10.32 (8)	18.03 - 20.27 (7)	8.57 - 9.8 (7)	7.82 - 8.96 (7)	4.92 - 5.34 (5)
FMNH	*Rusa marianna*	Luzon	12.8 - 15.24 (8)	9.6 - 10.97 (7)	10.46 - 11.6 (8)	15.8 - 18.34 (8)	11.05 - 13.18 (8)	11.12 - 12.46 (8)	23.3 - 25.28 (5)	11.4 - 12.77 (6)	10.52 - 12.94 (5)	5.86 - 7.46 (5)
FMNH	*Rusa unicolor*	SEA	16.65 - 18.33 (3)	12.81 - 13.27 (4)	12.52 - 13.88 (3)	19.46 - 20.93 (2)	14.74 - 15.32 (3)	14.24 - 15.09 (3)	28.28 - 28. 86 (2)	14.9 - 14.95 (2)	13.53 - 14.42 (2)	8.56 - 8.74 (2)
FMNH	*Muntiacus muntjak*	Borneo	9.32 - 9.77 (4)	6.67 - 7.04 (4)	6.9 - 7.72 (4)	10.05 - 11.0 (3)	7.97 - 8.56 (3)	8.11 - 8.28 (3)	14.64 - 15.2 (3)	7.65 - 8.15 (3)	7.23 - 7.78 (3)	4.41 - 4.76 (3)
18599	*Axis calamianensis*	Ille Cave							19.5	na	na	na
20058	*Axis calamianensis*	Ille Cave	10.98									
18438	*Axis calamianensis*	Ille Cave							20.65	8.54	7.67	7.02
2086	*Rusa* sp.	Ille Cave	13.04	10.3	10.96	16.35	12.14	11.84	27.63	12.74	11.78	7.55
818	*Rusa* sp.	Ille Cave				18.1	11.5	11.7				
1862	*Rusa* sp.	Ille Cave							22.88	12.06	11.36	5.99
2084	*Rusa* sp.	Ille Cave							24.15	12.2	10.97	6.81
18549	*Rusa* sp.	Ille Cave							24.18	11.32	9.96	na
9276c	*Axis calamianensis*	Pilanduk	10.45	7.85	8.39	12.83	8.8	\	16.12	\	7.31	3.36
5415	*Axis calamianensis*	Pilanduk	11.04	7.61	7.82							
9276d	*Axis calamianensis*	Pilanduk	9.85	\	8.13	12.9	9.01	8.47	16.66	8.98	7.96	3.47
9276h	*Axis calamianensis*	Pilanduk	9.9	7.53	8.59	12.93	8.94	8.43	17.95	9	8.6	4.21
4807	*Axis calamianensis*	Pilanduk	9.13	7.41	8.11	11.6	8.68	8.78	17.91	\	\	5.15
6162	*Axis calamianensis*	Pilanduk	11.01	7.4	7.56	12.92	8.65	7.44				
9276j	*Axis calamianensis*	Pilanduk							17.63	9.16	8.28	4.77
462	*Axis calamianensis*	Pilanduk							17.65	\	\	\
1976	*Rusa* sp.	Pilanduk	(erupting)	10.07	10.41							
9276a	*Rusa* sp.	Pilanduk	13.78	10.9	11.23	16.63	12.79	12.41	\	12.27	\	\
4555c	*Rusa* sp.	Pilanduk	14.74	9.63	10.34							
5114	*Rusa* sp.	Pilanduk				15.9	\	12.06				
8004a	*Rusa* sp.	Pilanduk				17.61	10.88	10.46				
9276b	*Rusa* sp.	Pilanduk				16.95	12.18	11.93	22.74	12.4	10.73	6.14
9276i	*Rusa* sp.	Pilanduk							23.03	11.45	10.29	5.53
5248	*Rusa* sp.	Pilanduk							23.37	11.14	10.7	6.39

5.4.7 *Rusa* sp.

Remains of a large-sized cervid in the Pilanduk Cave assemblage is attributed to the genus *Rusa*. There are presently no living sambar deer in the Palawan faunal region. Among the living *Rusa,* the Visayan species, *R. alfredi*, is the smallest in body size and most restricted in its present-day range within Negros and Panay. The other taxon, *R. marianna*, has a broader modern distribution, with a recorded historical translocation to the Mariannas Islands. Within its native range in the oceanic Philippines, *R. marianna* has substantial variation in size and pelage across the Luzon and Mindanao faunal regions (Heaney et al. 2010). Hence, further systematic study is needed for this species. A recent phylogenetic study of *R. marianna* from Luzon and Rota (Mariannas) and *R. alfredi* indicates that they form a monophyletic clade and are sister taxon to the other Southeast Asian rusine deer, *R. timorensis* and *R. unicolor* (Heckeberg et al. 2016). In the modern comparative measurements assembled for this study, Luzon and Guam individuals have larger tooth and post-cranial dimensions compared to Mindanao samples (Tables 5.7 and 5.8). Instead, *R. marianna* from Mindanao overlaps in dental dimensions with *R. alfredi*.

Since rusine deer are not presently known in the modern fauna of the Palawan region, verification of their presence is important. The Pilanduk Cave antler remains confirm the identification of *Rusa* in the Palawan fossil record (Figure 5.8). It was first identified in Ille Cave based on measurements of dental and post-cranial remains (Ochoa 2009; Piper et al. 2011), but there were no suitably well-preserved antlers from this site. In Pilanduk, numerous large antler fragments conform to the morphology of Southeast Asian *Rusa*. In contrast to *Axis* antlers, *Rusa* antlers are generally more robust, have rugose beams and tines, defined gutters, heavy pearling and often shorter pedicles relative to overall size (see Figure 5.7.4). Both *Axis* and *Rusa* have lyrate beams, but their curvature is different. Note in Figure 5.8 how the *Rusa* beam is more vertically straight compared to the *Axis* beam, which has a more pronounced outward/lateral curve. Note also the rugosity of the *Rusa* beam fragments compared to *Axis*. A conservative estimate of at least 48 antler fragments from across the sequence can be assigned to *Rusa.*

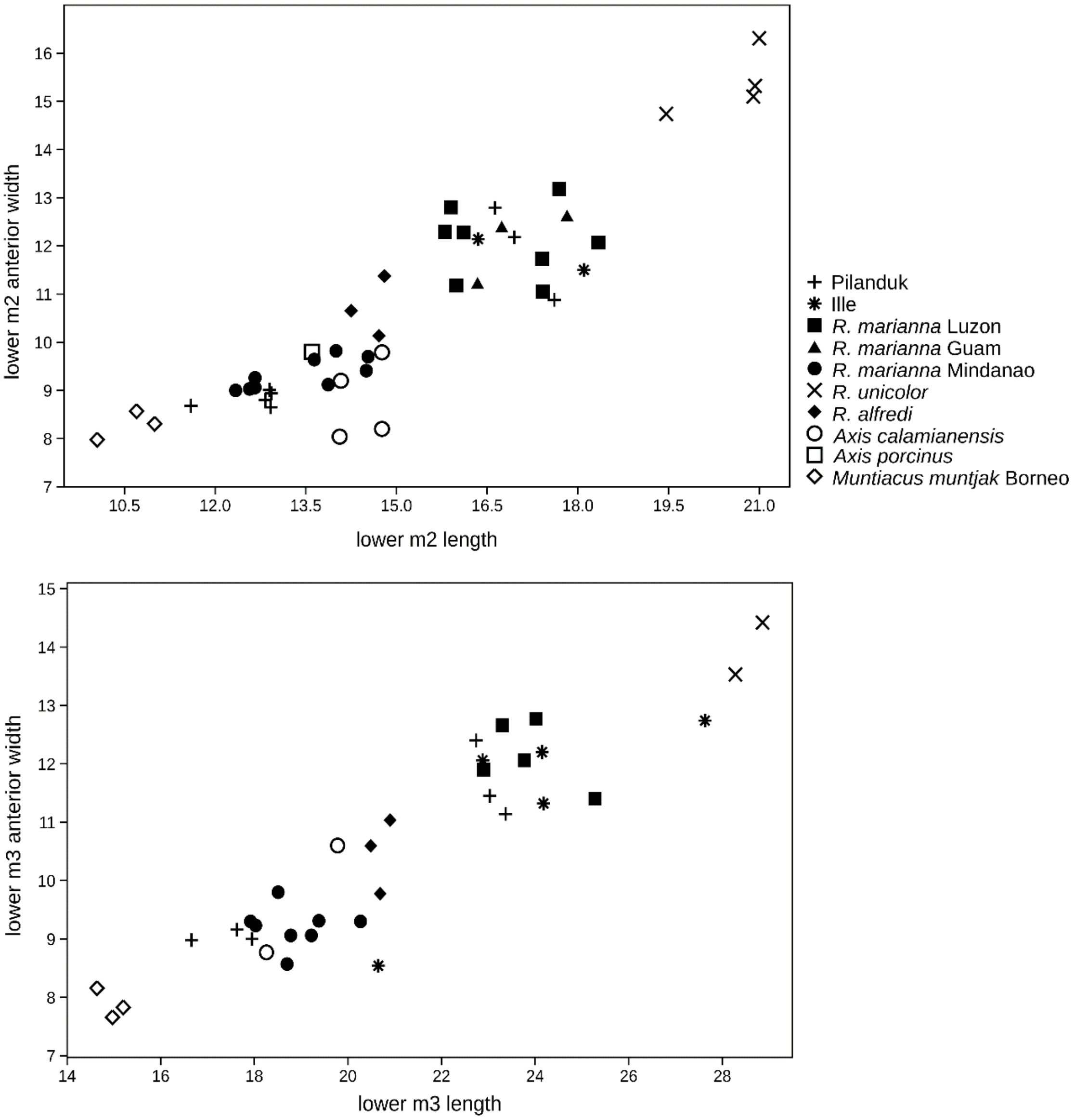


Figure 5.10 Bivariate plot of *Axis* and *Rusa* dental measurements (in mm) from archaeological (Pilanduk Cave and Ille Cave) and modern reference specimens. Above: mandibular m2 cervical length vs mandibular m2 width of anterior cusp. Below: mandibular m3 cervical length vs mandibular m3 width of anterior cusp. Extant cervid specimens are from the FMNH and MCZ. Comparatives from the FMNH and some Ille Cave specimens were measured with PJ Piper. Note how the Pilanduk specimens separate into two different size groups.

As mentioned above, cervid tooth measurements separate into two size groups, the larger of which overlaps in size with the extant *R. marianna* of Luzon and Guam (Figures 5.9 and 5.10, Table 5.7). For post-cranial measurements, most cervids in the assemblage overlap in size with extant *R. marianna* and there are relatively few small-sized elements (Table 5.8). This is to be expected because the assemblage is dominated by the larger cervid taxon. The majority of bones designated as 'large mammal' are also in the size range of the larger cervid. Note that in the small sample of limb measurements, all the *R. marianna* individuals measured are female (Table 5.8). For humeri, radii and femora measurements, all the measurable specimens are assignable to *Rusa*, and certain Pilanduk Cave specimens exceed the comparative sample range, possibly indicating sexual dimorphism. On the other hand, the spread of astragalus, metacarpal and tibia measurements possibly indicates interspecific variation between *Axis* and *Rusa*, as certain values overlap with or fall below the recorded size of *A. porcinus* (Figure 5.11). For astragali in particular, some small-sized specimens were verified to belong to adult individuals because they were found articulated *in situ* with a fused calcaneus, or adjacent to a fused calcaneus to which they could be aptly refitted.

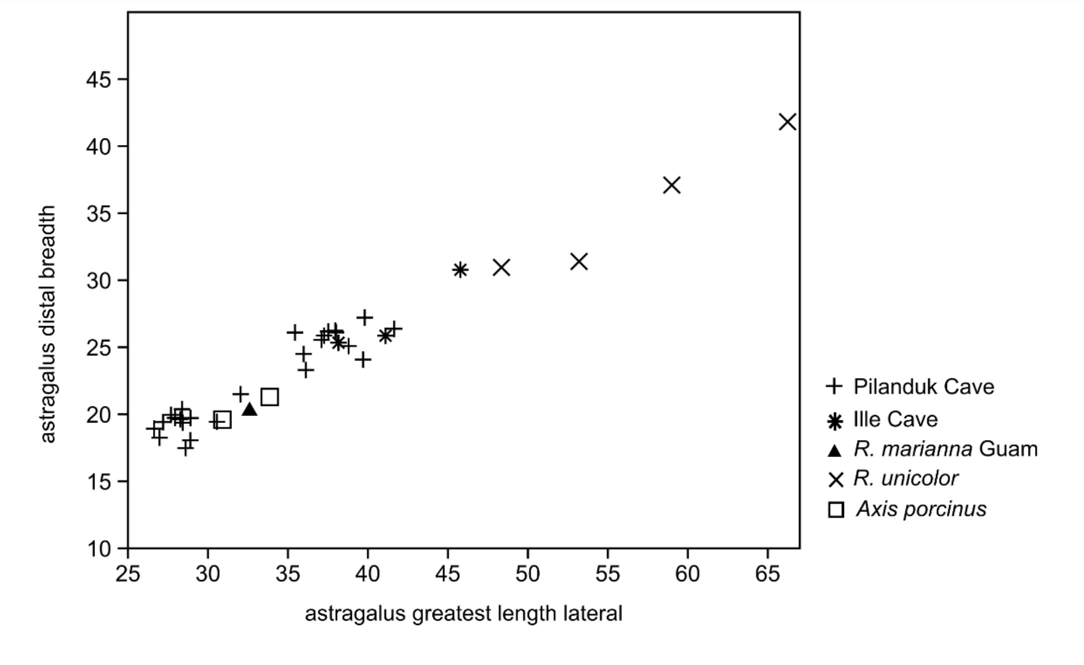


Figure 5.11 Bivariate plot of deer astragali measurements (in mm) from archaeological (Pilanduk Cave and Ille Cave) and modern reference specimens. Measurement of greatest length of lateral side and distal breadth follows von den Driesch's (1978) GLl and Bd.

Although the *Rusa* fossils overlap in dimensions with *R. marianna*, designation to this species cannot be easily given. Based on modern biogeographic distributions, Luzon and Palawan do not share artiodactyl taxa, and many other non-volant mammal taxa are not shared. For instance, among pig taxa, each major faunal region in the Philippines possesses its own endemic pig, which are not shared with other faunal regions. Phylogenetic studies on native Philippine pigs (Lucchini et al. 2005) show that there are five endemic species within the archipelago. Following these observed patterns, it is possible that the *Rusa* cervid in the Palawan record may represent a distinct species restricted to the Palawan faunal region. However, further morphological study is needed to differentiate dental and post-cranial remains, since the existing literature only focuses on cranial traits (Meijaard and Groves 2004). Such work is presently hampered by the rarity of comparative specimens for these Philippine taxa, and so ancient DNA or proteomics may be alternative options that can clarify the taxonomic and phylogenetic placement of the fossil rusine deer of Palawan.

5.4.8 Family Suidae

Sus ahoenobarbus

The Palawan bearded pig is the only extant artiodactyl on the main island of Palawan. In the Pilanduk Cave assemblage, it occurs in very small proportions across the sequence and accounts for only 6% of the identified taxa in the assemblage. Other confirmed fossil records of the bearded pig come from several other sites in northern Palawan (Ochoa et al. 2014; Piper et al. 2011) and southern Palawan (Reis and Garong 2001). In the Mid to Late Holocene record of the Dewil Valley in El Nido, the bearded pig is the most abundant prey animal, and deer is very scarce (Ochoa and Piper 2017). Presently, they are observed from sea level to 1500 m above sea level in a variety of forest habitats (Esselstyn et al. 2004). The wild pig is locally called *babuy* or *bjak.*

Table 5.8 Measurements (in mm) of cervid post-cranial elements from Pilanduk and modern comparative species. Pilanduk measurements in **bold** font indicate overlap with extant *R. marianna* (with +/- 1 mm of the sample range). Measurements shaded in grey are smaller than *A. porcinus*. Bt= breadth of trochlea, Bd=breadth of distal end, Bp=breadth of proximal end, DC= depth of caput of femur (after von den Driesch 1978). Breadth measurements are taken medio-laterally.

Taxon/Element	Locality	Specimen No.	Sex	Humerus (Bt)	Humerus (Bd)	Radius (Bp)	Radio-ulna (Bd)	Femur (DC)	Tibia (Bd)	Metacarpal (Bp)	Metatarsal (Bp)
Axis porcinus	India	FMNH-27447	M	30.72	32.85	31.67	\	\	24.53	\	\
Axis porcinus	India	MCZ-37003	F	25.8	29.7	27.4	\	19.8	\	21.4	21
Axis porcinus	India	FMNH-65802	F	32.74	34.61	\	30.96	\	31.29	\	\
Rusa marianna	Luzon	MCZ-14227	F	**34.4**	**39.9**	**36.8**	**33.1**	**23.3**	**30.9**	\	\
Rusa marianna	Luzon	USNM-49706	F	**38.16**	**40.91**	**38.41**	**34.02**	**24.4**	**33.66**	**27.4**	**27**
Rusa marianna	Mindanao	FMNH-61007	F	**29.03**	**31.92**	**28.85**	**23.1**	**18.9**	**29.94**	\	\
Rusa marianna	Guam	FMNH-186613	F	**34.06**	**39.62**	**34.6**	**28.54**	**24.19**	**28.1**	\	\
Rusa unicolor	Borneo	USNM-151861	M	52.79	55.1	49.65	42.22	33.1	44.23	35.81	34.1
Rusa unicolor	Borneo	MCZ-7282	M	47.8	55.6	51.5	47	33.7	44	36.6	34.8
Rusa unicolor	Borneo	USNM-151859	F	55.7	57.06	55.03	46.5	36.46	48.9	40.13	38.95
Rusa unicolor	India	MCZ-1381	M	56.4	66.2	63.7	53.9	40.7	55.1	43.1	39.5
Rusa unicolor	India	FMNH-27455	M	61.31	67.28	63	56.1	43.52	60.18	\	
distal humerus	Pilanduk	4503e		**31.64**	**33.28**						
distal humerus	Pilanduk	4503d		**35.57**	**38.18**						
distal humerus	Pilanduk	4503c		**39.94**	**41.9**						
distal humerus	Pilanduk	4503b		40.33	46.57						
distal humerus	Pilanduk	4503a		46.57	40.33						
proximal radius	Pilanduk	5369				**28.58**					
proximal radius	Pilanduk	4505f				**28.74**					
proximal radius	Pilanduk	5502				**28.95**					
proximal radius	Pilanduk	4505e				**29.43**					
proximal radius	Pilanduk	5740				**33.95**					
proximal radius	Pilanduk	3905				**34.32**					
proximal radius	Pilanduk	4505c				**34.48**					
proximal radius	Pilanduk	4505d				**34.66**					
proximal radius	Pilanduk	4505b				**36.44**					
proximal radius	Pilanduk	4505a				**36.8**					
distal radius	Pilanduk	1790					**26.5**				
distal radius	Pilanduk	1966					**27.3**				
distal radius	Pilanduk	4505h					**27.23**				
distal radius	Pilanduk	4505g					**31.8**				

Table 5.8 continued. Measurements (in mm) of cervid post-cranial elements.

Element	Locality	Specimen No.		Humerus (Bt)	Humerus (Bd)	Radius (Bp)	Radio-ulna (Bd)	Femur (DC)	Tibia (Bd)	Metacarpal (Bp)	Metatarsal (Bp)
proximal femur	Pilanduk	4514b						**21.03**			
proximal femur	Pilanduk	4514a						**22.19**			
proximal femur	Pilanduk	3900						25.82			
proximal femur	Pilanduk	4514d						28.72			
proximal femur	Pilanduk	4514e									
distal tibia	Pilanduk	1721							22.41		
distal tibia	Pilanduk	4513c							21.15		
distal tibia	Pilanduk	4513b							23.58		
distal tibia	Pilanduk	4513d							**27.34**		
distal tibia	Pilanduk	1792							**27.48**		
distal tibia	Pilanduk	4513a							**27.77**		
distal tibia	Pilanduk	1761							**27.9**		
proximal metacarpal	Pilanduk	6216								19.1	
proximal metacarpal	Pilanduk	5806c								19.62	
proximal metacarpal	Pilanduk	5371b								23.4	
proximal metacarpal	Pilanduk	5371a								25.8	
proximal metacarpal	Pilanduk	6011								26.1	
proximal metacarpal	Pilanduk	5464								**26.47**	
proximal metacarpal	Pilanduk	4508e								30.33	
proximal metacarpal	Pilanduk	4508f								30.9	
proximal metacarpal	Pilanduk	5806a								31.7	
proximal metatarsal	Pilanduk	5371d									21.51
proximal metatarsal	Pilanduk	4509i									**26.5**
proximal metatarsal	Pilanduk	4509g									**27.32**

5.5 Conclusion

This chapter has presented the fossil mammal identifications from Pilanduk Cave. The records of three extirpated large mammals – *Panthera tigris*, *Rusa* sp. and *Axis calamianensis* have been provided in detail. All identifications from the site currently represent the oldest confirmed fossils records for the seven identified taxa, dating to 25,000-20,000 years ago. In the case of the deer, differentiation of antler morphology confirms the taxonomic diagnoses for the two cervid taxa.

The identification and biometric analysis of nine pantherine fossils from Pilanduk Cave add greatly to the sparse inventory of tiger fossils from Palawan. The LGM presence of this species, as well as that of the macaque, support the hypothesis of their natural distribution on Palawan Island. We have previously argued for the tiger's native presence on the island based on initial evidence from Ille Cave in northern Palawan (Ochoa 2009; Ochoa and Piper 2017; Piper et al. 2008). A total of three phalanx specimens were identified in Ille Cave. The Pilanduk record lends further information regarding its past distribution, this time from a southerly geographic location and from an older period. The two oldest specimens described from Ille Cave are of Terminal Pleistocene age, *ca*. 14,000 BP, while another specimen derived from an Early Holocene layer. The Late Pleistocene presence of the tiger on Palawan runs parallel with the fossil presence of the tiger on Borneo (Piper et al. 2007), and this may likely be the population source of Palawan tigers. Based on GIS and bathymetric reconstructions, Palawan was likely not connected to Borneo during the LGM; however, only a short sea crossing of roughly 4.5 km would have been required during MIS 2 (Robles et al. 2015). In comparison, the present-day distance between the two islands is 140 km. Previous reconstructions, though, suggest a land connection (Sathiamurthy and Voris 2006). Tigers are known swimmers that can make sea-crossings and hence a landbridge between Borneo and Palawan would not have been necessary for colonisation, and the presence of this large carnivore on Palawan does not imply that a landbridge was present during MIS 2. In fact, all known fossil and extant large mammals (tiger, deer and pig) of the Palawan faunal region are capable of sea-crossings.

The Pilanduk Cave assemblage is not very speciose and is dominated by one taxon (*Rusa* sp.). This contrasts with the Holocene fossil assemblages of Ille and Pasimbahan Caves, which contain more macrovertebrate and microverterbate taxa. The diversity and abundance of taxa in Pilanduk Cave noticeably differ from these two sites. These features, along with palaeoecological, biogeographic and taphonomic issues, will be discussed further in Chapters 7 and 8.

Chapter 6 Holocene Archaeofaunas of Luzon Island

6.1 Introduction

In this chapter, I present the palaeozoological reconstruction of two terrestrial vertebrate cave assemblages in Luzon, with the primary aim of describing and examining the Late Quaternary history of the mammalian faunal community of the island. As presented here, the fossil record of Minori and Musang Caves provides evidence for the nature and composition of mammalian faunal communities in northeastern Luzon in the last 10,000 years. As discussed in Chapter 4, the two sites present Holocene sequences, containing two major cultural layers. The deeper aceramic layer contains flake assemblages and faunal remains that are older than 4000 BP. For Musang Cave, Thiel (1990) presented two ^{14}C dates that are of Terminal Pleistocene age (ca. 10,000 BC). Although the dates are not secure, they provide an indication that the aceramic levels of Musang are at least of Early Holocene age or slightly older. The younger cultural layers contain a similar flake assemblage, but with the addition of earthenware pottery that are younger than 4000 BP.

Accounts of species are presented here for Minori and Musang Caves, which include descriptions on systematics, morphology, distribution and ecology for each taxon. Biological data for the extant species are primarily derived from the most recent synopsis *The Mammals of Luzon Island* (Heaney et al. 2016). The fossil accounts focus on the non-volant mammalian taxa, since the assemblages consist primarily of mammalian remains. In the species accounts, native taxa are described first, followed by introduced/non-native taxa. In-depth accounts are provided for the Muridae due to the discovery of previously unknown and undescribed taxa. To provide the necessary background for these two assemblages, an overview of the Luzon faunal record follows.

6.2 The Vertebrate Fossil Record of Luzon

The fossil record of Luzon is primarily represented by sites from the Cagayan Valley. Early studies dealt with extinct megafauna (Beyer 1956; Koenigswald 1956). The fossils are often found redeposited within the alluvial plains of the valley and have not been securely dated but have been proposed to be of Middle Pleistocene age. Some of the fossil remains are said to be associated with 'Cabalwanian' pebble tools (Koenigswald 1958), but these associations are not well-established due to post-depositional processes in these alluvial settings. De Vos and Bautista (2001) previously examined the taxonomy of these fossil finds, identifying *Stegodon luzonensis, Rhinoceros philippinensis, Elephas* sp., a small bovid, a suid, a giant tortoise, and a crocodile. In the island of Cebu, bovid remains were found in 1958 in a mining tunnel and are of unknown age. These were described and assigned as *Bubalus cebuensis,* a diminutive buffalo that is smaller than the extant tamaraw (*B. mindorensis*) of Mindoro Island (Croft et al. 2006). Unidentified bovid remains are also found in some Luzon sites, and possibly represent a congener (coming from the same genus) of *B. cebuensis* and *B. mindorensis*.

Most recently, the hypothesis pertaining to the association of stone tools and Middle Pleistocene megafauna in Cagayan has been revisited and bolstered by the discovery of securely dated rhinoceros (*R. philippinensis*) remains found in association with stone tools (T. Ingicco et al. 2018). These were found in Kalinga site, which is located in neighboring Kalinga Province, although the geographic area still forms a contiguous part of the Cagayan Valley. Dating of the rhinoceros was done using electron spin resonance on tooth enamel and yielded an age of 709 ± 68 ka. The rhinoceros remains belong to a near-complete individual showing evidence of butchery-related cut marks and percussion marks. Associated with the articulated animal bones are 57 stone tools. These findings now represent the oldest evidence of hominin activity in the Philippine archipelago. Within the same vicinity, a novel species of fossil suid, *Celebechoerus cagayanensis*, was also diagnosed on the basis of an upper left canine found among surface remains (Thomas Ingicco et al. 2016).

The rest of the known fossil assemblages on Luzon date from the Late Pleistocene to the Holocene. The 67,000-year old sequence of Callao Cave provides the only Late Pleistocene record to date (Mijares et al. 2010). The deepest levels showed evidence of a human third metatarsal found with deer (*Rusa marianna)* and wild pig *(Sus philippensis)* bones*.* Two fossil murids (*Batomys* sp. and *Apomys microdon)* were also identified in these levels, providing the first description of fossil rodents on the island (Heaney et al. 2011). The Callao faunal sequence will be discussed further in the next chapter.

For the Holocene, an important and well-described assemblage comes from Nagsabaran open site in the Cagayan River Valley. Deer and wild pig remains dominate the assemblage, but the earliest identifications of three introduced domesticates are documented. These include the earliest record for domestic *Sus scrofa* in the Philippines, dated to 4000 cal. BP (Piper et al. 2009). In the Late Neolithic/Metal Period levels, the domestic water buffalo (*Bubalus bubalis)* and the domestic dog (*Canis lupus familiaris)* were also identified (Amano et al. 2013). Another site where *B. bubalis* has been identified is in Pintu/Busibus rockshelter. This site is located in the province of Nueva Vizcaya, also in northeastern Luzon. The site is near the Ngilinan River, a tributary of the Cagayan River. It was excavated in the 1960s and has tentative ^{14}C dates ranging from 4000 to 2000 BP. Mudar (1997) analysed the fauna, observing that deer is the most dominant taxa, followed by wild pig. Macaque remains were also identified in the same levels where the water buffalo occurs.

Holocene assemblages are further represented in the other cave sites in the Callao formation, including the two sites described here. In the case of Musang Cave, Thiel (1990) provided her identifications of the large mammal fauna in her analysis of finds from the site. This was limited to deer, wild pig and human remains. For majority of other sites in the Callao area, there are only unpublished manuscripts from the National Museum of the Philippines (NMP), with some of them giving preliminary descriptions of faunal composition. Such is the case for Minori Cave, where the vertebrate fauna for Chamber D was first analysed by De Vera (De Vera-Alba 1990) and the molluscan fauna by Bautista (1982). In her reports, De Vera noted that the lack of comparative material limited the number of specimens that could be identified to genus and species (Table 6.1). She also presented bone frequencies by arbitrary archaeological levels but was not able to segregate by cultural layers due to the lack of stratigraphic data at the time of her writing.

The research generated here for Minori and Musang Caves offers a re-analysis of these remains, producing additional genus- and species-level identifications. These include previously unidentified extant and extinct native taxa, as well domesticated and translocated non-native species. In the case of Musang, my analysis also includes some corrections for misidentified specimens. The following sections provide details of these determinations, which are based on morphological and morphometric analyses and comparisons with available modern references. The relevant ecological and systematic information is also summarised for the various taxa in order to provide the necessary basis for the discussion on biogeographic patterns and environmental changes in the next chapter.

Table 6.1 Specimen counts per taxa and excavated square in Minori Cave (Chamber D only) provided by De Vera-Alba. Column labels refer to the squares/excavation units. Adapted from Table 3 in De Vera-Alba (1990:5).

Taxon	27	40	41	44	50	57	58	Total
Cervus sp.	194	39	2	19	20	1	5	280
Sus sp.	54	13	2	2	12	3	10	96
Rodentia	106	25	\	193	139	13	287	763
Squamata	15	\	\	\	\	\	\	15
Carnivora	6	1	1	1	5	\	\	14
Macaca sp.	2	1	1	2	7	2	\	15
Bats	3	\	\	\	3	\	3	9
Aves	2	3	\	1	2	\	\	8
Fish	1	\	\	\	\	\	\	1
	383	82	6	218	188	19	305	1201

6.3 The Minori Cave Vertebrate Fauna: An Overview

A total of 1935 bone fragments were analysed from Minori Cave, coming primarily from two squares from the 1981-82 excavations (Table 6.2). The two squares represent the two main chambers of the cave: Square 27 for Chamber D, and Square 37 for Chamber A. These two squares were chosen because each has the greatest number of remains among all squares in the chambers and cover the known archaeological sequence for the site. Compared to the other squares, these two squares also had more archival archaeological records in the NMP and so it has been possible to some degree to reconstruct the provenance of the finds. The proportion of bone identified at the genus level comprises 20% for Minori Cave out of the total number of fragments (TNF) in the site.

Table 6.2 Number of identified specimens (NISP) in Minori Cave per square (Sq.) and chamber (Ch.). Counts for other squares (apart from the two main squares) are grouped together. *Extinct taxon.

Taxon	**Sq. 27**	**Ch. D other**	**Total Ch. D**	**Sq. 37**	**Ch. A other**	**Total Ch. A**	**TOTAL NISP**	**%NISP**
Rusa marianna	135	3	138	165	53	218	356	18.4
Sus philippensis	104	4	108	39	15	54	162	8.4
large mammal	956		956	138	1	139	1095	56.6
Phloeomys pallidus		1	1				1	0.1
Crateromys sp.*	2		2				2	0.1
Carpomys undescr. sp.*	6		6				6	0.3
Bullimus/Rattus sp.	2		2				2	0.1
Phloeomyin	33		33				33	1.7
Murid	13	2	15	2		2	17	0.9
Paradoxurus philippinensis					2	2	2	0.1
Canis lupus familiaris	2		2	1		1	3	0.2
Macaca fascicularis	4	20	24	14	15	29	53	2.7
intermediate mammal	8		8	6	4	10	18	0.9
Microchiroptera	1		1				1	0.1
small mammal	10		10	2			10	0.5
Varanus sp.	3		3				3	0.2
Turtle	1		1	1		1	2	0.1
Snake	8		8	1		1	9	0.5
Fish	1		1				1	0.1
Bird	2		2	1	1	2	4	0.2
macrovertebrate	82		82	41		41	123	6.4
microvertebrate	31		31	1		1	32	1.7
	1404	30	1434	412	91	501	1935	100

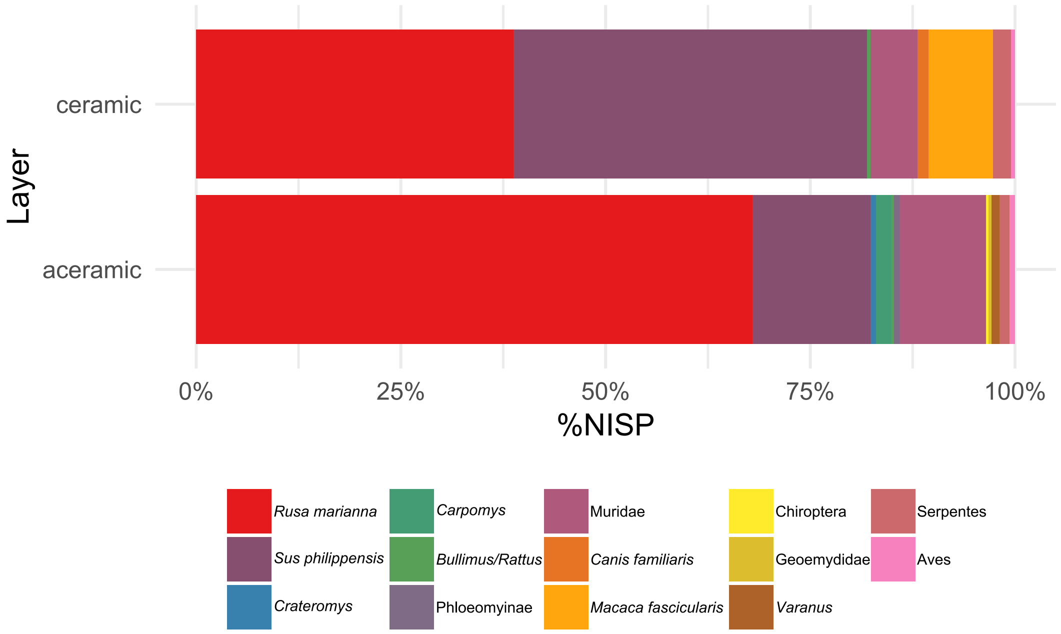


Figure 6.1 Relative taxonomic abundance (%NISP) of vertebrate taxa in Squares 27 and 37 of Minori Cave. NISP = number of identified specimens. NISP counts per layer are in Table 8.25.

A total of nine mammal species and two reptile taxa have been identified in the Minori Cave assemblage (Table 6.2). Of the nine mammal taxa, six are native species (*Rusa marianna*, *Sus philippensis* and four murid species) and three are non-native species (*Macaca fascicularis*, *Paradoxurus philippinensis* and *Canis lupus familiaris*). Of the native taxa, two species are novel endemic cloud rat species that are now extinct (*Carpomys* and *Crateromys*). Large mammals dominate the sequence (Figure 6.1, Table 6.2). In the aceramic layer, the native deer is the dominant taxon, whereas in the ceramic-bearing layer, pigs slightly outnumber deer. In the ceramic-bearing layers, the three introduced taxa appear (macaque, palm civet and domestic dog). Remains of turtles, monitor lizard and snakes also appear in small numbers across the sequence.

6.4 Minori Cave Accounts of Species

Species accounts for the non-volant mammal taxa of Minori Cave follows in this section. Detailed treatments are specifically provided for novel and extinct murid species discovered in the assemblage.

6.4.1 Order Cetartiodactyla

Family Cervidae

Rusa marianna

Measurements of dental specimens indicate that the deer remains in the assemblage are attributable to the Philippine brown deer, *Rusa marianna,* the extant cervid on Luzon (Table 6.3). Tooth specimens from Minori and Musang Caves overlap in dimensions with those of living *R. marianna* of Luzon (Figure 6.2). They also overlap in dimensions with archaeological specimens from two other Luzon sites, Callao Cave and Nagsabaran. All the Luzon specimens (modern and archaeological) generally separate from the other extant deer populations from other Philippine islands, although the sample size for the latter are small because of the rarity of these taxa. *Rusa alfredi*, a dwarfed sambar species, is restricted to the Negros-Panay faunal region, while *Axis calamianensis*, is the native hog deer of the Palawan faunal region discussed in the previous chapter. Both species are smaller than the Luzon deer and are single-island endemics of their own faunal regions.

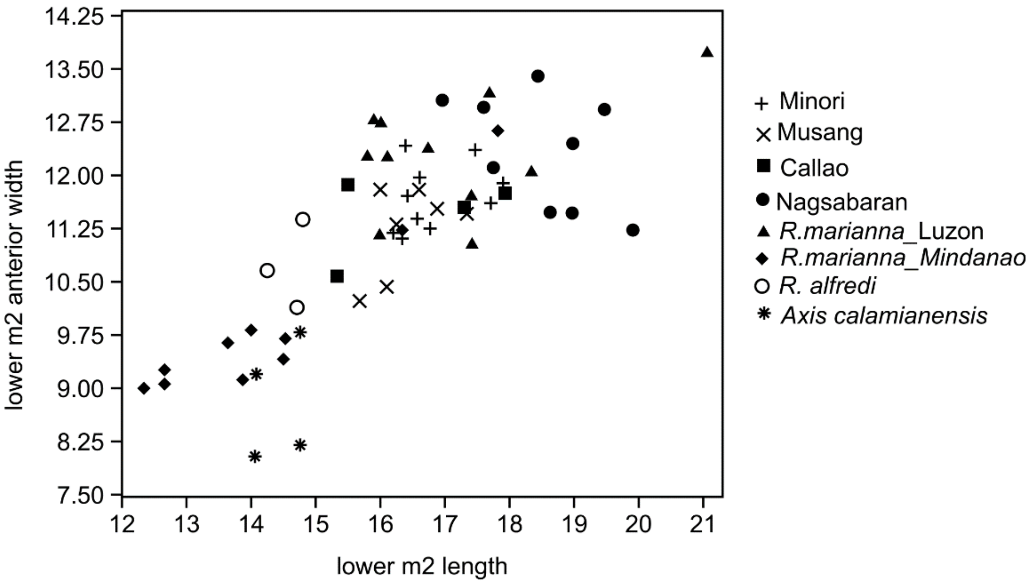


Figure 6.2 Bivariate plot of cervid mandibular m2 measurements (in mm) from Minori and Musang Caves compared with modern and archaeological specimens. Data for Callao Cave is from Piper et al. 2007 and data for Nagsabaran site is from Amano 2013. Modern comparatives of Philippine cervids are all from the FMNH and were measured with PJ Piper.

The Philippine brown deer (or Philippine sambar) is the most abundant taxon in the assemblage and is found across the sequence. It is generally common in archaeological assemblages in Luzon, and considered the major prey species along with the wild pig. *Rusa marianna* is presently widespread across the Luzon, Mindoro and Mindanao faunal regions, but historical extirpations on smaller islands have been observed (MacKinnon et al. 2015). The brown deer is noted as the largest living deer in the Philippines and its habitat ranges from sea level to 2900 m (Heaney et al. 2016). It is a forest species that can be found foraging in grassy clearings. It varies in size and pelage across its range and further investigation of systematic relationships is needed. Note that in Figure 6.2, most of the sample of *R. marianna* from Mindanao are relatively smaller than the Luzon population, and instead the former overlap in size with the smaller deer species of Negros and Palawan.

Table 6.3 Maxillary and mandibular molar measurements (in mm) of Minori and Musang cervids compared with extant cervid species. All measurements are cervical (taken above cementum/enamel junction). Anterior width = width of anterior cusp, Posterior width = width of posterior cusp. For modern reference, (N) refers to number of individuals. FMNH measurements were taken with PJ Piper.

Maxillary												
Source/ Specimen No.	Taxon	Locality	P4 Length	P4 Width	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width
FMNH	*Axis calamianensis*	Calamianes	7.36 - 8.61 (3)	9.15 - 11.15 (3)	11.02 - 13.26 (6)	10.5 - 12.93 (6)	10.72 - 13.42 (6)	13.3 - 14.84 (4)	11.45 - 12.68 (4)	11.78 - 13.3 (4)	15.08- 15.12 (2)	11.54 - 12.5 (2)
MCZ	*Axis porcinus*	India	8.6-9.2 (3)	11.3 -12.4 (4)	10.5 - 11.5 (3)	12.8-14.5 (3)	13.7-14.9 (3)	14.1-14.9 (2)	16.2-16.8 (2)	15.6-15.9 (2)	\	\
FMNH	*Rusa alfredi*	Negros	9.05 - 10.7 (3)	12.36 - 12.9 (3)	11.5 - 14.38 (5)	13.3 - 14.2 (5)	13.04 - 14.26 (5)	13.5 - 17.3 (4)	15.04 - 15.72 (4)	14.1 - 15.51 (3)	15.25 - 16.37 (3)	13.98 - 15.16 (3)
FMNH	*Rusa marianna*	Mindanao	7.7 - 9.27 (5)	10.72 - 11.91 (5)	10.28 - 12.39 (8)	12.49 - 13.8 (8)	11.8 - 14.34 (8)	11.63 - 14.58 (7)	13.32 - 15.09 (8)	13.1 - 14.78 (7)	13.17 - 15.67 (7)	12.9 - 14.38 (7)
FMNH	*Rusa marianna*	Luzon	9.03 - 11.17 (6)	13.4 - 15.2 (6)	12.4 - 15.12 (10)	13.75 - 17.03 (10)	13.95 - 17.04 (9)	15.06 - 18.28 (10)	15.84 - 18.66 (9)	15.3 - 18.68 (8)	16.12 - 18.3 (7)	16.8 - 17.94 (5)
FMNH	*Rusa unicolor*	SEA	12.34 -13.76 (3)	15.99 - 17.56 (3)	15.59 - 17.24 (4)	19.72 - 21.42 (4)	19.62 - 21.18 (4)	19.74 - 21.13 (4)	22.56 - 23.08 (4)	22.17 - 22.8 (4)	21.2 - 22.43 (3)	20.02 - 22.49 (3)
FMNH	*Muntiacus muntjak*	Borneo	6.34 - 7.86 (3)	9.03 - 9.95 (3)	8.4 - 9.68 (4)	10.22 - 12.23 (4)	10.61 - 12.02 (4)	9.15 - 10.62 (3)	11.33 - 13.06 (3)	11.0 - 12.76 (3)	9.97 - 10.88 (3)	10.98 - 12.62 (3)
2895	*Rusa marianna*	Minori Ch. A						15.67	17.15	\		
8502	*Rusa marianna*	Minori Ch. A			14.82	16.04	15.7					
1050	*Rusa marianna*	Minori Ch. A						15.44	16.29	17		
127	*Rusa marianna*	Minori Ch. A			15.65	14.96	16.76	16.63	18.04	17.06		
40	*Rusa marianna*	Minori Ch. A						16.32	17.66	16.09		
6061	*Rusa marianna*	Minori Ch. A						16.17	16.13	15.72		
8716	*Rusa marianna*	Minori Ch. A						17.06	16.63	15.22		
3144	*Rusa marianna*	Minori Ch. A			15.42	15.03	14.76	16.96	15.57	15.77		
962	*Rusa marianna*	Minori Ch. A			13.81	15.96	15.45					
488	*Rusa marianna*	Minori Ch. A			14.48	15.69	15.6					
632	*Rusa marianna*	Minori Ch. A						16.11	17.97	17.74		
4775	*Rusa marianna*	Minori Ch. A			13.18	\	\					
4734	*Rusa marianna*	Minori Ch. A			14.4	15.64	\					
3716	*Rusa marianna*	Minori Ch. A						16.21	\	\		
2815	*Rusa marianna*	Minori Ch. A									17.5	18.81
3148	*Rusa marianna*	Minori Ch. A						16.45	\	17.15		
73	*Rusa marianna*	Minori Ch. A									17.55	18.69
3660	*Rusa marianna*	Minori Ch. A									17.44	17.46
3664	*Rusa marianna*	Minori Ch. A						16.4	17.19	16.97		
269	*Rusa marianna*	Minori Ch. A			15.88	16	17.07					
3524	*Rusa marianna*	Minori Ch. A			15.33	17.15	17.12					
3276	*Rusa marianna*	Minori Ch. A						16.04	16.16	15.74		
3765	*Rusa marianna*	Minori Ch. A						18.88	19.22	19.82		
6193	*Rusa marianna*	Minori Ch. A						16.62	17.57	18.05		

Table 6.3 continued. Maxillary and mandibular molar measurements (in mm) of Minori and Musang cervids.

Maxillary													
Source/ Specimen No.	Taxon	Locality	P4 Length	P4 Width	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width	M3 Posterior width
8155	*Rusa marianna*	Minori Ch. A			13.39	15.09	14.37						
4533	*Rusa marianna*	Minori Ch. A			14.84	14.91	14.84						
3550	*Rusa marianna*	Minori Ch. A						16.45	17.63	16.75			
2661	*Rusa marianna*	Minori Ch. A						16.89	15.19	14.39			
3152	*Rusa marianna*	Minori Ch. A						16.29	17.29	17.15			
3321	*Rusa marianna*	Minori Ch. A			\	15.17	14.25						
2536	*Rusa marianna*	Minori Ch. A						16.31	17.25	15.35			
3693	*Rusa marianna*	Minori Ch. A									17.27	17.54	14.08
4421	*Rusa marianna*	Minori Ch. A			13.69	12.45	12.6						
182	*Rusa marianna*	Minori Ch. A			13.2	15.93	15.51						
2465	*Rusa marianna*	Minori Ch. A			13.47	15.59	15.74						
16732	*Rusa marianna*	Minori Ch. D			13.1	16	15.9						
9348	*Rusa marianna*	Minori Ch. D			14.2	16.4	16						
72	*Rusa marianna*	Musang						15.6	16.17	15.91			
1	*Rusa marianna*	Musang			13.64	12.87	13.13						
1	*Rusa marianna*	Musang						15.26	17.26	\			
74	*Rusa marianna*	Musang						16.24	17.43	17.14			
3	*Rusa marianna*	Musang	10.36	13.05									
75	*Rusa marianna*	Musang						17.14	14.82	15.87			
771	*Rusa marianna*	Musang						17.69	15.51	17.1			
594	*Rusa marianna*	Musang						17.54	15.64	15.08			
702	*Rusa marianna*	Musang						16.17	17.03	17.93			
596	*Rusa marianna*	Musang			14.98	14.2	14.46						
910	*Rusa marianna*	Musang			14.46	14.44	14.97						
10968	*Rusa marianna*	Musang			14.43	15.73	14.42						
197	*Rusa marianna*	Musang	10.25	12.16									
7071	*Rusa marianna*	Musang						16.05	15.46	14.02			
701	*Rusa marianna*	Musang									17.16	17.01	14.73
4369	*Rusa marianna*	Musang			15.61	\	14.54						
57	*Rusa marianna*	Musang	10	12.2									
60	*Rusa marianna*	Musang						15.6	16.7	16.5			

Table 6.3 continued. Maxillary and mandibular molar measurements (in mm) of Minori and Musang cervids.

Mandibular												
Source/ Specimen No.	Taxon	Locality	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width	M3 Width of middle cusp	M3 Posterior width
FMNH	*Axis calamianensis*	Calamianes	9.82 - 11.93 (6)	7.35 - 8.02 (6)	7.15 - 8.52 (6)	14.06 - 14.76 (4)	8.04 - 9.79 (4)	7.3 - 8.88 (4)	18.26 - 19.78 (2)	8.77 - 10.6 (2)	7.7 - 10.62 (2)	3.72 (1)
MCZ	*Axis porcinus*	India	11.6-11.7 (2)	7.9-8.1 (2)	8.2-8.7 (2)	13.6 (1)	9.8 (1)	9.5 (1)	\	\	\	\
FMNH	*Rusa alfredi*	Negros	11.22 - 13. 78 (5)	8.45 - 9.5 (5)	8.77 - 10.47 (5)	14.25 - 16.48 (4)	10.14 - 11.38 (3)	10.43 - 11.32 (3)	20.49 - 20.9 (3)	9.78 - 11.04 (3)	10.17 - 11.24 (3)	5.49 - 5.88 (3)
FMNH	*Rusa marianna*	Mindanao	10.24 - 12.96 (8)	7.76 - 8.7 (8)	8.5 - 9.44 (8)	12.34 - 14.53 (8)	9 - 9.82 (8)	8.91 - 10.32 (8)	18.03 - 20.27 (7)	8.57 - 9.8 (7)	7.82 - 8.96 (7)	4.92 - 5.34 (5)
FMNH	*Rusa marianna*	Luzon	12.8 - 15.24 (8)	9.6 - 10.97 (7)	10.46 - 11.6 (8)	15.8 - 18.34 (8)	11.05 - 13.18 (8)	11.12 - 12.46 (8)	23.3 - 25.28 (5)	11.4 - 12.77 (6)	10.52 - 12.94 (5)	5.86 - 7.46 (5)
FMNH	*Rusa unicolor*	SEA	16.65 - 18.33 (3)	12.81 - 13.27 (4)	12.52 - 13.88 (3)	19.46 - 20.93 (2)	14.74 - 15.32 (3)	14.24 - 15.09 (3)	28.28 - 28. 86 (2)	14.9 - 14.95 (2)	13.53 - 14.42 (2)	8.56 - 8.74 (2)
FMNH	*Muntiacus muntjak*	Borneo	9.32 - 9.77 (4)	6.67 - 7.04 (4)	6.9 - 7.72 (4)	10.05 - 11.0 (3)	7.97 - 8.56 (3)	8.11 - 8.28 (3)	14.64 - 15.2 (3)	7.65 - 8.15 (3)	7.23 - 7.78 (3)	4.41 - 4.76 (3)
4188	*Rusa marianna*	Minori Ch. A				16.57	11.39	\				
2041	*Rusa marianna*	Minori Ch. A				16.61	11.97	12.3				
2534	*Rusa marianna*	Minori Ch. A				\	11.89	\				
7744	*Rusa marianna*	Minori Ch. A	14.76	10	11.53							
698	*Rusa marianna*	Minori Ch. A							\	12.85	10.86	\
106	*Rusa marianna*	Minori Ch. A	14.72	9.57	10.26							
2988	*Rusa marianna*	Minori Ch. A				16.77	11.25	10.97				
228	*Rusa marianna*	Minori Ch. A				16.42	11.71	10.8				
2714	*Rusa marianna*	Minori Ch. A	15.2	9.75	10.23							
6194	*Rusa marianna*	Minori Ch. A										
4602	*Rusa marianna*	Minori Ch. A				16.2	11.19	11.15				
2212	*Rusa marianna*	Minori Ch. A	15.17	9.96	10.08							
840	*Rusa marianna*	Minori Ch. A							23.27	11.45	10.63	6.02
4636	*Rusa marianna*	Minori Ch. A										
4658	*Rusa marianna*	Minori Ch. A							24.85	11.24	11.2	6.44
229	*Rusa marianna*	Minori Ch. A	15.76	10	9.85							
6014	*Rusa marianna*	Minori Ch. A							22.7	10.95	10.04	6.07
2545	*Rusa marianna*	Minori Ch. A	\	9.81	10.72							
6054	*Rusa marianna*	Minori Ch. A	15.5	10.53	10.76							
3432	*Rusa marianna*	Minori Ch. A	13.87	10.42	10.78							
490	*Rusa marianna*	Minori Ch. A							22.7	12.74	11.29	7.1
2716	*Rusa marianna*	Minori Ch. A	13.93	10.54	10.1							
8000	*Rusa marianna*	Minori Ch. A							22.71	11.12	9.99	5.63
225	*Rusa marianna*	Minori Ch. A				17.9	11.89	12.38				
940	*Rusa marianna*	Minori Ch. A	14.37	10.26	10.84							
6006	*Rusa marianna*	Minori Ch. A										
6010	*Rusa marianna*	Minori Ch. A							22.25	11.93	10.92	6.5
6010	*Rusa marianna*	Minori Ch. A	15.2	10.28	11							
2291	*Rusa marianna*	Minori Ch. A				16.34	11.11	11.24				

Table 6.3 continued. Maxillary and mandibular molar measurements (in mm) of Minori and Musang cervids.

Mandibular												
Source/ Specimen No.	Taxon	Locality	M1 Length	M1 Anterior width	M1 Posterior width	M2 Length	M2 Anterior width	M2 Posterior width	M3 Length	M3 Anterior width	M3 Width of middle cusp	M3 Posterior width
2045	*Rusa marianna*	Minori Ch. A							23.32	11.08	10.77	5.5
2987	*Rusa marianna*	Minori Ch. A							23.33	\	9.98	5.11
7385	*Rusa marianna*	Minori Ch. A				17.47	12.36	11.65				
3151	*Rusa marianna*	Minori Ch. A				16.39	12.42	12.31				
3751	*Rusa marianna*	Minori Ch. A										
3746	*Rusa marianna*	Minori Ch. A										
3743	*Rusa marianna*	Minori Ch. A										
3400	*Rusa marianna*	Minori Ch. A										
2139	*Rusa marianna*	Minori Ch. A										
9626	*Rusa marianna*	Minori Ch. D	15.69	10.11	10.5							
9620	*Rusa marianna*	Minori Ch. D				17.71	11.61	11.87				
9624	*Rusa marianna*	Minori Ch. D										
16161	*Rusa marianna*	Minori Ch. D							20.8	11.2	9.9	5.3
16990	*Rusa marianna*	Minori Ch. D										
16733	*Rusa marianna*	Minori Ch. D	15	9.9	10.1							
1	*Rusa marianna*	Musang							\	\	11.22	6.28
1	*Rusa marianna*	Musang				17.34	11.46	11.81				
74	*Rusa marianna*	Musang							23.15	12.12	11.03	\
74	*Rusa marianna*	Musang				18.23	10.63	10.69				
74	*Rusa marianna*	Musang				15.68	10.23	10.4				
62	*Rusa marianna*	Musang										
73	*Rusa marianna*	Musang				16.25	11.31	10.35				
3	*Rusa marianna*	Musang										
58	*Rusa marianna*	Musang							18.11	10.52	10.34	4.12
75	*Rusa marianna*	Musang	14.41	10.34	10.05	16.1	10.43	10.31				
75	*Rusa marianna*	Musang				16.88	11.53	11.96				
64	*Rusa marianna*	Musang	14.76	9.92								
113	*Rusa marianna*	Musang	14.7	10.63	9.87							
110	*Rusa marianna*	Musang	15.29	9.92	10.59							
595	*Rusa marianna*	Musang							24.33	11.64	10.4	6.81
20102	*Rusa marianna*	Musang	13.25	9.13	9.21							
6900	*Rusa marianna*	Musang							23.9	10.97	10.84	6.39
6314	*Rusa marianna*	Musang							23.38	10.98	10.74	6.99
17129	*Rusa marianna*	Musang							22.49	11.6	10.31	6.11
10665	*Rusa marianna*	Musang							21.25	10.96	9.61	5.45
57	*Rusa marianna*	Musang				16	11.8	11.5				
57	*Rusa marianna*	Musang				16.6	11.8	11.1				
57	*Rusa marianna*	Musang										
55	*Rusa marianna*	Musang	13.3	9.7	10.2							

6.4.2 Family Suidae
Sus philippensis

The remains of pigs in the assemblage are attributed to the extant wild pig on Luzon Island, *Sus philippensis*. The Philippine warty pig is notably smaller than the introduced domestic *Sus scrofa*, and the Minori Cave teeth and postcranial remains are all relatively small (see Table 6.13 and Figure 6.15 under *S. scrofa* discussion in Musang Cave section). This smaller body size is characteristic of all the extant wild pig species in the Philippine archipelago, a phenomenon that follows the Island Rule (Foster's rule). There is no identified record of the domestic pig on Minori Cave, but there is a record described below for Musang Cave. The Philippine warty pig occurs in the Luzon and Mindanao faunal regions. Its range is from sea level to at least 2800 m elevation in nearly all terrestrial habitats.

6.4.3 Order Rodentia
Family Muridae
Tribe Phloeomyini

Four murid taxa were identified in the Minori Cave assemblage. Of these, three are ascribed to the tribe Phloeomyini (*sensu* Lecompte et al. 2008; Musser and Carleton 2005). Five genera are currently known from this endemic clade, and three of these – *Carpomys*, *Crateromys* and *Phloeomys* – were identified in the two assemblages. All fossil identifications are based on dental morphology, following the molar cusp terminology of Miller (1912) (Fig 6.2).

The Phloeomyini consist of arboreal and mostly herbivorous species native to the oceanic Philippines that are referred to as cloud rats, tree rats and tree mice. Twelve species are currently known in Luzon. Within the Phloeomyini, the '*Crateromys* group' (= Phloeomyini minus *Phloeomys;* after Musser and Heaney 1992) consists of four genera: *Batomys, Carpomys, Crateromys* and *Musseromys*. All of these genera are represented in the modern fauna of Luzon Island. Musser and Heaney (1992: 61-65) describe several shared derived traits in the molar morphology of the *Crateromys* group that distinguish them from other murid taxa:

1. a large discrete cusp t7 on each upper molar, which has an anterolingual orientation relative to central cusp t8 and forms a significant part of the lingual occlusal surface
2. a reduced or absent t9 in the labial margin of each upper molar
3. a large anteroconid forms the anterior one-third of each lower first molar

Identified cloud rat (*Carpomys* and *Crateromys*) fossil specimens possess these synapomorphies and further description and data are provided below to distinguish among the members within the *Crateromys* group.

6.4.4 *Carpomys* undescr. sp.

Carpomys is represented in Minori Cave by four maxillary specimens and two mandibular specimens, belonging to at least four individuals (Figure 6.4 and Table 6.5). An additional mandibular specimen was identified in Musang Cave (Musang-101). *Carpomys* are currently represented by two living species: *C. melanurus* (greater dwarf cloud rat) and *C. phaeurus* (lesser dwarf cloud rat). Both are limited in distribution to the Central Cordillera range of northern Luzon, particularly in mossy forest at 2100 to 2500 m. Like other cloud rats, dwarf cloud rats are so named because they inhabit montane rainforest and are largely or entirely arboreal. The ascription '*Carpomys'* is due to the short and broad hind foot (Thomas 1895).

The fossil specimens display the synapomorphies in molar morphology detailed above that distinguish the *Crateromys* group. The specimens are in the size range of the living *Crateromys schadenbergi*, but they have a brachyodont structure that contrasts with the hypsodont *Cr. schadenbergi*. The dental morphology of the four genera of the *Crateromys* group were compared with the fossils using comparative collections in the BMNH and FMNH. The BMNH collection includes the holotype for *Carpomys melanurus* and *Carpomys phaeurus*. The lamellate cusp pattern observed in the fossils (Figure 6.3) closely follows the morphology of the living *Carpomys*, as well as the members of the closely related *Musseromys*. The fossils and the extant *Carpomys* are observed to be distinctive from *Crateromys* and *Batomys* based on the following dental traits:

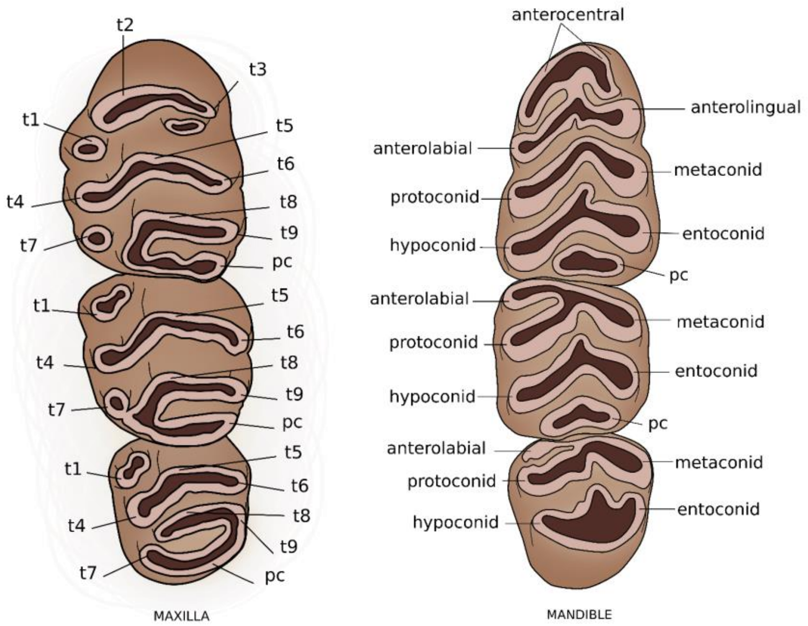


Figure 6.3 *Carpomys* cusp pattern diagram of the left maxillary and left mandibular toothrows using Miller's (1912) terminology.

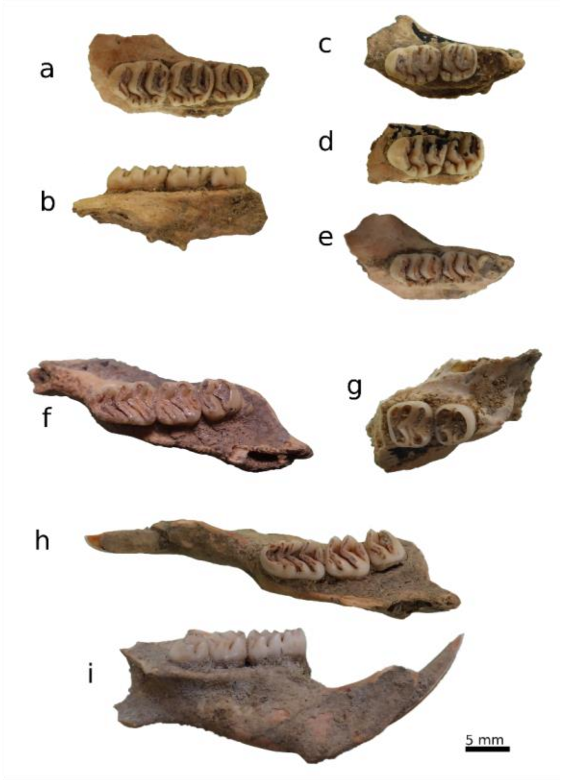


Figure 6.4 Fossil material referred to *Carpomys*: Minori-15997 (a-b), Minori-16481 (c), Minori-16825 (d), Minori-16447 (e), Musang-101 (f), Minori-16951 (g), Minori-16301 (h-i). (a-e) are maxillary specimens (f-i) are mandibular specimens. All are occlusal views except for b (labial) and i (lingual).

1. **General upper molar shape**. *Carpomys* have more elongate and narrower laminae in the upper molars, versus more angular and arcuate (or chevronate) in *Crateromys* and *Batomys*. The mesial cusps t2/t5/t8 are very broad in *Crateromys*. In *Batomys*, the mesial cusps are relatively intermediate in width – less broad than *Crateromys*, but still broader compared to *Carpomys*. In contrast, upper molars of *Carpomys* have an elongate form and narrow mesial cusps. Among the phloeomyins, the lopho-bunodont cusps of *Carpomys* are intermediate between the less lamellate *Batomys* and the lophodont *Phloeomys* (see molar topography classification in Lazzari et al. 2015).
2. **Number of laminae in molars**. *Carpomys* species possess an extra row of cusps or laminae in upper and lower first molars. Describing the holotype, Oldfield Thomas (1895) notes: "Teeth somewhat as in *Mus*, but upper molars each with an additional posterior lamina."
    a. There are four rows of laminae in upper and lower first molars in *Carpomys*, versus three rows in *Crateromys* and *Batomys*. Thomas (1898: 406) once again notes: "The last molar is normal, so that the laminar formula is 4-3-2." In contrast, the laminar formula for *Crateromys* and *Batomys* is 3-2-2.
    b. In the upper m1, the fourth row is the elongate and well-developed posterior cingulum.
    c. In the lower m1, the 'additional' row is the first lamina, the bicuspid anterocentral. In *Crateromys* and *Batomys* (and most other murid genera) the anterocentral has only one cusp that is fused with anterolabial and anterolingual cusp into a more typical triangular anteroconid (see below).
    d. The extra laminae are also present in maxillary second and third molars because of the elongate and well-developed posterior cingulum. *Carpomys* is distinctive among the *Crateromys* group in having a laminar posterior cingulum in all upper molars (see Figure 34 in Musser and Heaney 1992).
3. **Distinct morphology of the anteroconid**. Among various Southeast Asian taxa, the phloeomyin anteroconid is distinctive in having an expanded anterocentral cusp that forms the anterior half of a cordate anteroconid (Aplin and Helgen 2010; Musser and Heaney 1992). Within this form, *Carpomys* is distinctive in having a bicuspid anterocentral subdivided in two equal units (Figure 6.3; see also Figure 35 and 64D in Musser and Heaney 1992). This form produces an anteroconid with two distinct laminae: the bicuspid anterocentral lamina and the fused anterolabial and anterolingual lamina. In contrast, the anterocentral is more typically a single cuspid in

other phloeomyins (hence its name), and it is fused to the second lamina in a more typical cordate/triangular-shaped anteroconid such as that found in *Batomys* and *Crateromys.* Thomas (1898:406) describes: "In the lower jaw, m1 has an additional lamina in front, and both it and m2 have well-marked posterior supplementary cusps, while the last-named has in addition an antero-external one." This expanded form of the anterocentral is particularly observable in Minori Cave specimens 16961 and 16301 (Figure 6.4 f and h).

4. **Laminar posterior cingulum in all upper molars**. An elongate posterior cingulum is present in the upper molars, forming the 'additional lamina' of *Carpomys*, which is absent in *Crateromys* and the Luzon *Batomys*. A short, rounded/oblong posterior cingulum is present in *Batomys salomonseni*, a Mindanao Island *Batomys*, but this posterior cingulum appears more reduced and is only in M1-2. This form of the laminar posterior cingulum is labelled as a "posteroloph" by Aplin and Helgen (2010: 56) as they describe it for the Timor *Coryphomys*, noting that it is a singular trait shared with *Carpomys* and not found in other phloeomyins. This posteroloph also creates a deepened ''posterior fossette'' between the posterior cingulum and cusp t9 (Aplin and Helgen 2010). A substantial posterior cingulum to the rear of M3 is also a further specialization not observed in the other phloemyins.
5. **Anterior labial cusp in lower m2 and m3**. A well-developed anterior labial cusp ('antero-external' as labelled in Thomas 1898) is present in the lower m2 and m3 of *Carpomys* but is absent in *Crateromys* and greatly reduced or entirely absent in *Batomys*.
6. **Width of teeth**. *Carpomys* has relatively wide teeth compared to *Crateromys* and *Batomys*. In the upper and lower m2 and m3, the width of each tooth exceeds its length. This is also observed in the fossils but is not observed in *Crateromys*. In fossil and extant Luzon *Batomys*, the length often exceeds the width, or is nearly equal.

6.4.4.1 Comparison of *Carpomys* and *Musseromys*

The most closely related taxon to *Carpomys* is *Musseromys*, sharing a last common ancestor about 4 million years ago (Heaney et al. 2009; Lawrence R. Heaney et al. 2014). The fossil and extant *Carpomys* were compared with *M. gulantang* (holotype FMNH 178405), *M. inopinatus* (holotype FMNH 193838, FMNH 193840 and FMNH 214333), *M. anacuao* (FMNH 209523), and *M. beneficus* (FMNH 198857). *Carpomys* and *Musseromys* have extremely similar cusp patterns on upper and lower molars, such that the six traits outlined above also apply to

Musseromys. The main difference is that *Musseromys* is significantly smaller in all dimensions compared to *Carpomys*. A few traits were observed that align the fossil dentition with *Carpomys*, rather than *Musseromys* (Table 6.4). These are:

1. **Lower m1 morphology**. The second lamina (anterolabial + anterolingual) and third lamina (protoconid + metaconid) are more transversely oriented in *Musseromys* versus the bicuspidate and more arcuate form in *Carpomys* and the fossils. In *Musseromys*, only the fourth lamina (hypoconid + ectoconid) is clearly arcuate/chevron-shaped/chevronate. Furthermore, the anteroconid in the fossils and in two *C. phaeurus* individuals (including the heavily worn holotype BMNH 95.8.2.14) appear to have a different form. In these specimens, there appears to be a midline ridge (or narrow peninsula) connecting the anterocentral lamina to the second lamina.
2. **Lower m3 morphology**. In the lower m3, the anterior and posterior laminae have differing shapes in *Carpomys* and *Musseromys. Musseromys* species often have two transverse lophs in the m3. This contrasts with *Carpomys* individuals, which usually have a chevron-shaped anterior lamina and a more irregular shape ('W' shape) in the posterior lamina in some individuals (Figure 6.4 and Table 6.4). Another variation in the m3 morphology for *Carpomys* is a chevron-shaped anterior loph with a transverse posterior loph. Four fossils align with the *Carpomys* morphology (Minori-175565, 62291, 16301 and Musang 76-M-101) with a chevron-shaped anterior lamina and a 'W' occlusal pattern on the posterior lamina. The slightly worn specimen Minori-16301 (and see below Musang 76-M-101), shows that in the lower m3, an additional mesial cusplet is present between the anterior and posterior lophs. When worn down, the cusplet fuses with the posterior lamina and produces this 'W' pattern. The sample sizes are small for *Musseromys*, but the individuals available display transverse lophs in both lophs of the lower m3.
3. **Upper M3 morphology**. A well-developed posterior cingulum (pc) is observed on the upper m3 of the extant *Carpomys* and on a single fossil specimen with an M3 (Minori-15997). In *Musseromys*, it appears greatly reduced or absent altogether.

6.4.4.2 *Carpomys* and *Musseromys* Morphometrics

Measurements of fossil and comparative *Carpomys* and *Musseromys* specimens are presented in Table 6.5. Description of the method for taking *Carpomys* tooth measurements is provided in Appendix. The fossils are all substantially larger than the extant *Carpomys* and *Musseromys* species, greatly exceeding all length and width measurements of the living taxa (Figures 6.5 and 6.6). The specimens compared here encompass a broad size range of the cloud rat spectrum. On the one hand, the extant *Musseromys* (Philippine tree mouse) are the smallest known members of the cloud rats (Heaney et al. 2016). The body mass range for the four *Musseromys* species is 15 – 22 grams only, and their tooth dimensions are only 20-30% of the fossil measurements. The body mass range of the two living *Carpomys* (dwarf cloud rats) are 123 – 165 grams, and the tooth dimensions for both species are only 30-60% of the fossil dimensions. In the case of the fossils, the tooth measurements are closer to the size range of the living *Crateromys schadenbergi*, which has a body mass range 10x (1.35 – 1.5 kilograms) that of *C. melanurus,* the larger of the two *Carpomys* species. Within the fossil sample, five out six maxillary specimens are in a similar size range. One maxillary specimen, Minori-16447, appears to be relatively smaller than the other specimens.

On the basis of overall morphology and tooth measurements, the fossils represent a considerably larger-bodied version of the living *Carpomys*. The two extant *Carpomys* inhabit high-elevation mossy forest from *ca*. 2100 m in the Central Cordilleras, a separate mountain range that is on the opposite side (west) of the Cagayan River. The Callao system, on the other hand, is on the foothills of the Sierra Madre range. These two mountain ranges are known to be discrete sub-centres of endemism due to their complex geological histories and they harbour their own sets of endemic small mammals. *Carpomys* is not presently known in the Sierra Madre range; only *Musseromys and Phloeomys* are presently known in this mountain range. The extant *Carpomys* spp. are also not known to inhabit lowland forest habitats, which have characterized the environs of northern Luzon during the Holocene (see Stevenson et al. 2010). Holocene diminution in size for the living *Carpomys* is also unlikely to account for the size variation because of the great difference in size and because the fossil species persist into the Late Holocene.

Table 6.4 Summary of fossil traits compared with *Carpomys* and *Musseromys*. Traits listed are the state observed in the fossil specimens from Minori and Musang Caves. Counts indicate the number of modern individuals that display traits; otherwise, the opposite or alternative condition is listed. Mand = mandible, max= maxilla, M = missing tooth in specimen, HW = heavily worn, + = present.

Traits as observed in fossils	***Carpomys***		***Musseromys***				**Minori**						**Musang**
	C. melanurus	*C. phaeurus*	*M. gulantang*	*M. inopinatus*	*M. anacuao*	*M. beneficus*	16825	16481	16447	15997	16951	16301	101
	n=4	n=5	n=1	n=3	n=1	n=1	max	max	max	max	mand	mand	mand
LOWER M1													
arcuate to chevron-shaped second lamina	4	5	transverse	transverse = 3	transverse	transverse	\	\	\	\	+	+	+
chevron-shaped third lamina	4	5	transverse	transverse = 1; arcuate = 2	arcuate	transverse	\	\	\	\	+	+	+
mid-line enamel ridge inside the anteroconid (between anterocentral and second lamina)	0	2	0	0	0	0	\	\	\	\	M	+	+
LOWER M3													
chevron-shaped/ arcuate anterior lamina	4	2 (transverse =3)	transverse	transverse = 3	HW	transverse	\	\	\	\	+	+	+
W-shaped occlusal pattern of posterior lamina	2 (transverse = 2)	5	transverse	transverse = 3	HW	transverse	\	\	\	\	+	+	+
UPPER M3													
well-developed & elongate posterior cingulum	3	5	reduced	0	HW	0	M	M	M	+	\	\	\

The evidence suggests that the Minori fossils are ascribable to an undescribed novel species of *Carpomys*, representing a vastly larger species. It possibly had broader ecological tolerances than the living montane members of this genus, or it may have been particularly adapted to lowland forest environments. Of the living cloud rats on Luzon, there is a possible analogue in the two giant cloud rat species of *Phloeomys*, which tolerates a wide range of habitats from sea level to upper montane environments.

Figure 6.5 Fossil maxilla referred to *Carpomys* compared with extant taxa. L-R: Minori-15997, *Carpomys melanurus* holotype (BMNH 95.82.12), *Carpomys phaeurus* holotype (BMNH 95.82.14) and *Musseromys inopinatus* (FMNH 193838). All images are occlusal views of the left side.

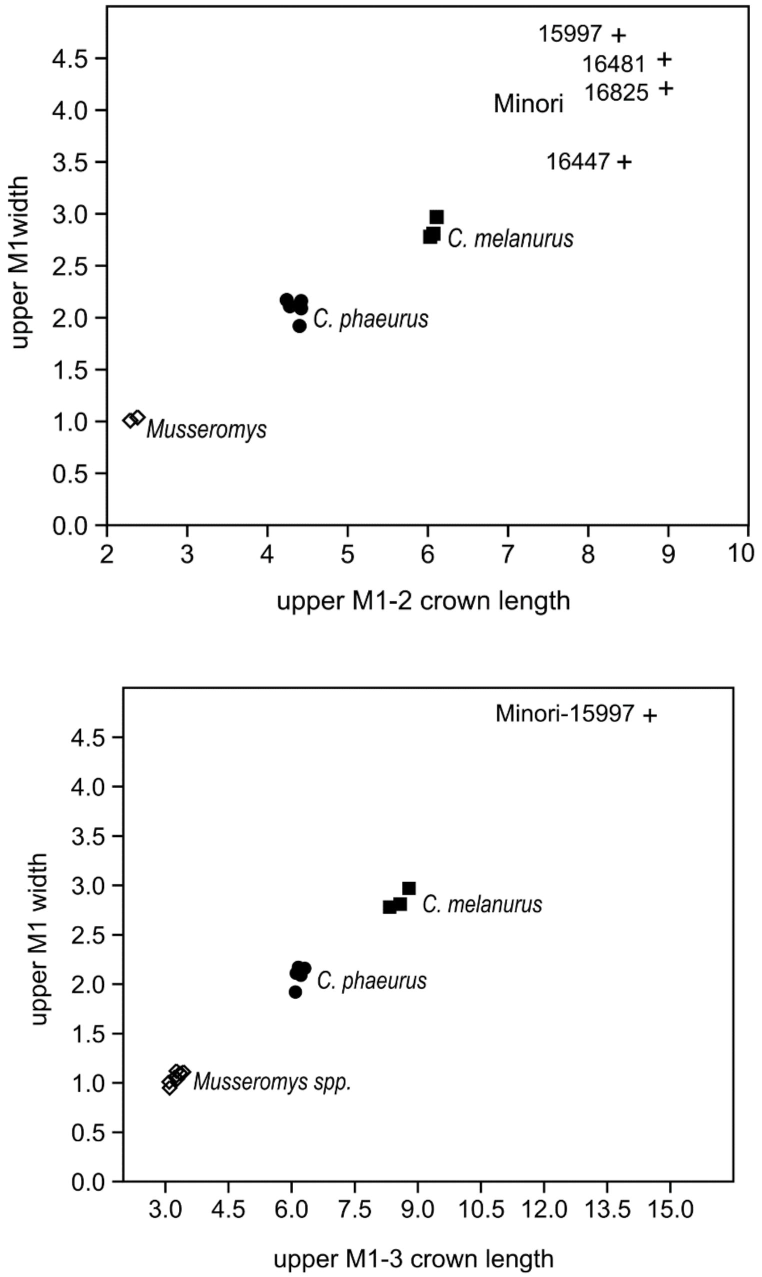


Figure 6.6 Bivariate plot of *Carpomys* dental measurements (in mm): A) maxillary M1-2 crown length vs maxillary m1 width of extant Carpomys, Musseromys and four Minori specimens; and B) maxillary M1-3 crown length vs maxillary m1 width which includes all known Musseromys spp. All measurements in are by the author except for upper M1-3 crown length measurements for Musseromys spp. in (B), which are from Heaney et al. (2009, 2014). Reference specimens are from the FMNH and the BMNH and measurements for extant taxa include the holotypes for the respective species.

Table 6.34 Measurements (in mm) of maxillary and mandibular molars of fossil *Carpomys* from Minori and Musang Caves, extant *Carpomys* and extant *Musseromys*. L = length, W = width, SD= standard deviation given for samples of 3 and more. *crown length measurement taken at the occlusal surface; ** crown length measurement taken immediately above the cementum-enamel junction.

		M1-M3 L occlusal*	M1-M3 L cervical**	M1L	M1W	M2L	M2W	M3L	M3W
maxillary									
Minori-16825				4.97	4.21	4.03	4.01		
Minori-16481				5.12	4.49	4.14	4.29		
Minori-15997		13.81	14.52	5.84	4.72	4.76	4.56	3.99	3.74
Minori-16447				4.52	3.5	3.82	3.39		
Fossil summary (n=4)	mean			5.11	4.23	4.19	4.06		
	SD			0.55	0.53	0.40	0.50		
C. phaeurus	mean	5.86	6.18	2.50	2.09	1.81	2.00	1.57	1.73
(n=5)	SD	0.21	0.09	0.16	0.10	0.12	0.06	0.11	0.04
	range	5.62-6.12	6.09-6.31	6.09-6.31	1.66-1.95	1.66-1.95	1.93-2.08	1.43-1.71	1.69-1.78
C. melanurus	mean	8.18	8.57	3.47	2.85	2.70	2.80	2.19	2.25
(n=3)	SD	0.23	0.23	0.09	0.10	0.08	0.12	0.14	0.05
	range	7.92-8.28	8.33-8.79	8.33-8.79	2.62-2.77	2.62-2.77	2.68-2.91	2.05-2.33	2.2-2.29
M. inopinatus FMNH 193838		3.12	3.28	1.37	1.04	0.87	1.02	0.73	0.82
M. anacuao FMNH 209523		3.00	3.09	1.45	1.01	0.87	0.97	0.67	0.69

Table 6.5 continued. Measurements (in mm) of maxillary and mandibular molars of fossil *Carpomys* from Minori and Musang Caves.

		M1-M3 L occlusal*	M1-M3 L cervical**	M1L	M1W	M2L	M2W	M3L	M3W
mandibular									
Minori-16951		\	\	\	\	4.33	4.46	3.49	3.9
Minori-16301		13.24	14.55	5.97	3.84	4.22	4.09	2.77	3.71
Musang-101		13.71	14.03	6.36	4.31	4.05	4.17	2.92	3.8
Fossil summary (n=3)	mean	13.48	14.29	6.17	4.08	4.20	4.24	3.06	3.80
	SD					0.14	0.19	0.38	0.10
C. phaeurus	mean	6.50	2.88	2.04	1.90	2.00	1.39	1.65	1.42
n=5	SD	0.13	0.05	0.10	0.10	0.12	0.10	0.07	0.13
	range	6.07-6.58	6.3-6.64	2.8-2.94	1.89-2.13	1.73-1.98	1.83-2.15	1.29-1.51	1.55-1.71
C. melanurus	mean	8.41	9.14	3.77	2.84	2.66	2.73	1.97	2.25
n=3	SD	0.23	0.06	0.08	0.12	0.08	0.11	0.20	0.08
	range	8.25-8.67	9.11-9.21	3.69-3.85	2.7-2.94	2.6-2.75	2.62-2.83	1.75-2.15	2.16-2.28
M. inopinatus FMNH 193838		3.23	3.31	1.51	0.99	0.95	1	0.8	0.8
M. anacuao FMNH 209523		3.25	3.26	1.47	0.97	0.91	1	0.7	0.83

6.4.5 *Crateromys* sp.

In overall appearance, two mandibular specimens (Minori -17018 and -16692) align in morphology with the *Crateromys* group, with its large, high-crowned, and chevron-shaped molar lophs (Figure 6.7). As mentioned above, a distinguishing feature of the *Crateromys* group is the large anteroconid of the lower m1 that is composed of a well-developed anterocentral cusp fused with anterolabial and anterolingual cusps. In comparison to *Carpomys*, the specimens have more arcuate, bicuspidate lophs akin to *Crateromys*, whereas *Carpomys* molar lophs are less arcuate. The lower m1 morphology is also very different. The anterocentral is composed of one cusp, such as is typical for *Crateromys* and *Batomys*, as opposed to bicuspid in *Carpomys*. In the specimens, the anterocentral is narrow and fused with the anterolabial and anterolingual cusps, expressing a large triangular anteroconid with a hollow core. The m2 and m3 do not possess an anterolabial cusp, as they do in *Carpomys*. The posterior cingula in the m1 and m2 are narrowly triangular, whereas these are much more elongate in *Carpomys*.

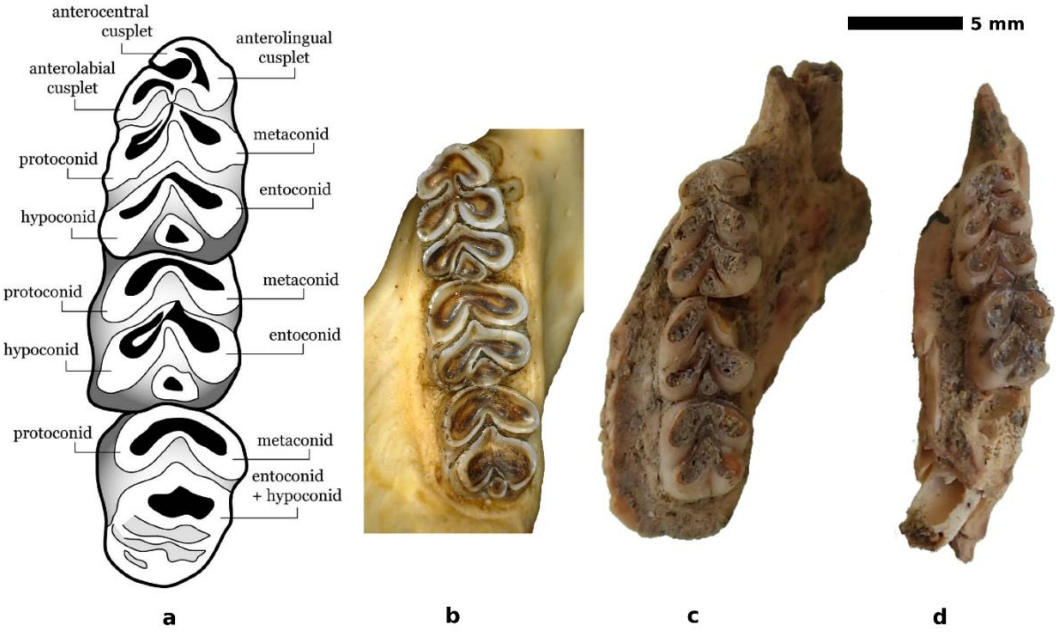


Figure 6.760 Mandibular specimens referred to *Crateromys* in occlusal view: Minori-17018 (c) and Minori-16692 (d). Modern reference is the Luzon native *Cr. schadenbergi* (b, FMNH 62294), with a diagram (a) of the cuspidation pattern of the m1-m3 adapted from Reyes et al. (2017).

The general features of the fossils align with *Crateromys* but it is necessary to compare them to the closely related *Batomys*. The specimens are markedly larger and more hyposodont compared to the Callao fossil *Batomys* (Heaney et al. 2011) and to the extant *B. granti* and *B. dentatus*. The m1 and m2 occlusal configurations are quite similar between the two genera, and the difference is mainly in size and height of the crowns. Only the m3 morphology in Minori-17018 (only one specimen has an m3) appears to differ with *Batomys* and align with *Crateromys*. The m3 anterior and posterior lophs are more arcuate in *Crateromys* and the specimen. In the Luzon *Batomys* spp., the anterior loph is not as arcuate and in some extant specimens are transversely oriented (Musser et al. 1998). The posterior loph is also more indented and chevron-shaped in *Crateromys*, as opposed to the transverse elongate loph in *B. granti* and fossil *Batomys*. This appears to be the case because there is sometimes a posterior cingulum on the m3 in *Crateromys* that has not been observed in any of the *Batomys* material. The trait, however, is variable and is absent in Minori-17018 and in several extant *Cr. schadenbergi* specimens (absent in all 7 BMNH specimens; present in 3 out 6 FMNH specimens).

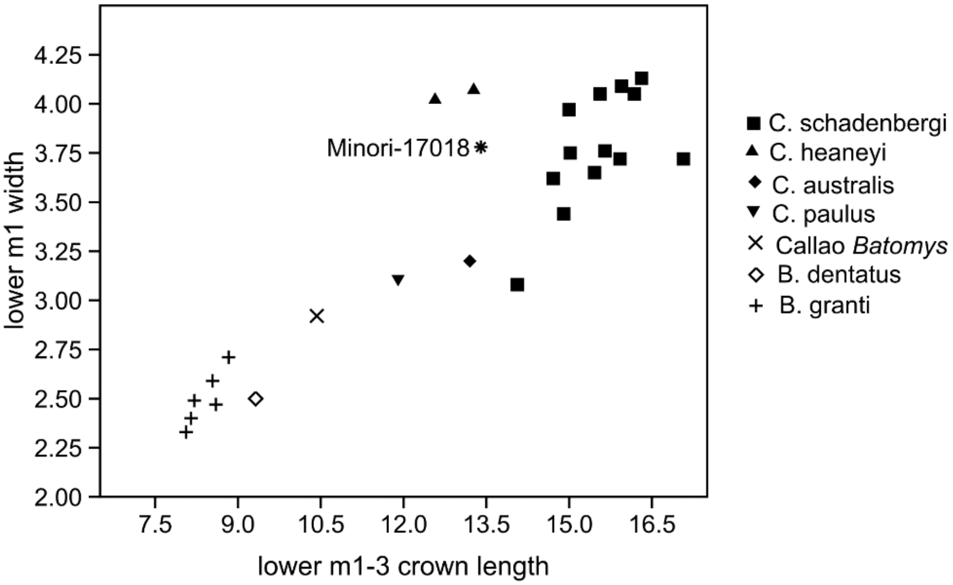


Figure 6.8 Bivariate plot of *Crateromys* and *Batomys* dental measurements (in mm) in comparison to fossil *Crateromys* Minori-17018. See Table 6.6 for data sources for modern and archaeological comparative material.

Table 6.6 Measurements (in mm) of mandibular molars of fossil *Crateromys*, extant *Crateromys*, extant *Batomys* and fossil *Batomys* from Callao Cave. L= length; W= width. Measurement parameters follow Heaney et al. (2011), except for cervical M1-3 crown length, which is taken above the cementum-enamel junction. Comparative data are from the ff. sources: *C. heaneyi* (Gonzales and Kennedy 1996); *C. australis* and *C. paulus* (Musser et al. 1985); fossil *C. paulus* (Reyes et al. 2017); fossil *Batomys* (Heaney et al. 2011).

Mandibular		M1-M2 L occlusal	M1-M3 L occlusal	M1-M3 L cervical	M1L	M1W	M2L	M2W	M3L	M3W
Minori-17018		9.12	13.05	13.40	5.47	3.78	3.57	3.67	3.49	3.52
Minori-16692		8.78	\	\	4.79	3.39	3.89	3.46	\	\
C. schadenbergi	mean	10.79	15.52	15.88	6.04	3.77	4.70	4.05	4.35	3.91
(n=13)	SD	0.28	0.79	0.68	0.22	0.30	0.24	0.36	0.63	0.56
	range	10.24-11.3	14.06-17.07	14.35-17.17	5.58-6.51	3.08-4.13	4.16-4.98	3.31-4.53	3.18-5.29	2.44-4.37
C. heaneyi	mean	\	12.90	\	\	4.10	\	\	\	\
(n=2)	range	\	12.57 - 13.27	\	\	4.03-4.08	\	\	\	\
C. australis (n=1)		\	13.20	\	\	3.20	\	\	\	\
C. paulus (n=1)		\	11.90	\	\	3.10	\	\	\	\
C. paulus fossils	mean	8.30	11.90	\	4.90	3.40	3.60	3.40	3.60	3.20
(n=96)	SD	0.43	0.48	\	0.33	0.23	0.19	0.23	0.23	0.21
	range	7.7-9.4	11-12.4	\	3.7-5.6	3-4.1	3.2-4	2.9-4.2	2.9-4.2	2.9-3.7
B. granti	mean	6.24	8.40	8.46	3.80	2.50	2.50	2.47	2.21	2.20
(n=6)	SD	\	\	0.11	0.20	0.14	0.14	0.14	0.15	0.15
	range	6.15-6.32	8.06-8.83	8.38-8.53	3.58-4.02	2.33-2.71	2.25-2.65	2.3-2.64	2.04-2.46	2.06-2.47
B. dentatus		\	9.32	\	3.72	2.50	2.76	2.73	2.74	2.70
Callao *Batomys*-7554		\	10.48	\	4.33	2.93	3.12	3.18	2.76	2.71
Callao *Batomys*-7573		\	\	\	4.35	2.74	3.14	3.02	\	\
Callao *Batomys* sp.	mean	\	\	\	4.34	2.84	3.13	3.10	2.76	2.71

Based on overall morphological features of the dentition, the two Minori Cave mandibular specimens are ascribed to the genus *Crateromys*. The fossils are intermediate in size and hypsodonty between *Cr. schadenbergi* and the two previously described *Batomys* fossils from Callao Cave. The specimens are smaller than the identified large fossil *Carpomys* and the extant *Cr. schadenbergi* (Table 6.6). The size difference against *Cr. schadenbergi* is apparent based on tooth lengths and size of the mandibular ramus. On the other hand, they are notably larger than all known Luzon *Batomys* species: the Callao fossil *Batomys*, *B. granti* and *B. dentatus* (Figures 6.7 and 6.8). Based on these observations, it is possible that a novel fossil species is represented by the Minori Cave fossils because of its relatively smaller dimensions and possible different or broader habitat tolerance compared to the living Luzon species, *Cr. schadenbergi.* The latter is currently only known from the Central Cordilleras, occurring from about 2000 to 2740 m elevation in mossy or pine forest. These are environments that have not so far been recorded in lowland environments of northern Luzon in the Holocene (Stevenson et al. 2010). Comparison with measurements in published literature indicates that the Minori Cave specimens overlap in size with *Cr. heaneyi* (Panay Island cloudrunner) and *Cr. australis* (Dinagat Island cloud rat). These two living species are known as single-island endemics of their respective islands and so it is uncertain whether the Luzon fossils can be ascribed to either. To ascertain species designation, further morphological comparison is needed with the other extant *Crateromys* species across the oceanic Philippines: *Cr. australis, Cr. heaneyi* and *Cr. paulus* (Ilin Island cloud rat). At the time of writing, access to modern specimens of these rare cloud rat species has not been possible, as they are housed in different museums overseas.

6.4.6 *Phloeomys pallidus*

A fragmented maxillary specimen (Minori-5707) with a complete toothrow is ascribed to *Phloeomys* (Figure 6.9). The specimen comes from Sq. 50 of Chamber D. It was found broken into three fragments and refitted. The teeth of the giant cloud rat are highly distinctive and unique, not only among the Phloeomyini or cloud rats, but among the Murinae. The specimen has high, lophodont molars consisting of thick, wide transverse plates without cuspidation, a morphology consistent with the traits of *Phloeomys* (Musser and Heaney 1992: 57-58).

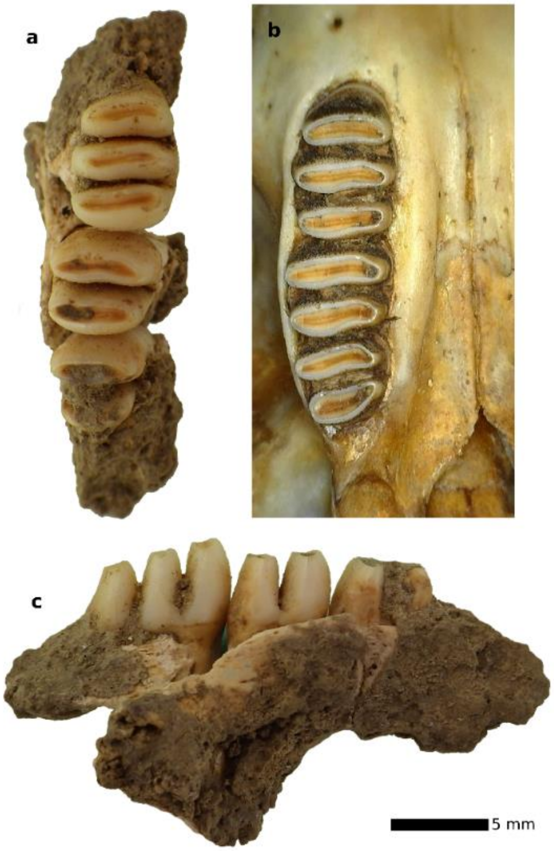


Figure 6.9 Maxillary specimen (Minori-5707) referred to *Phloeomys pallidus* in occlusal (a) and labial (c) views in comparison with modern specimen BMNH 97.52.20 (b).

Phloeomys is the largest of extant Philippine murids and also the largest within the living members of the subfamily Murinae (Heaney et al. 2016). They are highly arboreal and are found from sea level to about 2300 m elevation. Two living species are known. *P. pallidus* is widespread in north and central Luzon, while *P. cumingi* is widespread in southern Luzon. They overlap in distribution in central Luzon, namely in the southern Sierra Madre and Mingan Mountains (*ibid.*). One modern specimen (NM Osteo 880) of *P. pallidus* is housed in the National Museum Zooarchaeology section, and it has a provenance record from the Peñablanca area. Two individuals at the BMNH also have a provenance record in the northeastern tip of Cagayan province. Both records indicate that *P. pallidus* is or was present in the wider vicinity of Callao. *P. pallidus* is generally larger than *P. cumingi*, but the two overlap in size. The Minori Cave specimen is from a relatively small individual, and possibly represents a small *P. pallidus* (Figure 6.10 and Table 6.7). The smaller dimensions are likely affected by the damage on the specimen and refitting. On the basis of tooth morphology and known distribution of the extant species, the Minori Cave specimen is ascribed to *Phloeomys pallidus*, the northern Luzon cloud rat.

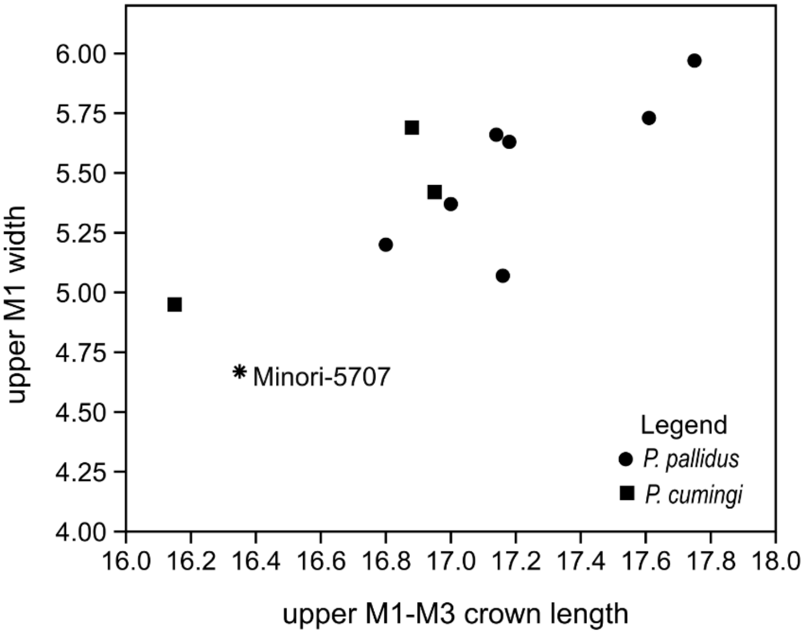


Figure 6.10 Bivariate scatterplot of modern *Phloeomys* maxillary measurements (in mm) with the single Minori specimen.

Table 6.7 Measurements (in mm) of Minori *Phloeomys* maxillary molars and extant *Phloeomys*.

maxillary		M1-M2 L occlusal	M1-M3 L occlusal	M1-M3 L cervical	M1L	M1W	M2L	M2W	M3L	M3W
Minori-5707		11.55	16.35	17.45	6.39	4.67	4.07	4.68	4.12	4.58
P. pallidus	mean	11.96	17.23	18.69	6.78	5.57	4.59	5.85	4.54	5.07
(n=7)	SD	0.42	0.33	0.50	0.38	0.33	0.35	0.17	0.37	0.25
	range	11.2-12.39	16.8-17.75	17.98-19.22	6.3-7.43	5.07-5.97	4-5.07	5.64-6.17	3.9-5.07	4.66-5.37
P. cumingi	mean	11.87	16.66	18.05	6.54	5.35	4.58	5.56	4.23	4.93
(n=3)	SD	0.28	0.44	0.52	0.32	0.37	0.37	0.30	0.19	0.38
	range	11.55-12.05	16.15-16.95	17.47-18.48	6.21-6.84	4.95-5.69	4.16-4.85	5.31-5.9	4.01-4.35	4.58-5.33
P. pallidus	97.5.2.19	12.39	17.75	19.22	7.43	5.97	5.07	6.17	5.07	5.15
P. pallidus	94.6.20.2	12.18	17.61	19.04	6.85	5.73	4.56	5.96	4.62	5.26
P. pallidus	97.5.2.20	12.23	17	18.48	6.83	5.37	4.48	5.72	4.29	4.66
P. pallidus	97.3.1.8	11.97	17.18	18.1	6.5	5.63	4.96	5.86	4.81	4.85
P. pallidus	97.3.1.7	12.17	17.14	17.98	7.02	5.66	4.64	5.8	4.49	5.37
P. pallidus	53.8.29.24	11.6	17.16	19.08	6.55	5.07	4.44	5.64	4.57	5.22
P. pallidus	NM Osteo 880	11.2	16.8	18.9	6.3	5.2	4	5.8	3.9	5
P. cumingi	55.12.26.200	12.05	16.95	17.47	6.84	5.42	4.85	5.48	4.35	4.88
P. cumingi	55.12.24.141	12	16.88	18.48	6.56	5.69	4.72	5.9	4.32	5.33
P. cumingi	42.2.15.236	11.55	16.15	18.21	6.21	4.95	4.16	5.31	4.01	4.58

6.4.7 *Bullimus/Rattus* spp.

Two mandibular specimens (Minori-15419 and -15998) represent one or two murid species belonging to a group of Philippine rats generally labelled as 'New Endemics'. A similar specimen (Musang I5a-1) is found in Musang Cave and described separately. Based on size and tooth morphology, two candidate species are possible: *Bullimus luzonicus* and *Rattus everetti* (see Figure 6.14 in Musang Cave Section). Both are forest rats that are common in low to medium elevations across a variety of habitats. *Bullimus luzonicus* is a Luzon endemic, whereas *R. everetti* is a Philippine endemic that is widespread across the archipelago. *R. everetti* is more closely related to the endemic members of the genera *Limnomys* and *Tarsomys* than to the members of the genus *Rattus*, and future phylogenetic work might place *R. everetti* in a different genus (Heaney et al. 2016a; Jansa et al. 2006). *Bullimus luzonicus* is generally the larger of the two, but they overlap in size.

The mandibular molar morphology of the two species is extremely similar and variation detected is based on size (Figure 6.14 and Table 6.8). As expected, tooth measurements of modern *B. luzonicus* are larger. In the very small sample of comparative metrics, one specimen (Minori-15419) groups with *R. everetti*. The other specimen (Minori-15419) slightly exceeds the dimensions of *B. luzonicus* samples, but this is due to the heavy wear on the specimen. The two specimens may represent the two species, respectively. Alternatively, both specimens may represent variable size range in *B. luzonicus* as this species has a larger body size range than *R. everetti.* Larger comparative samples may resolve species assignation in the future.

Table 6.8 Measurements (in mm) of Minori and Musang mandibular rodent molar specimens, extant *Bullimus luzonicus* and extant *Rattus everetti*.

Source/ Site	Taxon		M1-M2 L occlusal	M1-M3 L occlusal	M1-M3 L cervical	M1L	M1W	M2L	M2W	M3L	M3W
Minori	*Bullimus luzonicus*	15998	6.9	9.8	9.5	3.99	2.94	2.78	2.96	2.96	2.36
Minori	*Bullimus/Rattus* sp.	15419	6.37	\	\	3.57	2.24	2.57	2.5	\	\
Musang	*Bullimus luzonicus*	I5a-1	6.41	8.79	10.13	3.68	2.88	2.86	3.25	1.95	2.71
BMNH	*Bullimus luzonicus*	95.8.2.7	6.63	8.81	9.32	3.77	2.65	2.76	2.8	2.03	2.52
BMNH	*Bullimus luzonicus*	97.5.2.22	6.7	8.79	10.27	3.75	2.83	2.87	2.95	1.92	2.48
BMNH	*Rattus everetti*	77.10.6.20	6.29	8.32	8.91	3.71	2.05	2.45	2.18	1.75	2.03
BMNH	*Rattus everetti*	97.5.2.21	6.15	8.54	8.73	3.57	2.21	2.53	2.36	2.37	2.28
BMNH	*Rattus everetti*	95.8.2.8	6.26	8.51	8.86	3.56	2.24	2.56	2.44	2.18	2.33
BMNH	*Rattus everetti*	95.8.2.9	6.16	8.27	8.45	3.58	2.25	2.5	2.47	2.26	2.2

6.4.8 Order Primata

Family Cercopithecidae
Macaca fascicularis

A medium-sized primate identified in the assemblage is ascribed to *Macaca fascicularis* based on tooth and post-cranial morphology and dental measurements. The long-tailed macaque is the only known non-human primate on Luzon. They are obligate canopy dwellers found from sea level to montane forest. Fooden (1991) previously observed that dorsal pelage colour is one primary basis for differentiating Philippine subspecies. *M. f. fascicularis* is the lighter-coloured variant in the oceanic Philippines while *M. f. philippinensis* is the darker-coloured variant on Palawan Island. Tooth measurements (Figure 6.11; Table 6.9) indicate that the Minori Cave specimens overlap in measurements with both modern-day Luzon and Palawan macaques. Dental morphology or metrics do not appear to separate the two island populations.

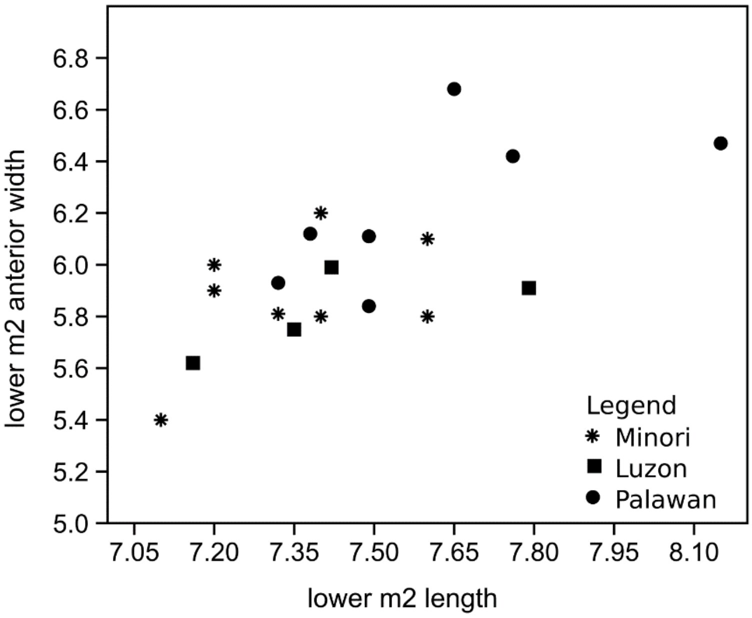


Figure 6.11 Bivariate plot of *Macaca fascicularis* mandibular second molar measurements (in mm) from Minori Cave and museum specimens. Anterior width refers to the anterior cusp of the molar. Luzon and Palawan reference specimens are from the FMNH and were measured together with PJ Piper.

Table 6.35 Maxillary and mandibular molar measurements (in mm) of Minori and Musang macaques compared with modern *Macaca fascicularis* in Luzon and Palawan. Wa = width of anterior cusp, Wp = width of posterior cusp. FMNH comparative measurements were taken with PJ Piper.

Site	Bone ID	Square/ Locality	Element	Side	P4L	P4W	M1L	M1Wa	M1Wp	M2L	M2Wa	M2Wp	M3L	M3Wa	M3Wp
maxillary															
FMNH	62275	Luzon					6.62	6.47	5.82	7.44	7.29	6.31	7.16	6.62	5.72
FMNH	62276	Luzon					5.98	6.45	6.03	7.43	7.3	6.52	7.65	7.02	6.23
FMNH	62274	Luzon					5.75	6.2	5.61	7.26	6.98	6.19	6.99	6.77	5.89
FMNH	62273	Luzon					6.64	6.25	5.85	7.09	7.17	6.31	7.27	6.84	6.01
FMNH	62901	Palawan					7.07	6.14	5.77	7.61	7	6.27	7.15	7.04	6.15
FMNH	62914	Palawan					6.83	6.21	5.84	7.72	7.09	6.59	\	\	\
FMNH	62913	Palawan					6.95	6.54	6.38	7.77	7.42	7.17	7.66	7.16	6.76
FMNH	62902	Palawan					6.95	6.44	6.25	8.24	7.61	7.11	7.87	7.04	6.33
FMNH	62905	Palawan					6.72	6.64	6.28	8.11	7.72	7.27	7.98	7.46	6.96
FMNH	62907	Palawan					6.59	6.26	5.84	7.61	6.94	6.39	7.8	6.54	6.09
FMNH	62908	Palawan					6.34	6.44	5.97	7.3	6.91	6.59	7.62	6.74	6.38
Minori Ch A	2082	37	p4	R	5.2	5.85									
Minori Ch A	2290	37	p4	R	4.97	\									
Minori Ch D	5606	50	p4	R	5.03	5.86									
Minori Ch D	5615	50	p4	R	4.54	6.12									
Minori Ch D	5614	50	p4	R	4.69	6.6									
Minori Ch D	17216	40	m1	R			6.6	6.52	6.12						
Minori Ch A	8524	7	m2							7.8	6.8	6			
Minori Ch D	9131	27	m2	L						7.3	\	6.2			
Minori Ch D	10800	27	m2	R						7.48	\	\			
Minori Ch D	5733	50	m2	L						7.5	7.7	6.95			
Minori Ch A	2047	37	m3	R									7.77	7.12	5.82
Minori Ch A	10045	50	m3	R									7	6.9	5.7
Minori Ch D	9039	27	m3	R									7.4	6.6	5.5
Minori Ch D	6177	58	m3	L									7.6	7	6.2

Table 6.9 continued. Maxillary and mandibular molar measurements (in mm) of Minori and Musang macaques.

Site	Bone ID	Square/ Locality	Element	Side	P4L	P4W	M1L	M1Wa	M1Wp	M2L	M2Wa	M2Wp	M3L	M3Wa	M3Wp
mandibular															
FMNH	62275	Luzon					6.88	5.03	5.22	7.79	5.91	5.77	9.33	5.83	5.6
FMNH	62276	Luzon					6.35	5.14	5.25	7.42	5.99	5.96	9.56	6	5.27
FMNH	62274	Luzon					6.03	4.82	5.12	7.16	5.62	5.36	8.59	5.49	5.03
FMNH	62273	Luzon					6.54	5.01	5.3	7.35	5.75	5.76	8.71	5.77	5.65
FMNH	62901	Palawan					6.76	5.13	4.88	7.32	5.93	5.47	9.19	5.65	5.24
FMNH	62914	Palawan					6.52	5.06	5.07	7.49	5.84	5.59	\	\	\
FMNH	62913	Palawan					6.53	5.13	5.25	7.76	6.42	6.17	8.82	6.22	5.89
FMNH	62902	Palawan					7.01	5.16	5.31	8.15	6.47	6.29	9.93	6.05	5.74
FMNH	62905	Palawan					6.59	5.25	5.57	7.65	6.68	6.35	9.98	6.79	5.95
FMNH	62907	Palawan					6.36	5.22	5.31	7.38	6.12	5.87	8.81	6.07	5.77
FMNH	62908	Palawan					6.43	5.15	5.07	7.49	6.11	5.86	9.28	6.05	5.73
Minori Ch A	4191	30	p4	R	5.3	4.2									
Minori Ch A	4253	30	p4	L	5.3	4									
Minori Ch A	4127	30	p4	R	5.1	3.8									
Minori Ch A	10077	50	p4		5.4	4.3									
Minori Ch D	6003	58	m1	R			6.6	5.3	5.6						
Minori Ch D	5765	50	m1	R			5.68	5.08	4.61						
Minori Ch A	4065	30	m2	R						7.4	6.2	5.5			
Minori Ch A	4258	30	m2	L						7.6	6.1	6			
Minori Ch A	8503	7	m2	R						7.2	6	5.8			
Minori Ch A	2296	37	m2	L						7.2	5.9	5.51			
Minori Ch A	8242	7	m2	L						7.1	5.4	5.6			
Minori Ch D	11057	27	m2	L						7.6	5.8	5.5			
Minori Ch D	6184	58	m2	L						7.4	5.8	5.5			
Minori Ch D	12394	57	m2	R						7.32	5.81	5.49			

In contrast to Palawan, where its native presence has been postulated (Piper et al. 2011), *M. fascicularis* has been recently proposed as a non-native species on Luzon and the oceanic Philippines on the basis of molecular phylogenetic data (Heaney et al. 2016). Philippine populations are said to differ little from Bornean populations, suggesting a possible recent introduction from the latter. For a long time prior to this, the macaque was considered by zoologists as a species native to the entire Philippine archipelago. In the Minori Cave sequence, all macaque remains are only found in the upper ceramic-bearing levels of the site. Their context will be discussed further in Chapter 7.

6.4.9 Order Carnivora
Family Canidae
Canis lupus familiaris

The dog, an introduced domesticate, is represented by three specimens in Minori Cave. These consist of a lower incisor (Minori-9733) and an upper third premolar (Minori-9069) from Sq. 27 and another lower incisor (Minori-2081) from Sq. 37. There are no known native canids in the oceanic Philippines, and only the domestic dog is encountered in the archaeological record. The dog remains are associated with the upper levels of the ceramic-bearing cultural layer in the site, which also contain other introduced taxa such as the macaque.

The antiquity of dog introduction in the Philippines is poorly known. Dog remains from the Nagsabaran site of the Cagayan Valley represent the oldest dated material, deriving from layers dating to *ca*. 500 cal BC (Amano et al. 2013). Of particular interest was a singular dog burial that was interred in the same area where human burials were found. Several bones found in the middens had dog-gnawing marks. Some fishing gorges found in the site were also fashioned out of dog canines (Piper et al. 2009). In Callao Cave, a left third metacarpal of a dog was found, possibly associated with layers dated to 1650 - 1470 cal BC (Mijares 2007). In Ille Cave in Palawan, dog remains are associated with 'Metal Period' pottery, but the layers or bones have not been directly dated (Ochoa 2009). A domestic dog cranial fragment was also identified in the Late Holocene levels of Pasimbahan Cave, also in Palawan. The layer in which it was found may be as old as 3704-3573 cal. BP (Ochoa et al. 2014), which is close to the possible age of the Callao Cave dog bone.

6.4.10 Family Viverridae
Paradoxurus philippinensis

The palm civet is represented by only two specimens: a right upper M1 (Minori-8039, Chamber A, Square. 7) and a left lower m1 (Minori-635, Chamber A, Square 32) (Figure 6.12). Both specimens were found in the upper cultural layer in their respective squares, which are ceramic-bearing layers. Macaque remains were also found in the same levels as the palm civet teeth.

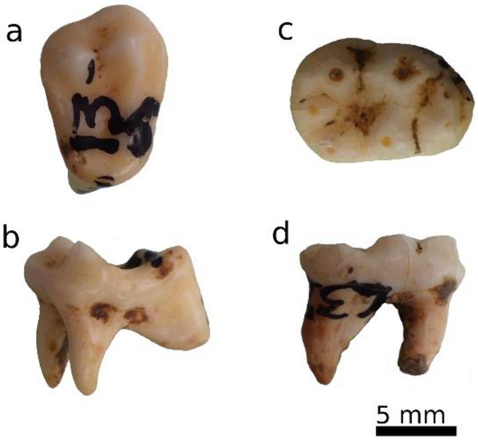


Figure 6.62 Molar specimens referred to *Paradoxurus* from Minori Cave. Minori-8039 is an upper right M1 (a-b, occlusal and distal views). Minori-635 is a lower left m1 (c-d, occlusal and lingual views).

Extant populations in the Philippines are ascribed as a distinct species *Paradoxurus philippinensis* based on recent genetic and morphological studies of Asian palm civets (Heaney et al. 2016a; Patou et al. 2010; Veron et al. 2015). The species is distributed across Borneo, Philippines and Mentawai, with Borneo posited as an evolutionary centre of origin for the clade. Within this clade, two groups were identified: ‘Philippines’ and ‘Borneo + Philippines’ (Patou et al. 2010). Luzon individuals grouped with Borneo and Palawan haplotypes. The lack of genetic divergence for Luzon and other oceanic Philippine populations from Borneo suggests recent human introduction (Veron et al. 2015). In contrast, Palawan individuals possessed three different haplotypes, one of them being more distant from the two and were found in both groups. This suggests one instance of natural dispersal and possibly another instance of human-mediated introduction in Palawan. On the basis of these studies, it is now hypothesized that the common palm civet has been naturalized on Luzon, occurring in agricultural and forested areas from sea level up to 2400 m (Heaney et al. 2016). They are mostly nocturnal and partly arboreal, feeding both on the ground and in trees.

6.5 The Musang Cave Vertebrate Fauna: An Overview

A total of 1163 bone fragments were analysed from Musang Cave, coming primarily from G4 trench (Table 6.10). All materials are from Barbara Thiel's 1976-77 excavations. The proportion of bone identified at the genus level comprises 27% for Musang Cave out of the total number of fragments (TNF) in the site.

A note has to be made regarding the differences in bone fragment counts in this study compared to Thiel's (1990) large mammal identifications (Table 6.11). Thiel only published counts for large mammals and records of other taxa are unavailable. There is a large discrepancy in the bone counts due to assemblage loss in the period after Thiel's analysis. The preserved assemblage in the existing storage facility in the NMP only accounts for 22% of the large mammal category.

I reserve some scepticism over Thiel's counts. During the identification process, I observed that some human bones were labelled as pig bones. Certain bones with 'pig' labels also consisted of undiagnostic specimens such as small rib and shaft fragments, which I would personally not ascribe down to genus or species because of insufficient distinguishing features that differentiate pig and deer. In my own counts, I place such fragments in the 'medium artiodactyl' category. In the remaining assemblage, pig bones are outnumbered by deer bones with a 1:2.6 ratio. This appears contrary to Thiel's claim that over 98% of the bone assemblage is from wild pig (Thiel 1990:73). Note that in the total NISP for *R. marianna* in Table 6.11, the current counts (N=169) outnumber Thiel's overall deer bone counts (N=116) even though the current assemblage size is only a fraction of Thiel's assemblage size. Thiel also curiously made no mention of bovid remains, which would have stood out in the assemblage based on their size. Based on these observations, I would argue that Thiel's counts for pig bones are overestimated. If assemblage loss was random (versus certain taxa deliberately chosen and separated from the current assemblage), then it may be arguable that deer is the more abundant taxa than the wild pig.

Table 6.370 Number of identified specimens (NISP) per excavated square (columns) in Musang Cave.

Taxon	G4	G5 se1m	G5 wcen1m	F3 se1m	F6	F6 east half	G7 nw1m	Total NISP	% NISP
Rusa marianna	102	18	22	4	17	3	3	169	14.5
Sus philippensis	51	4	4	2		1	2	64	5.5
Sus scrofa	2							2	0.2
Bubalus bubalis	2	2						4	0.3
Bos/Bubalus		4						4	0.3
large mammal I/ medium artiodactyl	516	50	8	5	13	17	10	619	53.2
large mammal II/ large artiodactyl	1	6						7	0.6
Carpomys undescr. sp.	1							1	0.1
Bullimus luzonicus	1							1	0.1
Phloeomyin	3	1						4	0.3
Murid	9							9	0.8
Macaca fascicularis	5							5	0.4
intermediate mammal	4	6	1					11	0.9
small mammal	4							4	0.3
Varanus sp.	6	1	1					8	0.7
Turtle	3	4						7	0.6
Snake	7	1			6			14	1.2
Fish	28	14				11		53	4.6
Bird	6							6	0.5
macrovertebrate	92	17	5	2	25	5	14	160	13.8
microvertebrate	3	2	2		4			11	0.9
	846	130	43	13	65	37	29	1163	100.0

Table 6.11 Comparison of large mammal counts from this study with bone counts from Thiel (1990: Table 1). Total NISP refers to counts from all trenches including G4.

Taxon	G4 Trench		Total NISP	
	Thiel	Ochoa	Thiel	Ochoa
Rusa marianna	77	102	116	169
Sus philippensis	3101	51	3826	64
Homo sapiens	73	8	78	23
bovid	\	1	\	7
medium artiodactyl	\	516	\	619
large artiodactyl	\	1	\	6
Total	3251	679	4020	888

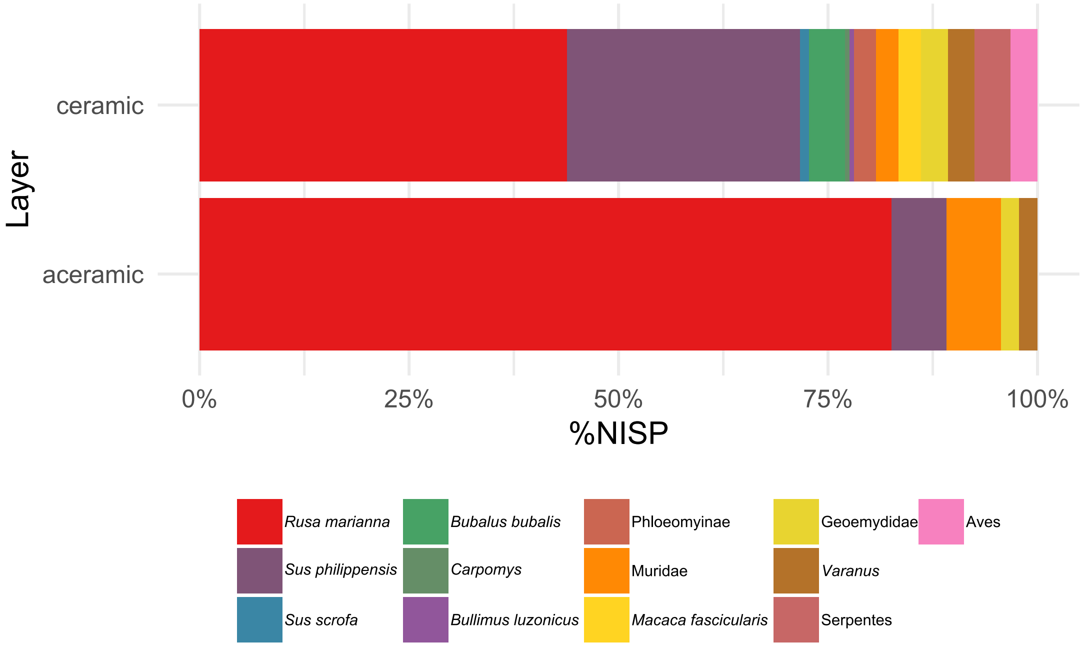


Figure 6.63 Relative taxonomic abundance (%NISP) of vertebrate taxa in Squares G4 and G5se1m of Musang Cave. NISP = number of identified specimens. NISP counts per layer are in Table 8.25 (Version 2).

A total of seven mammal species and two reptile taxa have been identified in the Musang Cave assemblage (Table 6.10). Of the mammal taxa, four are native species (*Rusa marianna*, *Sus philippensis* and two murid species) and three are non-native species (*Macaca fascicularis*, *Sus scrofa* and *Bubalus bubalis*). All the native species are shared with Minori Cave. However, for the non-native species, only the macaque is shared between Musang and Minori Caves. Large mammals dominate the Musang Cave assemblage (Figure 6.13, Table 6.10). In the aceramic layers, the native deer significantly outnumber pigs, whereas in the ceramic-bearing layers, the abundance of pigs increases (see Sections 6.6.4 and 8.5.2 for further discussion). Two species of endemic murids appear in the Musang record, one cloud rat (*Carpomys*) and the Luzon forest rat (*Bullimus luzonicus*). Regarding the introduced taxa (long-tailed macaque, domestic pig and domestic water buffalo), there is uncertainty with the stratigraphic provenance of these species and whether they can be clearly assigned to ceramic-bearing layers in the Musang sequence (see Sections 6.6.3 and 8.5.2). Turtle, monitor lizard, snake, bird and fish remains appear in small numbers in the assemblage.

6.6 Musang Cave Accounts of Species

Species accounts for the mammal taxa of Musang Cave follows in this section. The systematic, morphological and relevant ecological data for most of the taxa identified in Musang Cave have been outlined in the Minori Cave accounts of species and are not repeated here. Basic specimen descriptions are given for murids and macaques, as well as domestic taxa not found in Minori: *Sus scrofa* and *Bubalus bubalis*.

6.6.1 Order Rodentia

Family Muridae
Carpomys undescr. sp.

One phloeomyin (cloud rat) mandibular specimen was identified in the Musang Cave assemblage, 76-M-101 (Figure 6.4e). Based on the traits outlined among the Minori murids in Section 6.3, the specimen is ascribable to the genus *Carpomys*. The specimen has a complete toothrow, and tooth measurements are in the same range as the Minori Cave *Carpomys* specimens (Table 6.5). It is therefore ascribable to the same *Carpomys* taxon in the Minori Cave assemblage.

6.6.2 *Bullimus luzonicus*

One small murid mandibular specimen (G4-15a-1) from Musang Cave is ascribed to *Bullimus luzonicus*. As mentioned above, the tooth morphology of *B. luzonicus* and *Rattus everetti* is quite similar, and the distinction made here is based on size difference (Figure 6.14) between the two species. The Musang Cave specimen exceeds tooth dimensions of measured *R. everetti* and groups with *B. luzonicus* instead (Table 6.8), and on this basis, the specimen is ascribed to the latter.

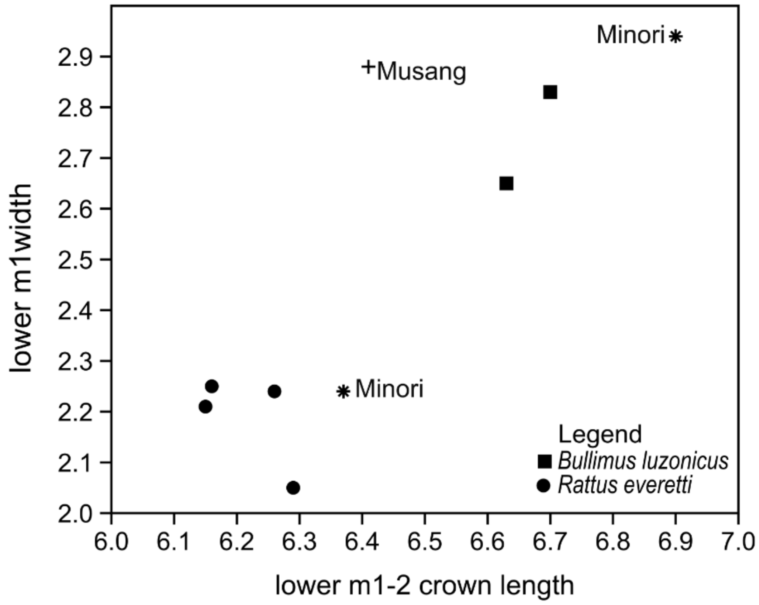


Figure 6.64 Bivariate plot of mandibular molar measurements (in mm) of murid fossils from Musang and Minori Caves, *Bullimus luzonicus* and *Rattus everetti*.

6.6.3 Order Primata

Family Cercopithecidae
Macaca fascicularis

Among the introduced intermediate-sized mammals described in Minori Cave, only the macaque has been identified in Musang Cave. Five post-cranial specimens are attributed to this primate recorded from G4 trench (Table 6.12). The specimens were found in three different layers. In the case of specimen 69e, it comes from Layer I4, which contains ceramics. The other four specimens are from Layers I4a and I7a, which are described by Thiel as aceramic portions of G4 trench. However, as discussed in Chapter 4, the stratigraphic integrity of layers I4a to I7a as aceramic levels is questionable and unverifiable, since in these same levels, pottery appears in the northwest portion of the trench. There is observed mixing of bones in Layer I4a, as evidenced by different states of preservation in bones that are bagged and labelled together as coming from the same layers. Several bone fragments appear to be of younger age than others based on their appearance. Butchery marks on certain elements are possibly derived from metal implements. Archaeological layers in Musang Cave that can be more confidently categorised as non-ceramic are from Layers 8 to 12 only. On the basis of these observations, it cannot be said for certain that the macaque remains are from an aceramic period.

Table 6.38 Macaque remains identified in Musang Cave.

Trench	Bone ID	Layer	Element
G4	69e	I4	humerus
G4	103a	I4a	clavicle
G4	103b	I4a	clavicle
G4	73a	I7a	femur
G4	73b	I7a	femur

6.6.4 Order Cetartiodactyla
Family Suidae
Sus scrofa

The suid remains from Musang Cave are predominantly from the extant endemic species, *Sus philippensis.* The exception, however, comes from two molar specimens that can be attributed to the introduced domestic, *Sus scrofa*. In contrast to mainland Asia, *S. scrofa* is not native to the islands of Southeast Asia and is recognized to have been introduced in the Late Holocene. Two specimens (69a and 69b) are referred to the domestic pig, consisting of a mandibular m3 and a maxillary M2 from Layer I4 of G4 trench. Layer I4 is a pottery-bearing layer that also contains one macaque specimen. Measurements of post-canine teeth specimens from Musang and Minori Caves are shown in Table 6.13. Species-level differentiation of teeth is based mainly on morphometrics. However, for the m3, it is also possible to distinguish *S. scrofa* based on the cusp pattern. Compared to endemic Wallacean pigs, *S. scrofa* has a more complex talonid in the lower m3, possessing an additional distal cusp (heptaconid) and a distinct segregation of the pentaconid and the hexaconid (Amano et al. 2013; Cucchi et al. 2008). The complex talonid in *S. scrofa* accounts for the greater length in the m3 compared to the reduced talonid in Wallacean and Philippine native pigs (Figure 6.15).

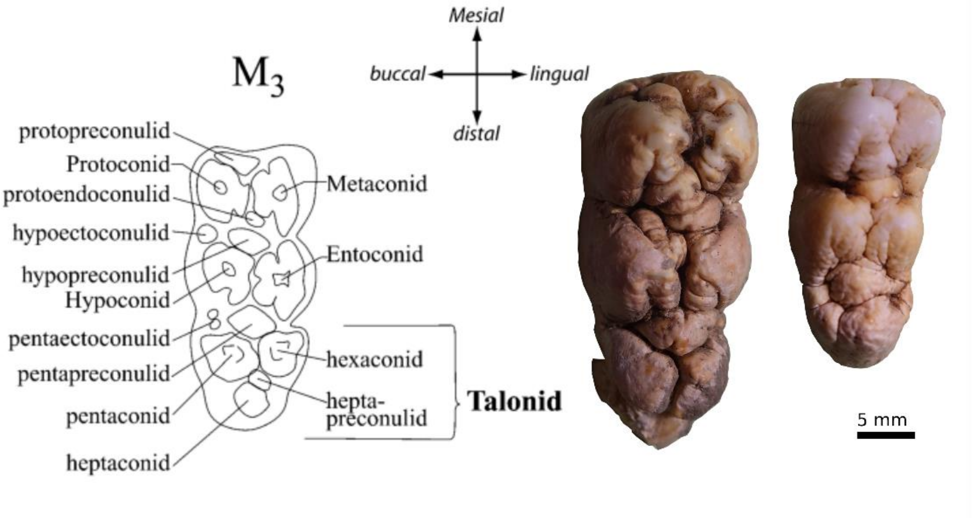


Figure 6.65 Comparison of mandibular m3 specimens of wild and domestic pigs from Musang Cave. Cusp pattern diagram is from Cucchi et al. (2008). Musang-69a (left) is ascribed to domestic *Sus scrofa* and Musang-69c (right) is ascribed to *S. philippensis*. Note that the heptaconid is present in Musang 69a but it has been damaged.

Apart from the third molar, cusp morphology of other molars and premolars do not appear to distinguish the various Southeast Asian pigs. Measurements are instead used and the data used here is from a large set of modern comparatives from Ingicco et al. (2017). This study successfully demonstrated the biometric differentiation of endemic Philippine pigs from domestic *S. scrofa* through linear metrics of post-canine teeth. Their statistical comparisons (one-way ANOVA) show that specific dimensions of tooth elements can confidently separate the domestic pig from Philippine wild pigs. The Luzon endemic, *S. philippensis*, easily separates from *S. scrofa* in their analysis. Measurements from the two dental elements of large-sized suids found in Musang Cave are among the most reliable metrics that enable differentiation. These are the length and mesial width of the upper M2 and length and distal width of the lower M3. In fact, in their one-way ANOVA pairwise comparison for differentiating *S. scrofa* and *S. philippensis*, all other length and width measurements from P4 to M3 produced highly significant *p*-values (Ingicco et al. 2017 Table S2). This indicates that the lengths and widths of the post-canine teeth can all be effectively used to separate the two suid species on Luzon, which is not always the case for other endemic suids from other Philippine islands (especially in the case of Palawan).

The oldest identification of the domestic pig in the Philippines and Island SEA comes from Nagsabaran site in northern Luzon. A premolar of *S. scrofa* from the site has a direct date of 3940 ±40 BP or 4500–4200 cal. BP (Piper et al. 2009). The suid remains from Nagsabaran clearly separate into two populations, with one being distinctly smaller than the other. The smaller-sized individuals were attributed to the wild pig and the larger individuals to the domestic pig. This identification was confirmed by the study of Ingicco and colleagues (2017). Similar to the case of Nagsabaran site, the combined suid dental measurements of Musang and Minori separate into two different populations of small (=wild) and large (=domestic) pigs (Figure 6.16). The two referred specimens (69a and 69b) represent larger individuals that group closer to modern and Nagsabaran *S. scrofa* comparatives. The other population consist of elements belonging to smaller individuals that group with modern *S. philippensis* comparatives. Ingicco et al. (2017:781) further observed that most of the archaeological *S. scrofa* they identified from Nagsabaran fall towards the lower range of size variation compared to modern *S. scrofa*. This size diminution has apparently been observed in other prehistoric domestic pig populations and appears to be a feature of selective breeding in managed pig populations. The Musang Cave specimens also fall in this lower size range, similar to the Nagsabaran domestic pigs.

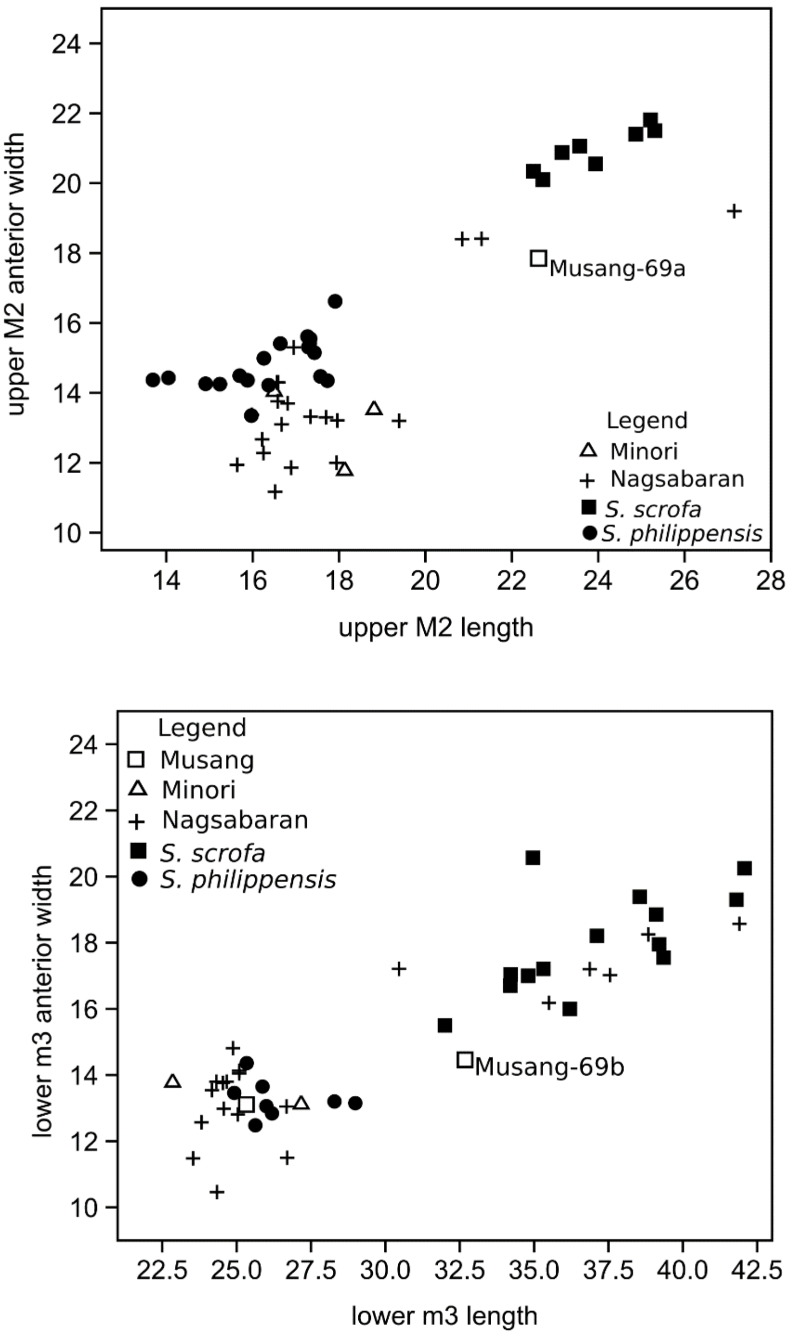


Figure 6.66 Bivariate plot of archaeological and modern suid teeth measurements (in mm) showing the distinction between wild *Sus philippensis* from domestic *Sus scrofa*. Above: maxillary M2; Below: mandibular m3. Data for modern Sus species are from Ingicco et al. 2016. Data for Nagsabaran site are from Piper et al. (2009) and Amano (2013). Musang specimens 69a and 69b are ascribed to *S. scrofa*.

Table 6.39 Measurements (in mm) of Sus maxillary and mandibular post-canine teeth from Musang and Minori Caves. L = length, W = width, Wa = width of anterior cusp, Wp = width of posterior cusp, Wm = width of middle cusp.

Maxillary	Number	P4 L	P4 W	M1 L	M1 Wa	M1 Wp	M2 L	M2 Wa	M2 Wp	M3 L	M3 Wa	M3 Wm	M3 Wp
Musang	69a						22.62	17.85	17.48				
Musang	9902									24.7	16.14	14.2	8.1
Minori	40						18.13	11.84	13.64				
Minori	9222			15.7	11.25	11.49	\	13.05	12.27				
Minori	9627									20.4	14.38	11.81	6.47
Minori	9133	10.4	12.46										
Minori	10274	10.6	12.21										
Minori	9221						18.81	13.58	14.28				
Minori	9005			13.9	\	\							
Minori	9130									25.5	15.36	13.25	9.26
Minori	9358			14.3	10.6	11.1							
Minori	9348			13.6	11.2	11.4	16.5	14.1	13.6				
Mandibular													
Musang	69b									32.7	14.46	14.3	\
Musang	69c									25.3	13.11	11.7	9.34
Musang	7996			17	10.33	11.16							
Minori	2023						16.39	\	13.39				
Minori	6010									22.9	13.84	11.93	8
Minori	3323			15.2	8.79	8.94							
Minori	2868	11.9	8.95	13.9	\	\							
Minori	3760	12.5	9.02										
Minori	2138			13.1	8.42	8.93							
Minori	2024									27.2	13.18	12.31	10.29
Minori	3529									\	\	\	11.05
Minori	9625	12	9.62										
Minori	15966			\	\	8.8							

6.6.5 Family Bovidae
Bubalus bubalis

Four phalanx specimens of a large bovid were retrieved from Musang Cave (Figure 6.17). Based on the size and robusticity of the specimens, they are ascribable to the domestic water buffalo or carabao, *Bubalus bubalis* (Table 6.14). The Musang Cave bovid specimens exceed the size of modern comparatives of the endemic tamaraw of Mindoro Island (*B. mindorensis*) and of domestic cows (*Bos taurus*). Instead, the Musang material are comparable in size to modern *B. bubalis* and to archaeological *B. bubalis* specimens from Nagsabaran site. This site provided the first evidence for the Late Neolithic introduction of this species to the Philippines, at ca. 500 cal BC (Amano et al. 2013). Domestic carabao remains were also reported by Mudar (1997) in the pottery-bearing levels of Pintu Rock shelter.

Figure 6.167 Musang bovid specimens (R side of each paired photo) ascribed to *Bubalus bubalis* compared with modern *B. bubalis* (NMP-1048, L side of each paired photo): 76-M-G4a abaxial fragment of proximal phalanx (that is longitudinally split) in abaxial (a) and plantar (b) views; 76-M-93 distal fragment of proximal phalanx in dorsal (c) and abaxial (d) views; 76-M-94 complete intermediate phalanx in dorsal (e) and plantar (f) views.

Table 6.140 Measurements (in mm) of phalanges of Musang Cave bovids, modern domestic bovids and the native *Bubalus mindorensis*. GL = greatest length, GL abaxial, greatest length of abaxial side, Bp = proximal breadth, Dp = proximal depth, Bd = distal breadth, Dd= distal depth.

Specimen No.	Taxon	Locality/Source	Description	GL	GL abaxial	Bp	Dp	Bd	Dd
Proximal Phalanx									
76-M-93	*Bubalus bubalis*	Musang	distal phalanx	\		\	\	33.89	24.56
76-M-G4a	*Bubalus bubalis*	Musang	longitudinally split, abaxial side		62.5		38.04		
II-1996-Z13-2009-414	*Bubalus bubalis*	Nagsabaran (archaeological)		70.4		32		33	
				70.6		31.9		34.3	
				70.4		32		33.7	
NMP-1048	*Bubalus bubalis*	modern			55.6	34.18	32.73	31.13	23.5
					55.47	33.95	33.75	32.27	24.93
					59.73	33	35.4	29.26	23.02
MCZ-29773	*Bubalus mindorensis*	modern		54.1		24.2	25.5	22.7	17.3
				51.5		25.8	24.3	24.7	16.8
MCZ-29772	*Bubalus mindorensis*	modern		50.3		27.4	25.3	25.9	18
				53.6		24.9	26.2	24.3	17.1

Table 6.14 continued. Measurements (in mm) of phalanges of Musang Cave bovids, modern domestic bovids and the native *Bubalus mindorensis*.

Number	Taxon	Locality/Source	Description	GL	GL abaxial	Bp	Dp	Bd	Dd
Intermediate Phalanx									
76-M-94	*Bubalus bubalis*	Musang	complete	49.5		37.82	40.85	28.68	31.83
NMP-1048	*Bubalus bubalis*	modern		46.11		32.44	33.83	26.9	28.61
				41.65		35.89	33.98	29.3	30.6
				44.45		32.74	33.62	26.53	28.63
ASP	*Bubalus bubalis*	modern		47.86		32.39		27.03	
				47.72		32.44		27.24	
				47.84		32.41		27.29	
ASP	*Bos taurus*	modern		37.89		24.08		19.94	
				37.74		24.06		19.95	
				37.73		24.15		19.96	
MCZ-29773	*Bubalus mindorensis*	modern		40.8		24.5	26.2	19.4	21.5
				40.4		24.7	26.5	20.5	22.3
MCZ-29772	*Bubalus mindorensis*	modern		40.7		25.7	27	20.4	22.8
				42		25.1	28	20.7	21.2
FMNH-18817	*Bubalus mindorensis*	modern		41.2		27.7	28	22.6	23.7
				42.8		26.5	27.1	20.9	22.3

6.7 Conclusion

This chapter has presented the taxonomic identifications for Minori and Musang Caves of Luzon Island. The morphological analyses provide evidence for new fossil records of previously unknown cloud rat taxa in northeastern Luzon. Identifications of introduced species are also documented. These include the domestic dog, pig, and water buffalo, as well as naturalised 'ethnospecies' such as the macaque and palm civet. Differentiation of the domestic pig from the Philippine warty pig was accomplished with the application of the method proposed by Ingicco et al. (2017). Both sets of identifications of endemic and introduced taxa have implications for understanding the modern mammalian fauna of Luzon. The species accounts lay the empirical foundations for examining questions on biodiversity, biogeography and faunal change that will be tackled in the next chapter.

Chapter 7 Island Biodiversity and Palaeoecological Changes in the Late Quaternary Record of the Philippines

7.1 Introduction

In this chapter, I investigate the timing and nature of faunal changes in the Philippines from the Late Pleistocene to the Holocene. This relates to the first research question of the thesis. Firstly, it must be demonstrated that changes did occur. The three assemblages described in Chapters 5 and 6 provide an opportunity to identify such changes, examine their nature, and gauge possible human impacts on the faunas of Luzon and Palawan. In this chapter, I expand the discussion on assemblage structure by presenting measures of taxonomic diversity and comparisons of the two island faunas. Combining these with data from other published sources, I provide a first attempt to construct Late Quaternary biostratigraphic sequences for the Philippines. These sequences facilitate the investigation of faunal changes through time. The changes occur against a backdrop of climatic and environmental fluctuations during the Pleistocene-Holocene transition, as well as possible anthropogenic impacts across the Holocene. As paralleled in many other cases across the globe, the Holocene disappearance of taxa occurs without replacement, which in turn implicates anthropogenic impacts. On this matter, I explore the hypothesis of a human extinction filter (Balmford 1996) in the Holocene as it applies to the Philippine fauna.

7.2 Species Diversity: An Overview

One of the most basic question in studies of biological diversity involves the question of 'How many species?'. Whereas taxonomic inventories of modern faunas may be well-known in many places, particularly in the case of mammals, many regions still require studies. Such is the case for many tropical islands of the Indo-Pacific region. This is particularly important for the tropics, which are known to harbour the most diverse and speciose habitats in the globe (Lomolino et al. 2016; Myers 1988).

A common characterization of oceanic island faunas is to describe them as depauperate, unbalanced and disharmonic because of the absence or low diversity of certain taxonomic groups such as the Carnivora, Primates and Cetartiodactyla (Flannery 1995; Lomolino et al. 2016; Morwood 2014; van der Geer et al. 2010). This assumption is partly rooted in received wisdom drawn from MacArthur and Wilson's (1967) influential equilibrium theory of island biogeography, which describes the one-way, downstream flow of colonists from species-rich continents. However, islands do vary greatly across the globe due to their dynamic evolutionary and geological histories, and unbalanced island faunas do not necessarily mean that these islands are species poor. Recent neobiological studies in tropical oceanic islands in Southeast Asia show unsuspected high levels of diversity and endemism than previously known. Such is the case for the large Philippine islands of Luzon and Mindanao and the Indonesian island of Sulawesi (Achmadi et al. 2013; Heaney et al. 2016; Rowe et al. 2016). As described in Chapter 2, the Philippines (as a country) is cited as possibly having the highest rate of endemism of a terrestrial region per square area in the world (Catibog-Sinha and Heaney 2006; Heaney et al. 2016a). Nearly two decades of systematic surveys on several mountain ranges across Luzon have doubled the number of Luzon mammal species known to science. Compared with 28 species known during the period of 1880-1999, another 28 species have been discovered during the period of 2000-2014 (Heaney et al. 2016b). Shown in this light, palaeozoological analysis of the fossil vertebrates of the archipelago is necessary in terms of understanding the history and modern assembly of this remarkable fauna. Apart from the discovery of tiger remains on Palawan Island (Ochoa 2009; Piper et al. 2008), the archaeofaunal record of the archipelago continues to produce surprises, as has been shown in Chapter 6 for the Luzon fauna.

7.2.1 Taxonomic Structure of Faunal Assemblages

Measures of taxonomic diversity for faunal assemblages in Luzon and Palawan are presented in Table 7.1 and provide an overview of the taxonomic structure of archaeofaunas. Description of measures are in Section 3.5. Counts are grouped into two ways: (A) for non-volant mammals only and B) for all terrestrial vertebrates (mammals, birds and reptiles). Both sets of measures exclude domesticated species. Comparative data for Palawan are derived from Ille, Pasimbahan and Tarung-tarung Cave sites (Ochoa 2009; Ochoa et al. 2014; Reis and Garong 2001, respectively). For Luzon, comparative data come from Callao Cave, Pintu Rockshelter and Nagsabaran site (Piper and Mijares 2007, Mudar 1997, Amano et al. 2013, respectively). The sites are also differentiated in broad temporal groups, as Late Pleistocene (LP) and Holocene (H). The taxonomic measures used are NTAXA for species richness, the Shannon-Weiner index (H) for taxonomic heterogeneity, Shannon index of evenness (e), and

Simpson's D and its reciprocal (1/D) for dominance. Further use of these taxonomic indices as it pertains to subsistence strategies is discussed in Chapter 8. Note though that due to the relative nature of these indices, values are comparable only among each other. There are no given thresholds to assess the strength of the difference between values and the indices are meaningful only relative to the sites included in the analysis. In addition, because the data is based on an ordinal scale value (NISP), the indices must also be considered as ordinal scale values (Lyman 2008). Keeping in mind these limitations, the indices remain instructive for providing a comparative and general overview of taxonomic structure among several sites that contain a variety of taxa.

Based on NTAXA for Palawan Island, the two Late Pleistocene assemblages (Pilanduk and LP levels of Ille Cave) are less speciose than the Holocene assemblages, particularly when all terrestrial vertebrate taxa are considered (Table 7.1 Palawan B). One possible reason for decreased diversity has to do with forest contraction during the MIS-2 stage that is recorded during this period on Palawan Island (Bird et al. 2007; Wurster et al. 2010; and see Section 7.4.1). Even though the LP faunas are not very speciose, they do contribute to the Late Quaternary record of Palawan biodiversity through the documentation of four extinct large mammals (tiger, rusine deer, hog deer and possible native dhole) that are only known from the fossil record.

In the Holocene, Ille and Tarung-tarung Caves have the highest number of species (NTAXA), and this has partly to do with the combination of natural and anthropogenic accumulation agents. The natural death assemblages of microvertebrate taxa in both sites increase the documented diversity, compared to the other sites which are predominantly human-accumulated. The Shannon indices (H) also show, as expected, that the llle and Tarung-tarung cave assemblages are the most diverse, particularly when all vertebrates are taken into account. The evenness index (e) shows that all the Palawan assemblages are uneven, with one taxon dominating each assemblage. Simpson's index and its reciprocal (1/D) show that the most uneven assemblages are the Late Pleistocene assemblages of Pilanduk Cave and 'Ille LP', as well as Holocene Pasimbahan Cave. In the case of Pilanduk and 'Ille LP', deer dominates the assemblages. In the case of Holocene Ille and Pasimbahan Cave, wild pig dominates. In the case of Tarung-tarung Cave, the macaque is the dominant taxon. These data have implications for temporal trends and subsistence practices, which are further considered and illustrated in Chapter 8.

Table 7.1 Measures of taxonomic diversity and composition for Palawan and Luzon archaeofaunas. NTAXA = number of taxa, NISP = number of identified specimens, H = Shannon-Weiner index, D = Simpson's index, 1/D = reciprocal of Simpson's index, e = Shannon index of evenness. Measures have been calculated in two sets for both islands using non-volant mammals only (A) and all terrestrial vertebrates (B). Temporal periods: LP = Late Pleistocene; Hol = Holocene. See Appendix B for NISP counts per site.

Palawan (A)	**NTAXA**	**NISP**	**H**	**D**	**1/D**	**e**
Pilanduk LP	7	446	1.15	0.40	2.53	0.45
Ille LP	8	326	0.54	0.78	1.28	0.21
Ille H	19	916	1.38	0.42	2.41	0.21
Pasimbahan H	9	720	1.00	0.50	2.01	0.30
Tarung-tarung H	10	138	0.87	0.65	1.53	0.24

Palawan (B)	**NTAXA**	**NISP**	**H**	**D**	**1/D**	**e**
Pilanduk LP	10	457	1.26	0.38	2.65	0.35
Ille LP	9	333	0.63	0.75	1.33	0.21
Ille H	29	1271	1.95	0.24	4.08	0.24
Pasimbahan H	14	835	1.33	0.39	2.59	0.27
Tarung-tarung H	32	218	2.10	0.28	3.55	0.26

Luzon (A)	**NTAXA**	**NISP**	**H**	**D**	**1/D**	**e**
Callao LP	5	151	0.37	0.85	1.18	0.29
Minori H	8	583	1.00	0.46	2.18	0.34
Musang H	5	240	0.73	0.57	1.76	0.41
Nagsabaran H	2	932	0.63	0.57	1.77	0.94
Pintu H	3	287	0.78	0.48	2.07	0.73

Luzon (B)	**NTAXA**	**NISP**	**H**	**D**	**1/D**	**e**
Callao LP	5	151	0.37	0.85	1.18	0.29
Minori H	8	583	1.00	0.46	2.18	0.34
Musang H	6	248	0.84	0.53	1.88	0.39
Nagsabaran H	6	937	0.66	0.56	1.79	0.32
Pintu H	4	292	0.86	0.47	2.14	0.59

Among the Luzon assemblages, Minori Cave has the most diverse fauna based on NTAXA and H. The Late Pleistocene assemblage of Callao is the most uneven based on the evenness index (e) and 1/D. In the Holocene, species richness appears to increase compared to the Late Pleistocene due to the presence of macaque and/or palm civet in these assemblages. It has been observed that in some depauperate oceanic islands, translocated species have tended to increase diversity in faunal communities, while palaeohistoric extinctions have had the impact of decreased diversity in modern faunas, further highlighting that such islands are species-poor (van der Geer et al. 2017; see Section 7.4.2 and 7.4.3). However, as a megadiversity island, these do not aptly fit the case for Luzon. The newly described extinct murid taxa further add to the documented high diversity and endemism on the island.

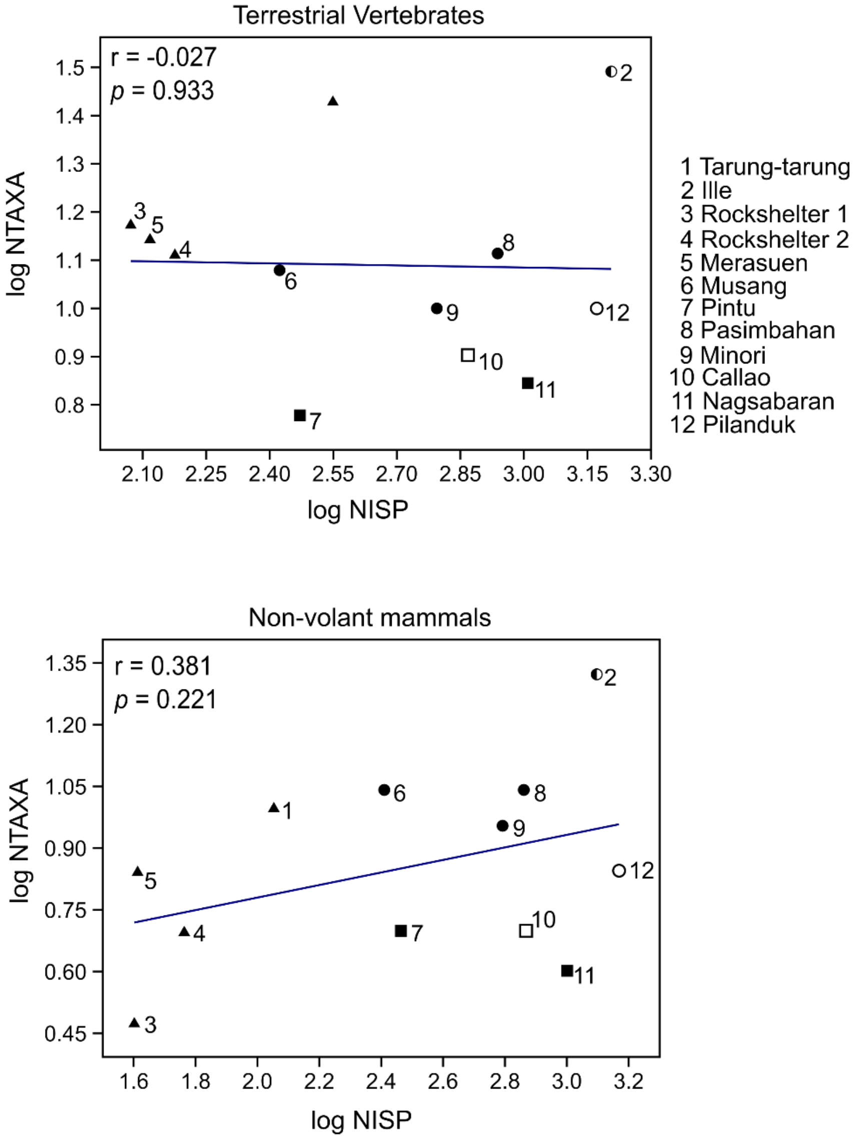


Figure 7.1 Linear model between species richness (NTAXA) and sample size (NISP) in 12 faunal assemblages from Luzon and Palawan (see Table 7.1. r = Pearson correlation coefficient. Data for sites (1, 3-5) are from Reis and Garong (2001), (2) Ille Cave from Ochoa (2009), (7) Pintu Rockshelter from Mudar (1997), (8) Pasimbahan Cave from Ochoa *et al*. (2014), (10) Callao Cave from Mijares and Piper (2007), and (11) Nagsabaran from Amano *et al*. (2013). Symbology denotes two sets of categories: by temporal period and by analyst that conducted the study. Filled shapes are Holocene sites, while unfilled shapes are Late Pleistocene sites. Sites denoted by circles were analysed by this author, triangles by Reis and Garong (2001) and squares are by other analysts.

7.2.2 Sample Size Effects

Is sample size driving measures of taxonomic diversity? A linear regression analysis was conducted to investigate sample size effects in twelve published faunal assemblages in Luzon and Palawan (Figure 7.1). Regression analysis allows detection of possible sample size effects on taxonomic diversity among independent samples of different size (Lyman 2008). NTAXA was computed in two ways: 1) for all terrestrial vertebrates, and 2) for non-volant mammals (NVM) only. In this estimation of taxonomic abundance, the target analytical unit is the identified assemblage, which forms a subset of the original death assemblage or thanatocoenose (see Lyman 2008). Faunal assemblages for both islands were all aggregated in one analysis due to the small number of published data available. Symbology in Figure 7.1 denotes two sets of categories: by temporal period and by analyst that conducted the study. Filled shapes are Holocene sites, while unfilled shapes are Pleistocene sites. The exception is Ille which has a Holocene sequence and a Terminal Pleistocene layer. Among twelve sites identified and pooled, five sites were analysed by this author, which are denoted by circles in the graph. Four sites were analysed by Reis and Garong (2001) (denoted by triangles), and three other sites were analysed by three different authors (denoted by squares). The spread of the points in the graph shows that inter-observer variation among analysts appears to have relatively minimal effect on sample size and richness.

The well-known species-area relationship predicts that richness increases with larger size (Arrhenius 1921; Lomolino 2000; Lomolino et al. 2016; McGuinness 1984; Rosenzweig 1995). On a log-log scale, the species-area relationship predicts a positive linear correlation. The linear regression analyses for all terrestrial vertebrates and for non-volant mammals both yielded non-significant correlations (Figure 7.1). This indicates that sample size is not significantly driving species richness, and that there are factors other than sample size influencing richness across the sites. Three sites (Nagsabaran, Pilanduk and Callao) show low diversity (NTAXA) despite relatively high sample size (NISP). Note that in this small sample, two sites are from the Late Pleistocene (Callao and Pilanduk). Linear regressions for Holocene sites only also yielded non-significant correlations (ten sites only, log-transformed, best-fit line for NVM: $r = 0.441$, $p = 0.202$). Linear regression analyses for when Ille site is split into Holocene and Pleistocene levels also produced non-significant correlations (13 assemblages, log-transformed, best-fit line for NVM: $r = 0.322$, $p = 0.282$). Caution is employed nonetheless, as the small number of available sample sites used here limits the inferences that can be drawn from the analyses.

A rarefaction analysis for non-volant mammals was also conducted for each island fauna (Figure 7.2). Rarefaction is a well-known tool in ecology and it allows two or more samples of different sizes to be compared as if they were the same size by reducing ('rarefy') the larger samples to a common small size (Lyman 2008). Calculations and plots were made using PAST and verified with Holland's (2003) Analytic Rarefaction program. In the case of the Palawan faunal assemblages, Pilanduk Cave is the outlier, falling well below expected values for NTAXA in relation to NISP. In the three Palawan sites of Pilanduk, Pasimbahan and Ille Caves, recovery methods were fairly similar in resolution, and yet many mammal taxa are absent from Pilanduk Cave. In contrast, Ille Cave is particularly speciose relative to the other sites. All of the Pilanduk Cave taxa are also found in Ille Cave. Both sites were analysed by this author, and so the variation in NTAXA and species identification is not just an artefact of inter-observer variation. In the case of Luzon, the largest outlier is the Late Holocene site of Nagsabaran, which has the highest sample size (NISP) but the lowest number of taxa.

There are also additional caveats to the sample size trends. As predominantly human-accumulated, a comparison of taxa present or absent in the different island assemblages is instructive not only about human subsistence patterns but also about community structure of the native fauna. In comparing the two islands, the archaeofaunas show that the Palawan assemblages are more diverse than the Luzon assemblages. A big contributor to the species diversity observed on Palawan is the intermediate-sized mammals, and many of these species do not have native congeners/conspecifics in Luzon. Outside of the Rodentia, at least ten mammalian genera are not present in Luzon, and six of these are carnivore taxa. Hence, these taxa are absent not because of the sample sizes, but because they are not native to and do not exist on Luzon. Instead, much of the renowned species diversity on Luzon lies in the Muridae (See Section 7.3.2). Because of their small size and ecology (see Heaney et al. 2016a), many endemic members of the murid clade do not as commonly get incorporated into human-accumulated cave assemblages and have not been recovered in these cave contexts (see Andrews 1990 for small mammal accumulations). In the Late Pleistocene levels of Callao, two murid genera are described by Heaney et al. (2011). More murid taxa are being described at present from additional excavated material that will add to the species richness in Callao (Heaney 2017 pers. comm.). Interestingly, the murid taxa encountered in the Holocene assemblages of Musang and Minori Caves belong to the cloud rat clade. Based on their large size and modern-day records (see Heaney et al. 2016a), giant cloud rats are typically preyed upon by humans. Other micromammal taxa are less represented in these human-accumulated assemblages.

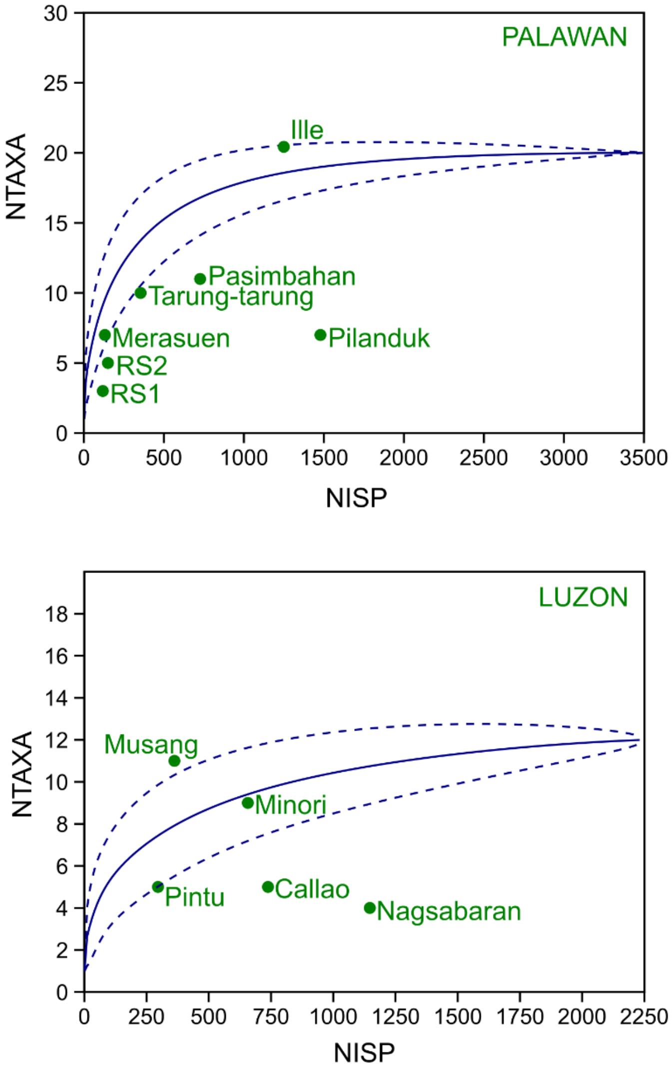


Figure 7.2 Rarefaction analysis for Palawan and Luzon island faunas using PAST and verified with Holland's (2003) Analytical Rarefaction program. Solid lines represent expected values and dashed lines show 95% confidence intervals.

7.3 Late Quaternary Faunal Sequences

Palaeoecological and palaeozoological records are necessary for understanding the native composition, ecological structure and evolution of present-day faunal communities. Combined with the data presented in this thesis, fossil discoveries and radiometric dates published in the last decade now allow for an initial biostratigraphy to be constructed for the mammal faunas of two faunal regions of the Philippines. These faunal sequences provide a baseline to examine patterns of faunal assembly, diversity and extinction in the archipelago during the Late Quaternary.

7.3.1 Palawan Faunal Sequence

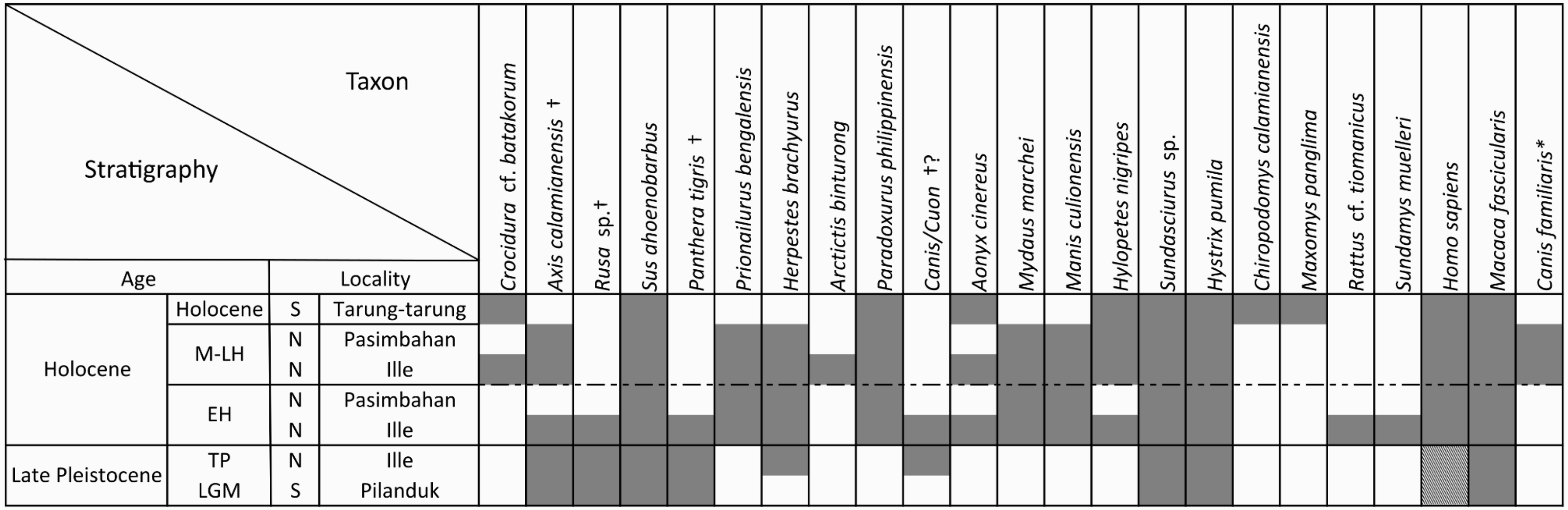
The faunal sequence for the mammals of Palawan Island presented here draws from records of four known vertebrate assemblages (Figure 7.3). Pilanduk and Tarung-tarung Caves represent the southern portion of the island, while Ille and Pasimbahan Caves cover the northern Palawan record. Pilanduk Cave provides a record for MIS-2, and Ille Cave provides a record at *ca*. 14,000 BP (Terminal Pleistocene). As shown in Figure 7.3, the Holocene records of Ille and Pasimbahan can be differentiated into Early, Mid and Late Holocene, and these are partitioned accordingly. In contrast, stratigraphic data for the Holocene sequence of Tarung-tarung Cave are not available and hence, it is unpartitioned. The oldest vertebrate fossils are those of *Homo sapiens* remains from Tabon Cave, which range in age from 50,000–16,000 years ago. Tabon Cave was not included in this synthesis, however, because none of the other vertebrates were described. The presence of *Homo sapiens* is deduced for Pilanduk and Ille Caves, based on the presence of stone tools and other artefacts, taphonomic evidence (see Chapter 8), and the data from Tabon Cave (see Chapter 4). No other species of human is known on Palawan Island during this period. As shown in the Palawan fossil faunal sequence, most of the extant non-volant mammals of the island have been identified in the fossil record. The exceptions include *Tupaia palawanensis*, *Haeromys pusillus* and three other montane taxa (*Sundasciurus rabori*, *Palawanomys furvus* and *Palawanosorex muscorum)*. The absence of montane taxa is explicable since all fossil assemblages are from lowland localities.

The continental affinities of Palawan's extant fauna have long been recognized by biologists (Dickerson 1928; Esselstyn et al. 2004; Heaney 1986). Palawan is considered as a part of the Sunda Shelf both in terms of its geology and biogeography, as represented in Huxley's modification of Wallace's Line (Huxley 1868). Palawan shows relatively high endemism and high diversity for an island fauna. This is related to its proximity to Borneo, which is the main continental source of its fauna. A maximal interpretation of bathymetric data indicates that a narrow Middle Pleistocene land-bridge connection may have possibly connected Borneo and Palawan, but an LGM connection was likely not present (Robles et al. 2015). During the LGM, the nearest distance between the two landmasses is estimated at around 4.5km. This palaeogeographic record coincides with the degree of species endemism observed on Palawan, wherein it shares many genera with Borneo but there has been sufficient divergence that Palawan taxa are attributed as separate species. In the fossil records collated here, nearly all genera identified are shared with Borneo and the Sunda Shelf. On the other hand, more recent phylogenetic studies have drawn attention to certain oceanic affinities of Palawan's fauna, particularly based on reptile and amphibian taxa (Brown and Guttman 2002b; Evans et al. 2003). Most Palawan taxa are indeed shared with Borneo, but there are a few lineages that are exclusively shared with the oceanic Philippines and Sulawesi (Esselstyn et al. 2010). Palawan endemism is partially attributed to Pleistocene sea-level high-stands separating the island from Borneo during interglacial periods (Heaney 1985, 1986). It has also been observed that for certain Palawan vertebrate lineages, the divergence pre-dates the Pleistocene and that there was also invasion of taxa from the oceanic Philippines (Oliveros and Moyle 2010; den Tex et al. 2010). These imply that such divergences occurred much further back in geological time and that these occurrences lend some oceanic affinities to the Palawan herpetofauna (Esselstyn et al. 2010). Nonetheless, the non-volant mammal components reinforce Palawan's Sundaic affinities (Esselstyn et al. 2004). The degree of endemism on Palawan can be linked to the question of a land bridge connection to Borneo and how long since Palawan has been isolated from Borneo (Piper et al 2011), which palaeogeographic reconstructions suggest is the Middle Pleistocene (Robles et al. 2015). Given these mix of attributes, Esselstyn et al. (2010:2054) have previously suggested to view Palawan as a filter zone which has played multiple biogeographic roles, including a young and old extension of the Sunda Shelf.

As described in Chapter 5, Palawan's terrestrial vertebrate fossil record only reaches as far back as *ca*. 50,000 years ago. In terms of its geological history (see Chapter 2), this is a period when Palawan was already part of the Sunda Shelf and is considered a Sundaic peninsula. The extinct fossil species described here (*Panthera tigris, Rusa* sp., *Axis calamianensis*) all belong to genera that are shared with Borneo, Java and the Asian mainland. These records lend further support to Palawan's Sundaic affinities. In the case of the tiger, its presence runs parallel with fossil and historical records showing that it is/was present on all other large Sundaic Islands (Borneo, Java, Bali and Sumatra). In Borneo, it is only represented by Holocene fossil records from two sites (Harrison 1998; Piper et al. 2007). To date, available fossil records show that the tiger did not cross east of Huxley's or Wallace's Lines. Molecular phylogenetic data suggest that the basal South China tiger is the likely source population of living tigers, including those of the Sundaic islands (i.e., Java, Bali and Sumatra), and that divergence estimates indicate that this was a Late Pleistocene occurrence, as recent as 108,000–72,000 years ago (Luo et al. 2004; Xue et al. 2015). One implication of this is that, although there are Early and Middle Pleistocene records of *Panthera* on Java, the current genetic evidence suggests that they are not the direct ancestors of the modern tigers of Java. For Borneo and Palawan, although there are no phylogenetic data available, it is likely that the tiger populations that were present in these two islands derive from the same dispersal event across the Sunda region.

In the case of artiodactyl taxa, the lineages on Palawan are old ones representing pre-Pleistocene colonization. Phylogenetic reconstruction of suid species of the Philippines indicates that they are all ancient taxa that diverged from other SEA pigs during the Pliocene (Lucchini et al. 2005). In this reconstruction, the Palawan bearded pig (*Sus ahoenobarbus)* groups with other Philippine pigs. Furthermore, the basal position of the Palawan pig in the phylogenetic model in relation to other Philippine pigs implies that the colonization occurred via Palawan. In the case of rusine deer, divergence estimates are not yet available. Available molecular data support a Philippine *Rusa* clade that is separate from *R. unicolor* (mainland SEA and Borneo) and *R. timorensis* (Java and Bali) clade (Heckeberg et al. 2016). In the case of *Axis (=Hylelaphus) calamianensis,* molecular phylogenetic data are, to date, unavailable and its relationship to other SEA deer remains unclear.

The fossil evidence across the island clearly shows that deer are part of the natural ecological community of Palawan Island. Additional records for deer come from Tabon and Guri Caves, as observed by Fox (1970) and Heng (1998), respectively. However, it is not known what taxon these deer belong to as no further studies were made on the bones from these two sites. The work from Ille and Pilanduk Caves has previously demonstrated that two species are represented (*Rusa* sp. and *Axis calamianensis*). Based on their contemporaneous occurrence in several archaeological layers in both sites, the range of the two deer species possibly overlapped. From what is currently known of the modern and Late Pleistocene fossil records, all other faunal regions in the Philippines support only one endemic deer per region. Palawan is thus unique in harbouring two deer species in the Late Quaternary. Each faunal region also possesses one endemic pig each. In contrast, Luzon and Cebu Islands appear to harbour their own extinct buffalo (*Bubalus* spp.), similar to the extant tamaraw (*Bubalus mindorensis)* of Mindoro. To date, native bovids have not been found in the Palawan fossil record.



Age			Locality	*Crocidura* cf. *batakorum*	*Axis calamianensis* †	*Rusa* sp.†	*Sus ahoenobarbus*	*Panthera tigris* †	*Prionailurus bengalensis*	*Herpestes brachyurus*	*Arctictis binturong*	*Paradoxurus philippinensis*	*Canis/Cuon* †?	*Aonyx cinereus*	*Mydaus marchei*	*Manis culionensis*	*Hylopetes nigripes*	*Sundasciurus* sp.	*Hystrix pumila*	*Chiropodomys calamianensis*	*Maxomys panglima*	*Rattus* cf. *tiomanicus*	*Sundamys muelleri*	*Homo sapiens*	*Macaca fascicularis*	*Canis familiaris**
Holocene	Holocene	S	Tarung-tarung	■			■					■		■			■	■	■	■	■			■	■	
	M-LH	N	Pasimbahan		■		■		■	■		■			■	■	■	■	■					■	■	■
		N	Ille	■	■		■		■	■	■	■		■	■	■	■	■	■					■	■	■
	EH	N	Pasimbahan				■		■	■		■			■	■		■	■					■	■	
		N	Ille		■	■	■	■	■	■		■	■	■	■	■	■	■	■			■	■	■	■	
Late Pleistocene	TP	N	Ille		■	■	■	■		■			■					■	■					▨	■	
	LGM	S	Pilanduk		■	■	■	■										■	■					▨	■	

Figure 7.3 Late Quaternary faunal sequence for non-volant mammals of Palawan Island. Data are derived from four cave assemblages. Shaded areas denote presence of taxa. Native taxa are listed before non-native species (*). M-LH = Middle to Late Holocene, EH = Early Holocene, TP = Terminal Pleistocene, LGM = Last Glacial Maximum, N = northern Palawan, S = southern Palawan, † = extinct on Palawan Island, †? = possibly extinct but taxonomic designation is uncertain between *Canis* and *Cuon*. Data for Tarung-tarung Cave are from Reis and Garong (2001) but data for further subdivision of Holocene levels in this site are not available. The presence of *Homo sapiens* in the Late Pleistocene is inferred from the Tabon Cave record.

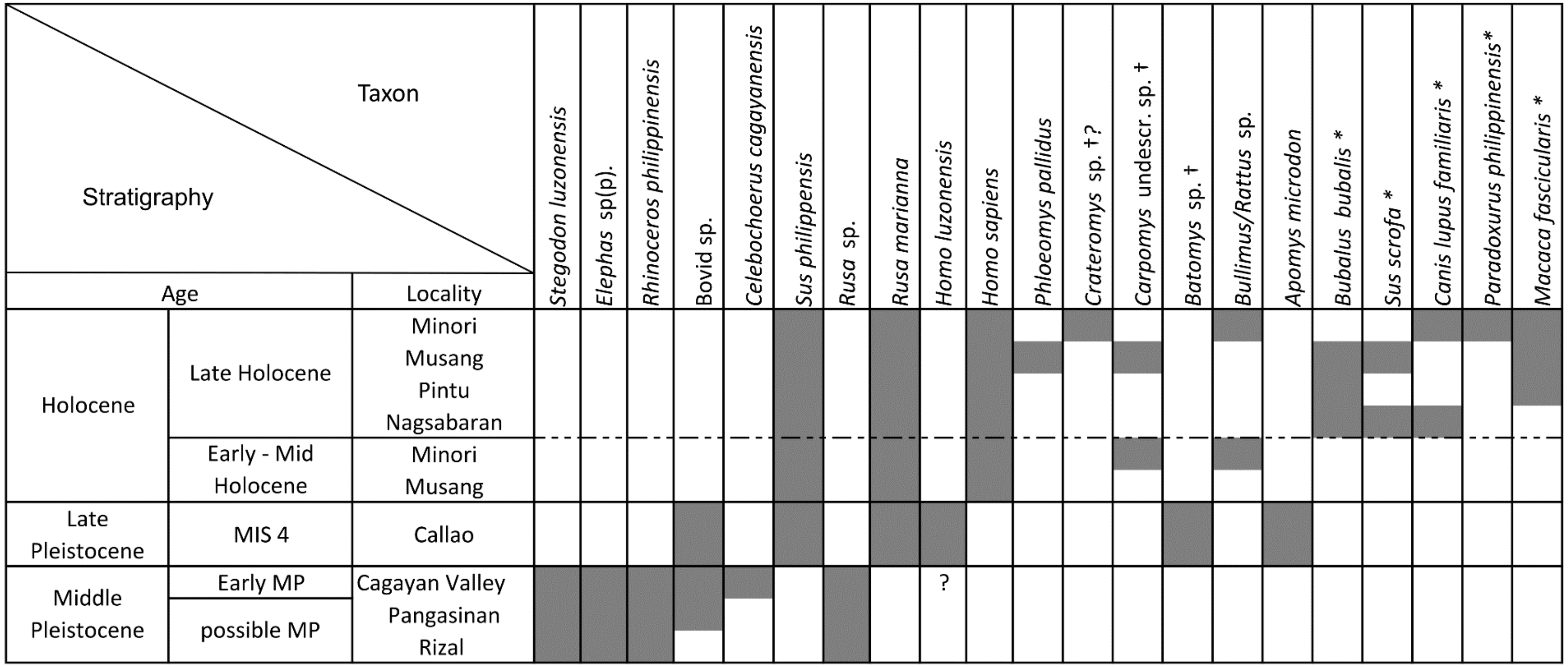
As its name denotes, the Calamian hog deer is presently considered endemic to the Calamianes, a group of small islands north of Palawan. The fossil data drawn from two sites clearly show that it was also once part of the main Palawan Island. For the hog deer, this is unsurprising, given that during sea-level low-stands, the smaller islands surrounding the main island all joined to form the Pleistocene aggregate called ‘Greater Palawan’. Nonetheless, this finding has significance for the conservation of this species, which is listed as Endangered in the IUCN database. Its known habitat is currently restricted to its modern range in the small northerly islands of Calamian, Calauit and Busuanga. It is continuously threatened by habitat loss due to human land conversion and hunting pressure. Based on the previous fossil evidence presented from Ille Cave regarding the presence of *Axis calamianensis* (Piper et al. 2011), reintroduction to the main island of Palawan is now considered by assessors to be a possible means to reduce extinction risk of the Calamian hog deer (Widmann and Lastica 2015).

7.3.2 Luzon Faunal Sequence

The known fossil records of Luzon provide a faunal sequence that extends from the Middle Pleistocene to the Holocene (Figure 7.4). The recent discovery and radiometric dating of rhinoceros remains in the Cagayan Valley have provided a chronostratigraphic anchor for megafaunal remains found in this area. The dating is 709,000 BP (T. Ingicco et al. 2018), placing it in the early stage of the Middle Pleistocene. This record is used as a tentative proxy for the megafaunal record of the Cagayan Valley. Other megafaunal remains purported to be of Middle Pleistocene age have been recovered in the Cagayan Valley in previous decades, but their stratigraphic associations and dating remain uncertain. These include remains of extinct *Elephas, Rhinoceros* and *Stegodon*. Similar megafaunal finds are also found in undated localities in Luzon, such as Rizal and Pangasinan provinces. In this faunal sequence, these are also tentatively assigned to the Middle Pleistocene. I refer the reader to de Vos and Bautista (2003) and van der Geer and colleagues (2010) for details on the provenance and taxonomy of the Middle Pleistocene taxa.

For the Late Pleistocene, Callao Cave provides an assemblage dated to 67,000–52,000 BP and is the only site in the archipelago with dates of this age (Mijares et al. 2010). For the Holocene, four sites are collated and divided into Late and Early Holocene. With my own data on Minori and Musang Caves, I add data for Nagsabaran site from Amano et al. (2013) and Pintu Rockshelter from Mudar (1997). Within these sites, archaeological layers with pottery, metal artefacts and known trade items are assigned to the Late Holocene. Aceramic levels are assigned to the Early Holocene. On Luzon, the earliest appearance of pottery and introduction of the domestic pig is dated at *ca.* 4500–4000 BP (Hung 2005; Mijares 2005; Piper et al. 2009).

Much like the fauna of other oceanic islands of Southeast Asia, the mammal fauna of Luzon is unbalanced, with numerous bats and non-volant small mammal taxa, but very few intermediate and large species. There are no native carnivores, but among other vertebrates, top predators include the Philippine eagle (*Pithecophaga jefferyi*), monitor lizard (*Varanus* spp.), and python (*Python reticulatus).* Nonetheless, Luzon Island is known as a hotspot for diversity and endemicity (see Chapter 2). Of the non-volant mammals, a total of 56 extant species are currently recognised (Heaney et al. 2016a). Half of these taxa only became known to science in the last two decades, indicating a very high rate of species discovery (Heaney et al. 2016b). In contrast to Palawan, which is adjacent to a continental faunal source, much of the diversity on Luzon is derived from speciation and *in situ* diversification, particularly within the Muridae (Heaney et al. 2016a). The living members of the Muridae on Luzon currently number 47 described species, displaying a wide variety of ecological and morphological specialisations. Two geologically old murid clades are recognized: the 'cloud rat' clade (=Phloeomyini) and the 'earthworm mice' clade (=Chrotomyini) (Fabre et al. 2015; Musser and Heaney 1992; Rowsey et al. 2018). The ancestors of these clades colonized Luzon *ca*. 14 and 7 million years ago, respectively. They are collectively referred to as 'Old Endemics' because they colonized the archipelago earlier in geological time and have diversified within the archipelago. Apart from these two endemic clades, four additional colonisations have taken place in the last five million years. The members of this group are referred to as 'New Endemics' (Heaney et al. 2016a; Musser and Heaney 1992).



Stratigraphy / Age		Locality	*Stegodon luzonensis*	*Elephas* sp(p).	*Rhinoceros philippinensis*	Bovid sp.	*Celebochoerus cagayanensis*	*Sus philippensis*	*Rusa* sp.	*Rusa marianna*	*Homo luzonensis*	*Homo sapiens*	*Phloeomys pallidus*	*Crateromys* sp. †?	*Carpomys* undescr. sp. †	*Batomys* sp. †	*Bullimus/Rattus* sp.	*Apomys microdon*	*Bubalus bubalis* *	*Sus scrofa* *	*Canis lupus familiaris* *	*Paradoxurus philippinensis**	*Macaca fascicularis* *
Holocene	Late Holocene	Minori						▨		▨		▨		▨			▨				▨	▨	▨
		Musang						▨		▨		▨	▨		▨				▨	▨			▨
		Pintu						▨		▨		▨							▨				▨
		Nagsabaran						▨		▨		▨							▨	▨	▨		
	Early - Mid Holocene	Minori						▨		▨		▨			▨		▨						
		Musang						▨		▨		▨											
Late Pleistocene	MIS 4	Callao				▨		▨		▨	▨					▨		▨					
Middle Pleistocene	Early MP	Cagayan Valley	▨	▨	▨	▨	▨		▨		?												
	possible MP	Pangasinan	▨	▨	▨	▨			▨														
		Rizal	▨	▨	▨				▨														

Figure 7.4 Late Quaternary faunal sequence for non-volant mammals of Luzon Island. Data derive from five assemblages. Shaded areas denote presence of taxa. Native taxa are listed before non-native species (*). MP = Middle Pleistocene, † = extinct on Luzon Island, ? = uncertain status. See text for data sources for each locality.

The current Middle Pleistocene record consists of large mammals that include endemic forms of *Elephas, Stegodon, Rhinoceros, Bubalus* and *Celebochoerus*. There are no murid fossils from this period, although based on the genetic phylogeny of Philippine murids, relatives of Old Endemic and New Endemic taxa would also have been part of the Middle Pleistocene fauna. Megafaunal extinctions occurred on Luzon, as is recorded in many parts of the world. However, the timing of this faunal turnover on the island is unknown. Whether megafauna persisted into the Late Pleistocene remains a question. The relationship of the Middle Pleistocene cervid, suid and bovid remains to Late Pleistocene and Holocene taxa is also unclear. Bovid remains were found in the Late Pleistocene levels of Callao, but species designation was not possible due to the fragmentary state of the remains (Mijares et al. 2010). It is possible that the bovid represented in Callao maybe congeneric/conspecific to the Middle Pleistocene bovid found in the Cagayan Valley. Apart from the extant deer and pig, this bovid record represents the latest dated occurrence of the Middle Pleistocene megafauna.

In the case of the genus *Homo,* Middle Pleistocene human fossils have not been found, but an inferred human presence is postulated based on stone tools and animal butchery marks on bones found in the Kalinga rhinoceros site (Ingicco et al. 2018). The Callao human metatarsal fossil dated to 67,000 BP was ascribed to the genus *Homo* (Mijares et al. 2010). Nonetheless, the fossil represents a diminutive individual, akin to the case of *Homo floresiensis* on the oceanic island of Flores. As mentioned previously, additional fossil remains were found in the same layers, which have now been described and ascribed to a new human species, *Homo luzonensis* (Détroit et al. 2019).

Among the living native mammal species, only five (Figure 7.4: *Rusa, Sus, Phloeomys, Bullimus, Apomys*) have reported fossil records. These records also occur within the known geographic distribution of these living species. Of the cloud rat clade, five species have been identified in the fossil record, three of which are previously unknown extinct/extirpated taxa (undescribed species of *Carpomys*, *Crateromys* and *Batomys*). Of the Chrotomyines and 'New Endemics', only one species of each (*Apomys microdon* and *Bullimus luzonicus*, respectively) has so far been reported in the fossil record. Clearly, the diversity of the small mammal fauna is underrepresented in the fossil record, and the bias has partly to do with the fact that the latter derive from human-accumulated assemblages in cave settings. These assemblages are biased towards human prey species that belong to larger-bodied taxa and to species living in the lowlands. Of the Muridae, the large-bodied cloud rats are better represented compared to other smaller-bodied murids.

As described in Chapter 6, the fossil records of Minori, Musang and Callao Caves have produced records of three extinct species belonging to the cloud rat clade. A previously unknown *Batomys* sp. was described in Callao Cave (Heaney et al. 2011), which is slightly larger than the living *Batomy granti.* The latter is a montane species only known to occur today above 1300 m elevation and only in the Central Cordillera mountain range. The Callao Cave complex is located at the western foothills of a separate mountain range, the Northern Sierra Madre. These two mountain ranges comprise separate 'sky islands' or distinct areas of endemism within Luzon. Biologists now currently recognize eight centers of local endemism within this single island, and they all harbour local endemics not found elsewhere (Heaney et al. 2016b).

This current pattern of diversity and endemism is attributed to the geological history and topographic complexity of Luzon (Hall 2013; Heaney et al. 2016a). Although it is well beyond the time scale covered by this research, it is worth reviewing in brief the geological background that has set the distinct evolutionary stage of Luzon (see Chapter 2). The oldest geological unit of the island which existed above sea level is the Central Cordillera, emerging as a set of scattered islands during the Miocene. The Central Cordillera was the only portion of Luzon that had a substantial highland area from the period of 15 to 7 million years ago. This coincides with the modern molecular phylogenetics of the oldest murid clades on Luzon, which originated in the Central Cordillera. The Northern Sierra Madre coalesced around 5 million years ago and much of the other areas of Luzon would join together mostly within the last three million years. As a caveat, the Luzon faunal sequence represented in the fossil record actually only covers a limited geographic coverage, i.e. the Northern Sierra Madre and Cagayan region in the northeastern part of the island. This means that most other local centres of endemism (seven out of eight) have not been sampled in the fossil record, and future studies will hopefully remedy this.

Because of its geological age and complexity, the Central Cordillera harbours the most biodiversity among all centers of endemism on Luzon, containing all known genera of the cloud rats and earthworm mice (Heaney et al 2016a). These include the extant *Crateromys schadenebergi* and two species of *Carpomys.* The two extinct fossil cloud rat species identified in the Holocene record of Minori and Musang Caves belong to these two genera. The presence of the two species in the Peñablanca area of Cagayan is notable for several reasons. First, the three living congeners are only known to presently inhabit the Central Cordillera, which is a separate area of endemism from the Northern Sierra Madre range. It has been previously noted that the Sierra Madre region has less non-volant mammal diversity compared to the Central Cordillera (Balete et al. 2011). The only living members of the cloud rat clade presently found in the Sierra Madre belong to *Phloeomys* and *Musseromys.* The Holocene archaeological record of the Peñablanca area can now confirm that all five genera of the Luzon cloud rat clade

(*Phloeomys, Crateromys, Carpomys, Batomys* and *Musseromys*) that are present in the Central Cordillera are also found in the Cagayan and Sierra Madre region.

Secondly, all three living species of *Carpomys* and *Crateromys* are montane taxa inhabiting mossy forest at 2000 m elevation and above. In fact, of the twelve living species of cloud rats on Luzon, nine species occur above 1400 m elevation. The three living lowland cloud rats consist of two species of *Phloeomys*, which are the largest of all cloud rats. The other lowland species is *Musseromys gulantang,* an inhabitant of Mt. Banahao in the Southern Sierra Madre, which is another separate area of endemism. The Callao limestone formation (where Minori and Musang Caves are located) has an elevation range below 600 m and is characterized by karstic lowland forest. Most of the cave sites lie below 300 m elevation. As discussed in Chapter 5, there are no known climatic events or records of environmental change on Luzon that would have lowered habitat elevational gradients to such an extent during the Late Holocene. Hence, taking these biogeographic and ecological considerations into account, the extinct fossil records of *Batomys*, *Crateromys* and *Carpomys* in the Callao formation are significant because they extend the known distribution of the three genera not only beyond the Central Cordillera, but also beyond montane forest into lowland environments. Among living cloud rats, ecological parallels do exist: two *Phloeomys* species and the three *Crateromys* species of Ilin, Dinagat and Panay Islands are elevational generalists, and all occur in lowland forests.

Furthermore, the presence of three fossil species in the lowland environs of Callao indicate previously unknown lowland diversity for Luzon small mammals. It also draws attention to the exercise of estimation of species richness in island biogeography, which is largely based on data from extant biotas. Various authors have already observed that many modern faunas are heavily transformed faunas impacted by humans (Helmus et al. 2014; Steadman 2006; Zalasiewicz et al. 2011). The last two decades of modern biological surveys in the Philippines have produced exceptionally large numbers of new species discoveries (Heaney et al. 2016b). This is said to be unsuspected because mammals are typically viewed as well-described groups compared to other classes of organisms. It appears that the Holocene vertebrate record is revealing added numbers to previously unsuspected biodiversity in the archipelago. Another important aspect of species richness relates to distribution of taxa along elevational gradients. Among Philippine small mammals, a curvilinear pattern of increasing species richness is observed as elevation increases, such that relative abundance rises by a factor from two to ten from the lowlands to 1500–2200 meters above sea level (Heaney 2001). The peak in species richness of non-volant small mammals is said to occur at the transition from montane to mossy forest, which is also the likely point where rainfall peaks (Heaney

2001). The description of three extinct fossil species inhabiting the lowlands of Cagayan adds to the inventory of lowland species on Luzon, and this raises the question of whether lowland small mammal diversity is masked by an extinction filter. This extinction phenomenon is further discussed in Section 7.4. Lowland faunas appear to be the most heavily impacted by human activities and the invasive species that humans have introduced. On the other hand, the karstic environment of the Callao formation may also harbour additional and unknown diversity that requires further investigation. This is evidenced by the discovery of an unnamed member of the genus *Apomys* found in recent field surveys in the karsts near Callao Cave (Heaney et al. 2016a).

7.3.3 Body Mass Estimation of Fossil Murids

Body size difference is one of the main criteria that distinguishes extinct murid taxa identified in the Luzon record from the living congeners. These size differences among the extinct taxa further substantiate the remarkable repertoire of morphological niches with the Phloeomyini. Members of the Phloeomyini range in size from 2.7 kg for the largest cloud rat *Phloeomys*, to 15 g for the tree mice of the genus *Musseromys*.

Body mass of fossil murids was estimated based on toothrow lengths using regression equations by Hopkins (2008) and Freudenthal and Martín-Suárez (2013) (Table 7.2). Calculations were also made for extant species for which body mass is known in order to test for accuracy of estimations. Body mass range is based on data provided by Heaney and colleagues (2016a) for each species. For *Musseromys*, actual body mass for each individual is available and provided separately for each specimen. Hopkin's method allows estimation from mandibular toothrow lengths, and two equations are provided: one for larger murids (<5kg) and another for smaller murids (<500g). Both were used according to the size of the living murids measured. For fossil specimens, the equation for <500g murids were used for *Bullimus* and the rest of the fossil murids fall in the <5 kg category. For Freudenthal and Martín-Suárez' method, equations were available for mandibular (inferior) and maxillary (superior) toothrows. Using their method, regression equations for the 'Muridae' and for 'All Rodents' were both calculated, as shown in Table 7.2.

When actual body mass and estimated body mass of living species are compared, both sets of methods significantly underestimate the body weight of the large phloeomyines (*Crateromys* and *Phloeomys*) (Table 7.2 and Figure 7.5). Hopkins' equations show the lowest values, while the 'All Rodents' equation from Freudenthal and Martín-Suárez (2013) provides the largest values. Note that known body mass records of modern specimens derive from taxonomic descriptions of living taxa (Heaney et al. 2016a) and do not correspond to individual museum specimens measured. Regardless, there are large discrepancies between the known body mass of living Philippine murids drawn from existing data in the literature compared to the results for the regression estimates. This has implications for the body size estimation of the two large fossil cloud rats, *Carpomys* undescr. sp. and *Crateromys* sp. Comparing the toothrow lengths of the fossil *Carpomys* to the living species, the former falls in the lower range of the living *Crateromys schadenbergi*. Hence, it is possible that the fossil *Carpomys* may also fall in the body weight range of *C. schadenbergi*. The lowest end of this range is recorded at 1350 g, while the calculated body mass estimates range only from 684-1045 g. A possible solution (for future work) is to gather body weight data for the Phloeomyini and calculate regression equations tailored according to this endemic murid clade. Hopkins' equations have been used to estimate body size of fossil rodents from Sumba and Timor Islands (Indonesia) (Turvey et al. 2017). The results for Luzon put into question whether such calculations also underestimate body size for Wallacean rodents.

Despite these discrepancies in body mass estimation, the extinct fossil murids provide evidence for further morphological specialization within the Phloeomyini. The difference in size of the fossil *Carpomys* from the living *Carpomys* is particularly remarkable (see Chapter 6). Among the living species that have existing molecular phylogenetic and divergence estimates, such discrepancy in size between taxa of similar dental morphology appears to warrant differentiation at the genus level. Such is the case for *Carpomys* (120-165 g) and *Musseromys* (15-22 g), which have similar tooth morphologies. This is also the case for *Crateromys* (1350-1550 g) and *Batomys* (182-226g). The size difference between the living *Carpomys* and the extinct fossil *Carpomys* runs parallel to the size difference between living members of *Crateromys* and *Batomys* on Luzon.

Table 7.2 Body mass estimation of Luzon fossil and extant murids using equations from Hopkins (2008) and Freudenthal and Martinez-Suarez (2013). Estimations for modern murids with known body mass are provided to compare with the results of regression equations. *Indicates data from Heaney et al. 2016a. (N) indicates number of modern specimens under toothrow lengths (TRL). Note the large differences between the estimations using different equations, and the differences between the estimations and known body mass for living taxa (modern).

Site/Source	Bone ID	Element	Taxon	M1-3 TRL (mm)		Hopkins 2008	Freudenthal and Martinez-Suarez 2013	
						body mass (g)	body mass (g)	body mass (g)
Fossil							Muridae equation	All rodents equation
Minori	16301	mandible	*Carpomys* undescr sp.	14.55		755.5	868.8	1045.9
Musang	101	mandible	*Carpomys* undescr sp.	14.03		684.4	791.7	947.2
Minori	17018	mandible	*Crateromys*	13.4		604.1	704.1	835.9
Heaney et al. 2011	7554	mandible	*Batomys* sp.	10.21		288.7	351.7	398.7
Minori	15998	mandible	*Bullimus/Rattus*	9.5		235.9	292.6	327.6
Musang	I5a-1	mandible	*Bullimus luzonicus*	10.13		280.6	344.7	390.2
Minori	15997	maxilla	*Carpomys* undescr sp.	14.52		N/A	919.4	1035.9
Minori	5707	maxilla	*Phloeomys pallidus*	17.45		N/A	1512.5	1719.5
Modern					known body mass			
FMNH and BMNH		mandible	*Crateromys schadenbergi*	14.35-17.17 (13)	1350-1550*	727.7-1184.6	789.6-1325.8	838.6-1641.7
FMNH and BMNH		mandible	*Carpomys melanurus*	9.11-9.21 (3)	165*	211.8-218.2	262.9-270.3	292.3-302.2
FMNH and BMNH		mandible	*Carpomys phaeurus*	6.3-6.64 (5)	123*	77.8-89.7	102.5-117.3	107.1-123.5
BMNH		mandible	*Batomys granti*	8.38-8.53 (2)	182-226*	168.8 -177.2	212.4-222.2	232.8-244.3
BMNH		maxilla	*Phloeomys pallidus*	17.98-19.22 (6)	2200-2700*	N/A	1491.4-1768.3	1867.3-2244.3
FMNH	193839	mandible	*Musseromys inopinatus*	3.31	19.5	13.7	19.8	17.6
FMNH	209523	mandible	*M. anacuao*	3.26	17	13.1	19.1	16.9
Heaney et al. 2014	1933839	maxilla	*M. inopinatus*	3.37	19.5	N/A	17.6	18.5
Heaney et al. 2014	209523	maxilla	*M. anacuao*	3.09	17	N/A	13.9	14.5
Heaney et al. 2014	178405	maxilla	*M. gulantang*	3.23	15.5	N/A	15.7	16.4
Heaney et al. 2014	193840	maxilla	*M. inopinatus*	3.43	17	N/A	18.5	19.4
Heaney et al. 2014	198714	maxilla	*M. beneficus*	3.26	22	N/A	16.1	16.9
Heaney et al. 2014	198857	maxilla	*M. beneficus*	3.35	22	N/A	17.3	18.2
Heaney et al. 2014	209522	maxilla	*M. anacuao*	3.1	21	N/A	14.0	14.7

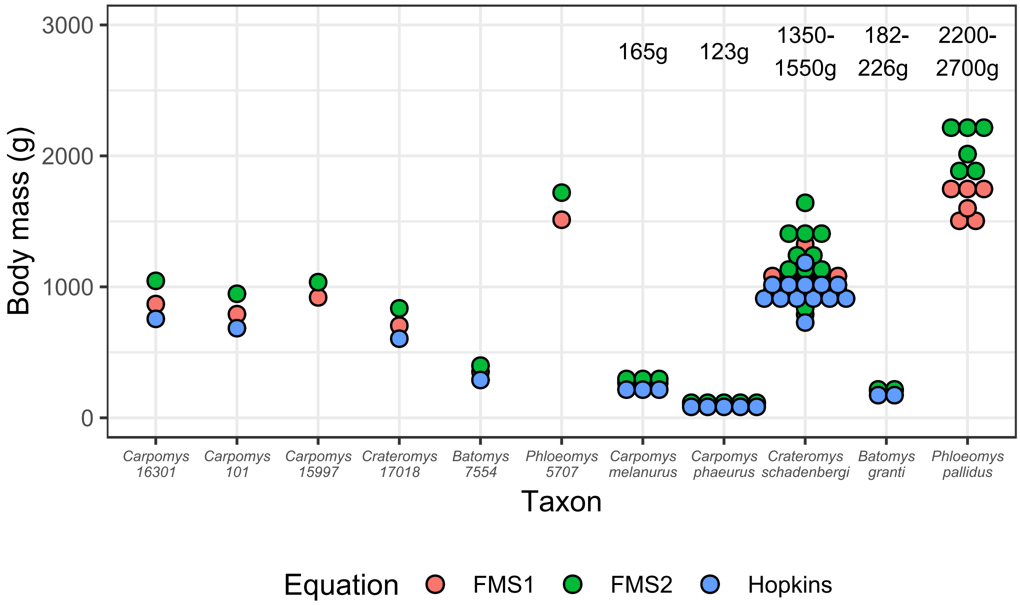


Figure 7.20 Body mass estimations (in g) of fossil and modern cloud rats of Luzon. Body mass were estimated using the regression equations of Hopkins (2008) and the 'Muridae equation' (FMS1) and 'All rodents equation' (FMS2) of Freudenthal and Martinez-Suarez (2013). Known body mass of living species are indicated. See Table 7.2 for data and sources. Note that certain estimations for *Crateromys schadenbergi* and *Phloeomys pallidus* fall well below the known body mass of living species.

7.4 Holocene Faunal Changes and Mammal Extinctions in the Philippines

Understanding faunal changes and extinctions requires robust fossil records and chronologies. For the Philippines, there is much work needed to resolve chronologies. A few radiometric dates and palaeoenvironmental data are available for the Late Pleistocene and the Holocene. In this section, I present the extinction records of Luzon and Palawan within the broader palaeoecological and archaeological contexts in the Philippines and Island Southeast Asia. Globally, the Late Quaternary has witnessed massive levels of extinction, particularly for large-bodied vertebrates. It has been vigorously debated whether climatic change or human impacts are the major cause of these events; however, it is now widely accepted that human involvement played its role in varying degrees in megafaunal extinctions across several parts of the world (Koch and Barnosky 2006; Martin and Steadman 1999; Sandom et al. 2014; Turvey 2009; Wroe et al. 2004). Massive extinctions have continued into the Holocene, occurring during an epoch with reduced climatic fluctuations. Palaeohistoric extinction events in the Holocene, therefore, offer the potential to investigate the varying impacts of humans in the last 10,000 years and understand the extent of anthropogenic extinction drivers. Here, I focus on specific taxa from Luzon and Palawan to investigate local extinction chronologies and explore factors that have influenced their demise.

7.4.1 Extinct Tiger and Deer of Palawan

The Palawan faunal sequence (Figure 7.3) documents the presence of three extirpated large mammals. The last occurrence record for the tiger is from an Early Holocene context of Ille Cave (context 1839 of West Mouth trench) with an associated age of ca. 11,000 cal BP (Lewis et al. 2008; Paz et al. 2008). The last occurrence records for the rusine deer are also from Early Holocene levels of Ille Cave (West Mouth contexts 1530, 1532, 1560 and 1626; East Mouth context 807). For the extant Calamian hog deer, the last occurrence records on the main island of Palawan are from the Late Holocene levels of Ille and Pasimbahan Caves. A radiocarbon age of 3704–3573 cal BP is associated with a Late Holocene level (context 71) from Pasimbahan Cave, where hog deer remains are still present in small numbers (Ochoa et al. 2014). It is possible that the hog deer survived much later since a midden deposit (context 403) in Trench J of Pasimbahan Cave contains deer remains, Indo-Pacific glass beads and ceramic tradeware. However, as caves in this area are used as burial sites during the Middle to Late Holocene, it is possible that the ceramics and beads are intrusive materials and are not associated with the deer remains. If associated, though, this may even indicate a much later extinction date within the last millennium.

The asynchronous timing of Palawan Island extinctions signals different dynamics of extinction (Ochoa and Piper 2017). The apparent Early Holocene disappearance of the tiger and rusine deer happens against a backdrop of extensive environmental changes during the Pleistocene-Holocene transition. The inundation of Greater Palawan initiates after ca. 19,000 years ago, and eventually the land area of the main island was reduced by approximately 85% at the end of the Pleistocene (Robles et al. 2015). Shallower areas were progressively drowned, leading to the loss of land connections of several island groups (Cuyo, Calamianes and Busuanga) to the main island. Present-day Palawan has a land area of 11,578 km^2, while Greater Palawan had a land area of 79,440 km^2. Palaeoenvironmental records from Gangub Cave (southern Palawan) and Makangit Cave (northern Palawan) also indicate a shift in vegetation communities (Bird et al. 2007; Wurster et al. 2010). Forest contraction and the presence of more open vegetation regimes are reported during the LGM, based on stable carbon isotope composition of guano profiles in both caves. Closed forest canopy is said to expand again during the onset of the Holocene. More open environments were possibly favourable to both deer species, and the maintenance of both populations would have been beneficial to the tiger. Deer are typically eurytopic taxa that tolerate a wide range of environments and can also adapt to climatic variation through time. The extirpation of the deer on Palawan has long been a conundrum since all other Philippine faunal regions retain their endemic rusine deer populations. Smaller oceanic islands (that were separated from larger islands after the last glacial due to sea level rise) had deer populations up to recent historic times. Present-day ecological traits of the modern Calamian hog deer show that it prefers grassland habitats. While it was present on the main island of Palawan, rusine deer appear to have been intensively hunted by humans since they were the dominant prey taxon in the Late Pleistocene to the Early Holocene. A resource switch is evident during the Middle Holocene, when the Palawan bearded pig became the main prey of humans, the hog deer became very rare in the record, and the rusine deer is absent from the record (Ochoa 2009; Piper et al. 2011). The rarity of *Rusa* deer was likely caused by the extensive reduction of habitat brought about by palaeogeographic changes and vegetation shifts at the end of the Pleistocene. This, coupled with direct predation by humans of a diminishing population, possibly drove the extinction of the rusine deer. Future work to test this hypothesis can focus on deer palaeodiets. My initial attempt to conduct microwear studies on deer teeth from Pilanduk was unproductive due to the scarcity of well-preserved teeth from the 2016 excavation.

Was the reduction of land area and habitat sufficient to drive the extinction of the tiger on Palawan? Bali, an island of only 5780 km^2, retained its tiger population until the mid-20th century. It also retains an autochthonous rusine deer population (*Rusa timorensis renschi*). Palawan is a larger island at over 11,000 km^2 that has not retained either tiger or deer. Bali and its fauna are generally perceived as an extension of East Java due to the recurring Pleistocene land connections between the two islands. Bali's land connection to Java was likely drowned by the Early Holocene, when rising sea levels reached -20 meters below present sea level (from an LGM level of -116 mbpsl; see Sathiamurthy and Voris 2006; Voris 2000). During connectivity in times of low sea-levels, savannah vegetation likely prevailed on Bali (Bird et al. 2005; Heaney 1991). However, Bali presently has a different natural lowland environment to Palawan. In the former, ever-wet rainforests are confined to upper elevations of mountains (Flenley 1998). These differences in post-Pleistocene environments between Bali and Palawan likely influenced the maintenance of rusine deer and tiger populations. Borneo is another island that harboured tiger populations in the past that became extinct in the Holocene (Piper et al. 2007). This large island also retains native deer, bovid and bearded pig population up to the present, and these are prey taxa that could have supported a tiger population. Of the large Sundaic islands, only Palawan and Borneo lost their tiger populations prior to recent historic times.

On Palawan, diminishing deer populations may have elevated the extinction risk of the tiger population. A possible scenario is that in the Late Pleistocene, there was a prey-enriched landscape populated by deer that supported tiger populations, and a prey-depleted landscape by the onset of the Holocene. Tigers prey on pigs and bovids, but deer appear to be the most important prey across its range (Mazák et al. 2011). Modern assessments indicate that the availability of a sufficient prey base of large ungulates is the tiger's major habitat requirement, in order that they may survive and reproduce (Hayward et al. 2012; Sunquist 2010) (Hayward et al. 2012; Sunquist and Sunquist 2002). These assessments also indicate that tigers prefer prey that are closer in size to their own. In the case of Palawan tigers, the rusine deer would be the prey closest to its size, whereas the endemic (and dwarfed) bearded pig and hog deer are much smaller in size that both the rusine deer and the tiger. The combination of these factors – decreased habitat, diminished prey base and human predation – possibly drove tiger extirpation on Palawan in the Early to Middle Holocene.

The situation of the Calamian hog deer markedly differs from that of the rusine deer. The hog deer persists into the Late Holocene on Palawan, and at present, retains a relictual distribution in the Calamianes Islands. The environments of the Dewil Valley of northern Palawan in the Middle to Late Holocene are described by O'Donnell (2016), who presents the only pollen record for Palawan Island. The >5000-year Makinit sequence shows the continuity of open landscapes (in the form of seasonal tropical lowland forest of an open structure) amidst a mosaic of riparian and mangrove communities. Within the last 2750 cal BP, the sequence shows evidence of patches of true closed lowland forest. The causes (anthropogenic or climatic) for the maintenance of open landscapes during the Middle to Late Holocene is not known due to problems of equifinality. Potentially, the presence of a mosaic of open and closed forest types would have been suitable to deer populations. The presence of open forest types is also said to contrast with other proxy evidence (Bird et al. 2007; Wurster et al. 2010) indicating the increasing presence of closed forest on Palawan during the Holocene.

The condition of the Calamian hog deer is mirrored in the condition of the hog deer on Bawean Island, *Axis (=Hyelaphus*) *kuhlii*. Fossil records indicate that the Bawean hog deer was also present on Java (van den Bergh et al. 2001), and Bawean Island also lost its land connection to Java due to post-glacial sea level rise. As paralleled in many cases of extinctions around the globe, there is less extensive natural climatic variation recorded in the Late Holocene of the archipelago and environmental conditions appear broadly similar to modern regimes (see Turvey 2009). Hence, it appears that anthropogenic factors are the main drivers of Late Holocene extinction events.

The regional picture for large mammal extinctions in Southeast Asia depicts environmental factors as the main causes (Louys et al. 2007). Post-glacial sea level change drowned a large portion of the Sunda Shelf, and separated land connections between islands. The consequent loss of more open environments and other floristic changes are thought to be responsible for most large mammal extinctions. A broad range of large-bodied taxa became extinct or extirpated in the Late Quaternary (e.g. *Stegodon, Hexaprotodon, Pongo, Crocuta, Hyaena, Palaeoloxodon, Ailuropoda, Rhinoceros,* etc.). Extinction chronologies are poorly resolved for most of these taxa. In the case of anthropogenic impacts, it is suggested that humans were likely to have more direct impacts on the fauna in Island Southeast Asia than in the mainland (Sondaar 1987). This appears to be the case for Palawan, where environmental and anthropogenic impacts appear to be both implicated.

7.4.2 Translocation of Non-native Species on Luzon

An important Late Holocene ecological process that relates to faunal assembly and extinction is the translocation of non-native species. On Luzon, the taxa in question are the long-tailed macaque (*Macaca fascicularis*) and palm civets (*Paradoxurus philippinensis* and *Viverra tangalunga*). These species were long considered by biologists as native species of the archipelago (Fooden 2006; Heaney et al. 1998). More recently, they have been re-classified as invasive taxa that have been naturalised across the oceanic Philippines primarily based on morphological and molecular genetic data that indicate that Philippine populations differ little from those on Borneo (Heaney et al 2016a). On Palawan, these species are considered natives of the island based on biogeographic, phylogenetic and fossil evidence (Section 5.4.1).

Geneticists point to a Sunda Shelf origin for Philippine macaques (Blancher et al. 2008; 2012; Liedigk et al. 2015; Tosi et al. 2003). Blancher et al. (2008, 2012) show that Philippine sequences have low genetic and nucleotide diversities and that these are encompassed by one sequence from Indonesia (Sunda Shelf portion). The authors say that precise dating of Philippines colonisation cannot be assessed from their results but suggest a colonization date of 110,000 years ago. A more specific study of Philippine macaques focused on comparing populations from Luzon and Mindanao islands that represent two subspecies in the Philippines, *M. f. philippinensis* and *M. f. fascicularis*, respectively (Smith et al. 2014). The subspecies distinction is primarily based on pelage consisting of a lighter variant (*fascicularis*) and a darker variant (*philippinensis*) (Fooden 1991). The study by Smith et al. (2014) does not support sufficient genetic distinction to warrant sub-specific designation of regional populations. Both Philippine populations were most closely related to two different mtDNA haplotypes from Sarawak (Borneo) from which they are apparently derived. They also suggest that there are two independent immigration events of the macaque into the archipelago. These genetic studies note that the long-tailed macaque has been introduced by humans to many islands beyond Wallace's Line; however, they suggest a natural colonization scenario for the Philippines. Blancher et al. (2012) characterise the Philippine macaque populations as an isolated population that experienced a founding effect followed by a probable rapid initial expansion of the population. Based on the current fossil evidence from Luzon, I suggest that this low genetic diversity, close relation to Indonesian macaque populations and founder effect likely derive from a Late Holocene human introduction of this species to the oceanic Philippines. The suggested colonisation date of 110,00 years ago (derived from baboon-macaque divergence time) may pertain to divergence estimates in reference to the founding Sundaic population and not actual colonisation into the Philippine archipelago.

As noted in Chapter 6, the common palm civet (*P. philippinensis)* populations of Luzon are genetically indistinguishable from Bornean civets. Unlike the case of long-tailed macaques, geneticists suggest that the low diversity among Philippine palm civets and the lack of genetic divergence for Luzon and other oceanic Philippine populations from Borneo indicate recent human introduction (Veron et al. 2015). The palm civets in Sulawesi and Lesser Sunda islands have also been attributed to human introductions (Patou et al. 2010). Reis and Garong (2001) also proposed that leopard cats (*Prionailuris bengalensis*) and viverrids (*Paradoxurus* and *Viverra*) were introduced by humans in the oceanic Philippines similar to the view proposed for Lombok by Kitchener (1990). The Malay civet (*Viverra tangalunga*) and the leopard cat are also present in the oceanic Philippines, but fossil records on Luzon have not been reported or identified yet. Genetic data for the Philippine and Wallacean populations of Malay civet also suggest recent translocation (Veron et al. 2014). In the Philippines, two haplogroups for the common palm civet were identified, indicating at least two colonisation events. One haplogroup is only separated by one mutation step from a Bornean haplotype, possibly indicative of recent introduction. The other haplogroup is separated by three mutation steps from Borneon haplotypes, possibly attributable to a natural dispersal event on Palawan Island.

In various Wallacean islands, such as Sulawesi and the Lesser Sundas, macaques and palm civets were introduced in the past and are recognized as translocated species or 'ethnotramps' – economically and culturally favoured wild animals that humans carried around and introduced into other habitats (Heinsohn 2003). The proposed reason for the introduction of the macaque is as a pet and food animal, whereas the palm civet may have been a rat catcher. It is also suggested that these translocations occurred in the latter half of the Holocene, with the Austronesian expansion or in later 'protohistoric' periods. The actual timing of introductions is, however, still poorly resolved and an unpacking of the Austronesian package is necessary. On Flores Island, macaques and palm civets appear in the faunal sequence during the Late Holocene in the same levels where pottery and polished stone adzes are found (van den Bergh et al. 2009). In Tron Bon Lei site on Alor Island (Lesser Sundas), a viverrid bone was identified in levels dated at *ca*. 3200 BP. In Matja Kuru 1 in Timor Leste, the palm civet has been identified and directly dated to 2741±27 BP (O'Connor 2015). A possible example of an earlier translocation comes also from Flores, where a single Sulawesi warty pig (*Sus celebensis*) tooth has an associated charcoal date of *ca*. 7000 BP (Larson et al. 2007). However, because this is not a direct date on the warty pig specimen, caution must be taken before assigning a Middle Holocene translocation.

The current work on Minori and Musang Caves provides fossil and stratigraphic evidence that substantiates the process of translocation and documents the timing of introductions in the oceanic Philippines. Apart from anecdotal evidence implying that invasive taxa were part of a 'Neolithic package', actual evidence for translocation has not been demonstrated for the Philippines. The faunal sequence for Luzon (Figure 7.4) shows that remains of endemic species of cervids, suids and murids are present in the fossil record during the Mid to Early Holocene and the Late Pleistocene. In contrast, records for proposed translocated species indicate that they appear only during the Late Holocene. If macaques and civets are native on Luzon, we would expect to have Early Holocene or Pleistocene records for them; however, such records are absent in all reported sites (Figure 7.4). Mijares (2008) also reports the presence of deer and pigs in Eme and Dalan Serkot Caves, but no other large or intermediate mammals were reported. Both sites also lie within the Callao formation and range in age from *ca*. 7000 to 3000 BP. This absence cannot be simply attributed to low sampling effort or poor preservation, since smaller murid taxa are preserved in these assemblages. In contrast, macaque and small carnivores remains are found in the Early Holocene and Late Pleistocene record of Palawan Island, and they appear to be frequently hunted throughout the Holocene. At present, macaques and civet cats are still the frequent prey of human hunters on Luzon.

The stratigraphic data presented for Minori Cave show in detail the occurrence of particular mammal taxa throughout the archaeological sequences (Tables 7.3 and 7.4). For Musang Cave, records for the stratigraphic location of macaques are in Table 6.10 (Chapter 6). The data for Minori Cave are reconstructed from logbook and inventory records from the 1981

– 1983 excavations. Detailed records were available for Square 37 and Square 27, and these are shown in Table 7.3. These two excavation units also had the greatest number of remains among all squares. Data for all Minori Cave excavation units are summarized in Table 7.4. The records show that native deer, pigs and murids are present throughout the sequence. They also indicate that macaque, palm civet and domestic dog remains only appear in pottery-bearing levels and are not found in deeper layers. In fact, these taxa only appear in the uppermost levels that are no deeper than 20 cm from the surface.

As mentioned in Chapter 3, direct ^{14}C dates were obtained from macaque remains in Minori Cave. Two tooth specimens from Square 37 that had the lowest depths were chosen. These had the corresponding depths of -226 and -227 cm from site datum or approximately 10-15 cm below the surface. The specimens yielded the ages of 1827–1706 cal BP (OxA-36333) and 305–14 cal BP (or cal CE 1762–1803; OxA-36334), respectively. The incongruence of dates for the two specimens of similar depths is not surprising, given the shallowness of the levels and the acknowledged post-depositional processes that have contributed to the mixing of finds in the upper levels (see Chapter 4). This is also the reason why direct dates on the targeted taxon were taken due to this suspected problem. Presently, these are the only two direct dates on archaeological macaque remains from the archipelago.

In the case of the palm civet, only Minori Cave has secure identifications for this species. Two specimens of teeth were identified in Squares 7 and 32 of Chamber A (Table 7.4). The recorded depths for the specimens come from levels that also contained pottery. Note that palm civet remains were not found in Squares 27 and 37, and hence this taxon is not included in Table 7.3. It has not been identified or recorded in other Luzon faunal assemblages. Direct dating was not attempted due to the scarcity of the finds.

The record from Musang Cave shows a similar pattern to Minori Cave. Large mammals are found throughout the sequence and macaques only appear in levels that had pottery as well. The stratigraphic record for Musang, however, is not straightforward. All the macaque remains were identified in Trench G4 (Table 6.10). Thiel (1990) ascribes ceramic and aceramic portions for similar levels, denoted by the addition of ‘a’ to the aceramic portions (e.g. I4a, I6a, I7a) of the trench. Bones of varying preservation states are found within these levels, which appear to indicate post-depositional disturbance. As described in Chapter 3, I question the separation of finds and levels based on certain grounds and suggest that the well-defined aceramic levels are only those below Layer 7a (i.e., those that are not divided into non-ceramic and aceramic portions).

Only one other Luzon site has published records for the presence of macaque and this is Pintu Rockshelter (Mudar 1997). Similar to Minori and Musang Caves, the macaque is only identified in pottery-bearing levels. Mudar did not comment that the macaque may have been translocated. In the same levels as the macaque, Mudar also identified remains of domestic carabao, *Bubalus bubalis*.

The appearance of macaques and civets in the archaeological record of Luzon coincides with the presence of introduced domesticates. The timing of domestic introductions also bears weight to understanding the nature of translocations. Nagsabaran site is the only site in the archipelago that provides data on the varied timing of domestic introductions. Domestic pig is the earliest known introduced species, directly dated to 4000 cal BP (Piper et al. 2009). In the Late Neolithic/Metal Age layers of the same site, domestic dog, carabao and cow also appear. The Metal Age layers are dated to *ca*. 2500 cal BP (Amano et al. 2013). The Nagsabaran data show that the domestic pig was introduced first and the domestic dog and bovids appear considerably later. It is notable that in Minori, Musang and Pintu sites, macaque and palm civet remains are found in the same layers where introduced domesticates have also been identified. It is not known though whether they were introduced at the same time as some of these domesticates due to uncertainties in stratigraphic associations. What is also notable from the data from Nagsabaran is the absence of macaque and civets, despite the excellent preservation in the site and the presence of other smaller vertebrates. The data are quite limited, but the single date of 1800 cal BP on the Minori macaque tooth raises the possibility that the translocated animals may have been introduced even later than other domesticates in this part of Luzon. This might potentially explain their absence in Nagsabaran site. Data and dating from other sites may clarify the timing of these introductions in the future. Initial data from on-going research in Munsayac Cave in southern Luzon show that macaque remains are also limited to pottery-bearing layers (Mijares pers. comm.).

Where are the introduced animals from? The molecular phylogeny for modern populations has implications not only for understanding the non-native status of these species, but also for the possible directionality of ancient introductions. Initial genetic evidence for domestic pigs shows an instance of a possible north-to-south Taiwan connection. Older/traditional stocks of black domestic pigs (locally called 'native' pigs) in the Cordillera region of Luzon have genetic affinities with the Lanyu domestic pigs of Taiwan, indicating that this haplotype was introduced to Luzon in the past (Herrera 2010). For macaques and palm civets, modern haplotypes in the Philippines group mainly with Borneo and other Sunda Shelf populations (Blancher et al. 2008, 2012; Liedigk et al. 2015; Veron et al. 2015). Borneo is the likely source of introduced populations, although the role of Palawan populations in the process of translocation remains unclear since the latter have not been sampled in the genetic studies.

Table 7. 3 Distribution of taxa (number of identified specimens) and pottery (total number of fragments) per level (depth in cm from site datum) in Squares 37 and 27 of Minori Cave. Records of depth are all negative values. Dashed lines indicate the last occurrence of pottery. In Square 37 of Chamber A, the last occurrence of pottery is recorded at -241 cm. For Square 27 of Chamber D, inventory records are unavailable, but logbook records indicate that the last occurrence of pottery is at -112 cm. Ground surface for Square 37 is at 213-219 cm below datum, while that for Square 27 is not indicated in the records.

Chamber A Square 37

Depth	*Rusa*	*Sus*	Large mammal	Murid	*Macaca*	*Canis*	Pottery
surface to 220	5	3	3		6		30
221-230	27	13	29		8	1	241
231-241	9	3	4				25
242-250	9	3	16				
251-260	25	2	30	2			
261-270	31	3	18				
271-280	19	3	18				
281-290	15		7				
291-300	4	2					
301-310	1	1					
311-320	5		2				
321-330	7		1				
331-340	3	1					
341-350							
351-360	1						
361-390							
391-400			1				
401-450		1	2				

Chamber D Square 27

Depth	*Rusa*	*Sus*	Large mammal	Murid	*Macaca*	*Canis*	Pottery
surface to 80		1	10		1		inventory records not available, last record at -112 cm
81-90	27	41	222	2	1	2	
91-100	13	23	144	8	2		
101-112	6	11	81	4			
113-120	3	4	50	\			
121-130	24	11	139	7			
131-140	21	8	134	6			
141-150	15	2	68	8			
151-160	14	3	48	10			
161-170	9	2	16	7			
171-180	3		6	4			
181-190			2				
191-200			2				

Table 7.18 Distribution of taxa and pottery (depth in cm below site datum) across all squares in Minori Cave. Stratigraphic data were sourced from the NMP logbook (Log) and inventory (Inv) records of the 1981-83 excavations of Minori Cave. Records of depth are all negative values. ^ = occurrence based on excavation records, * = occurrence based on NISP of selected taxa identified by the author, \ = absent, ~ = approximate depth, ? = no data available. Occurrence records for *Macaca* show the elevation ranges with NISP in brackets. Deepest remains refer to artefacts recorded in the trench and maximum depth refers to the lowest depth reached in each excavation unit.

	Chamber A Squares					
Taxon/Entry	37	7	32	30	50	4
data source	Log, Inv	Log, Inv	Log	Log, Inv	Log	Log
local datum point	188	60	157	160	202	60
Macaca	219-229 (14)	92-100 (4)	185-194 (2)	196-204 (5)	248-251 (2)	92 (1)
Canis	221	\	\	\	\	\
Paradoxurus	\	86	195	\	\	\
last occurrence of pottery	241	193	215	213	?	110
deepest bone recorded^	449^	202*	250*	270*	251*	178*
deepest remains	449	202	255	315	252	?
maximum depth	~459	~196	397	~350	?	?
	Chamber D Squares					
Taxon/Entry	27	44	58	57	40	50
data source	Log	Log	Log	Log	Log	Log
local datum point	40	101	148	130	65	110
Macaca	80-94 (4)	149 (1)	193-197 (7)	186-190 (2)	126-129 (2)	146-162 (6)
Canis	82, 88	\	\	\	\	\
Paradoxurus	\	\	\	\	\	\
last occurrence of pottery	112	?	239	~190	158	below 173
deepest bone recorded^	212^	?	?	?	?	?
deepest remains	?	193	290	~240	212	?
maximum depth	?	?	410	256	248	344

7.4.3 Small Mammal Extinctions on Luzon

The Holocene extinction record of Luzon differs from that of Palawan and suggests that other factors may be in play. Luzon retains its Late Pleistocene large mammals up to the present, and only small mammals are recorded to have gone extinct during the Holocene. As mentioned above, a turnover for the Middle Pleistocene megafauna also occurred, but the timing of these changes is unknown. The latest possible occurrence of any member of the Middle Pleistocene megafauna is recorded in the MIS-3 layers of Callao Cave in the form of bovid remains that might be attributable to an endemic *Bubalus.*

The recognition of and evidence for translocated species that were previously cast as native taxa has significant implications for understanding the faunal assembly of the terrestrial vertebrate fauna of Luzon and for small mammal extinctions. The remarkable endemic small mammal fauna of Luzon appears to have evolved without native carnivores or primates, which could have acted as predators or competitors for arboreal and other forest niches. Currently, there are eleven non-native mammals that occur on Luzon (Heaney et al. 2016a). As discussed above, two of these – macaque and common palm civet – have archaeological evidence for their Late Holocene introduction. These two species, along with the Malay palm civet, have become successfully naturalised throughout the Philippines due to the fact that there are no other carnivores or primates known in Luzon. Macaques and civets occur both in disturbed and old-growth forests and across elevational gradients. The introduction of palm civets has specific implications for predation on small mammals. Although little is known about their local ecology in the Philippines, the palm civets are noted to prey on smaller vertebrates, including murids. A single scat record for the common palm civet on Mt. Isarog on Luzon showed the presence of large (*Phloeomys*) and small (*Apomys* and *Rattus*) murids (Heaney et al. 1999). It is suspected that the Malay civet is more carnivorous than the common palm civet and is the main mammalian predator of small mammals in lowland and montane forest (Heaney et al 2016a). There is no fossil record yet for the Malay civet on Luzon, but genetic evidence also suggests that it may have been a later introduction (Veron et al. 2014).The introduction of domestic dogs also has implications, since they can prey on small mammals and are also known to be used by humans to hunt forest animals.

The timing of small mammal extinctions on Luzon is currently not known, and hence it is also difficult to attribute causes for extinction. In Minori and Musang Caves, last occurrence records cannot be pinned down due to post-depositional disturbances in the Late Holocene layers. Based on the evidence, we can say that these taxa occur in pottery-bearing layers. Nonetheless, we can explore certain archaeological and ecological patterns on Luzon and in Southeast Asia to address the question of extinction.

On Luzon, biologists have observed the resiliency of the living endemic mammal fauna in the face of habitat disturbance and presence of non-native species (Heaney et al. 2016a; Rickart et al. 2011). Native murids are variably abundant in old growth forests and in disturbed habitats. They can also re-colonise areas that have been severely disturbed. This is true for ecological generalists (e.g., *Crocidura grayi, Bullimus luzonicus* and *Rattus everretti*) that tolerate disturbance well, but also for certain ecological specialists (e.g. *Chrotomys* spp.). In contrast, non-native small mammals (rats and shrews) are often only abundant in human settlements and deforested habitats. They become much less common in secondary forests and are not recorded in old-growth forests. The non-natives are in fact markers of habitat disturbance, as these are the places where they thrive. Certain native murids (particularly the New Endemic rodents) appear to compete well with non-natives in disturbed habitats. Contrastingly, the non-natives are unable to successfully invade secondary and old growth forests where there are established native murid communities (Rickart et al. 2007).

With Late Holocene extinction records of three lowland small mammals, it appears that this overall picture of resiliency needs to be re-assessed. The three species in question – *Carpomys* sp., *Crateromys* sp. and *Batomys* sp. – belong to the 'Old Endemic' cloud rat clade. The Old Endemics are recognized as competitively superior to the New Endemics in natural habitats, but it is the latter that fare better in disturbed or anthropogenic habitats (Heaney et al. 2016a; Rickart et al. 2011). The living members of *Carpomys, Crateromys* and *Batomys* on Luzon are ecological specialists presently restricted to montane habitats. In terms of reproduction, cloud rats are *K*-selected species that reportedly give birth to only one or two young each year (Heaney et al 2016a). It is very likely that the extinct fossil taxa were also slow-breeding species, and this would have contributed to their vulnerability. Their disappearance indicates that there were vulnerable native taxa that became recently extinct in the Late Holocene, and what appear to remain among the extant community are the more resilient taxa.

This phenomenon – whereby susceptible species have long disappeared in places of high human population density leaving a fauna consisting of resilient species – has been attributed to the effects of an extinction filter (Balmford 1996). In an examination of the Holocene extinction record, Turvey and Fritz (2011) have observed that their global data patterns support this human extinction filter hypothesis. This scenario is also supported by evidence for the widespread disappearance of large mammal populations from regions of high human population density (Cardillo et al. 2005). On Luzon, the recorded extinct taxa are all lowland species and human activity appear to be most concentrated in the lowlands. Many other Luzon mammals are either montane or elevational generalists (i.e. occurring across elevational gradients), including the native pig and deer (Heaney 2001; Heaney et al 2016a). This is one possible factor for their observed persistence up to the present day.

There are several classes of anthropogenic activities that impact local faunas. In this discussion, I focus on the introduction of non-native taxa since archaeological evidence is now available for this ecological process. On Luzon, the disappearance of certain small mammals appears to coincide with the appearance of translocated non-natives. I propose that there is a previously unrecognised palaeohistoric human extinction filter on Luzon. One component of this filter relates to predation and competition brought about by human-introduced taxa on Luzon in the last few thousand years. This is an ecological event on Luzon that can be contrasted to the Palawan case. Whereas macaques and civets are introduced taxa on Luzon, these taxa appear to be native to Palawan on the basis of current zooarchaeological evidence. The possible impacts of invasive predators and competitors have been documented in various Pacific islands (e.g., Pregill and Steadman 2009; Steadman 2006; Towns and Daugherty 1994). Among the invasives, rats and carnivores are the major culprits. The Pacific rat (*Rattus exulans)* caused the extinction of numerous bird and invertebrate taxa across east Polynesian islands (Liebherr and Porch 2015; Steadman 2006). Introduced rats are also implicated in the decline of the New Zealand herpetofauna (Towns and Daugherty 1994). Dogs and rats are also linked to the extinction of the moas of New Zealand (Worthy and Holdaway 2002).

Elsewhere in Wallacea, extinction records of small mammals have also come to light in sites from Flores, Timor, Sumba and Alor Islands. On Flores, the Liang Bua sequence documents the presence of at least six endemic murid species from five genera (Locatelli et al. 2012; H. J. Meijer et al. 2010; Musser 1981; G. D. van den Bergh et al. 2009). Two species, *Papagomys theodorverhoeveni* and *Spelaeomys florensis*, went extinct late during the Holocene. Across the Liang Bua sequence, a distinct drop in abundance of giant rats occurs in two levels that range in age from 4180 to 3620 BP (Locatelli et al. 2012). Within these levels, introduced species are identified: *Rattus exulans, Hystrix javanica, Macaca fascicularis, Paradoxurus hermaphroditus,* and *Sus scrofa* appear in the sequence*.* Prior to the introduction of these mammals on Flores, the giant rats were the largest Holocene mammals on the island, since the endemic stegodon is reported to have gone extinct in the Late Pleistocene.

On Timor, Aplin and Helgen (2010) describe two extinct giant rats belonging to the genus *Coryphomys* that are found in various excavated sites across Timor. An additional eight undescribed murid taxa also went extinct on the island (Turvey 2009). These murid remains are said to co-occur with Neolithic artifacts, bones of animal domesticates, and bones of commensal murines (*Rattus exulans* and *R. rattus*). On Sumba Island, two extinct giant murids have also been identified in Holocene sequences. These are *Milimonggamys juliae* and *Raksasamys tikusbesar,* which are both described as novel genera and species known only from Sumba (Turvey et al. 2017). Lastly, on Alor Island, an extinct giant murid, *Alormys aplini*, is recorded from the LGM and Holocene levels of Tron Bon Lei rockshelter and Makpan Cave (Hawkins et al. 2018; Julien Louys et al. 2018b). An unusually early record of domestic dog is also presented in Tron Bone Lei site, dated at *ca.* 8000 BP. Remains of a viverrid are also reported in levels dated from 3600–3200 BP. It is hypothesized that the extinction of the large murids on Timor, Sumba and Alor Islands was brought about by increased aridity in the late Holocene and the introduction of metal tools that may have accelerated deforestation (Louys et al. 2015). The period of the earliest Neolithic introduction is said to coincide with a drier climate around the Indian Ocean (Locatelli et al. 2015).

On the Philippine island of Ilin, fossil records of an endemic cloud rat, *Crateromys paulus*, were recently identified from two rockshelters (Reyes et al. 2017). The Ilin cloud rat was only known from a single specimen reported in 1953 and subsequently described by Musser and Gordon (1981) as a distinct species. Ilin Island would have been connected to the larger island of Mindoro during times of lower sea levels, as the water depth between the two islands is down to 24 meters only. The archaeological record confirms the natural presence of the cloud rat on Ilin, with numerous fossils derived from layers dating from 11,000 to 500 cal BP. The cloud rat is suspected to have become recently extinct (Pritchard 1989).

Direct predation, introduction of exotic species and habitat transformation are the recognized major drivers of extinction in island ecosystems during the Holocene (Wood et al. 2017). For the Lesser Sunda Islands, habitat transformation through deforestation is the hypothesized filter for human-induced extinctions of small mammals (Louys et al. 2015). In the case of Philippine cloud rats, available evidence for human hunting in the archaeological record is relatively limited. In Minori and Musang Caves, the archaeological context of large murids possibly suggests that they were incorporated in the cave assemblages as human prey. However, they are comparatively rare in Holocene sequences. Hence, evidence for intensive hunting of cloud rats is so far lacking. Across several sites, native deer and pigs are consistently the leading target prey, and these taxa are still extant. This contrasts with certain Wallacean islands in the Lesser Sundas, where giant rats were the largest native mammals recorded in the Holocene. Consequently, these would have also been the largest mammal prey that humans would have encountered on these islands.

In terms of habitat transformation and habitat loss, unequivocal evidence for large-scale anthropogenic forest disturbance is yet to be demonstrated for the Neolithic or Metal periods of Luzon (from *ca.* 4000 BP). Historical sources indicate that prior to European (Spanish) colonization in the 16th century, the Philippines retained about 90% of its forest cover (Bankoff 2007). Two Holocene palynological records are available for Luzon (See Chapter 2). The 7000-year record from Paoay Lake in northwestern Luzon indicates pine-related disturbance in sub-montane forests at *ca.* 5000 BP (Stevenson et al. 2010). This record is westward of the Central Cordillera and does not directly reflect changes in the Sierra Madre or Cagayan Valley where the study sites of the thesis are located. Charcoal is abundant throughout the Paoay record, but it spikes during this disturbance at around 6500-5000 BP. The other palynological record comes from Laguna de Bay, a lake in the southwest section of the island (Ward and Bulalacao 1999). The record indicates forest decline at around 5000 BP, which parallels with the Paoay record. The results from both studies are interpreted as climate-driven changes, possibly during a period of higher temperatures and lower rainfall in the mid-Holocene. For the Paoay record, it is suggested that forests appear to have slowly recovered in the succeeding 3000 years. It is of interest to note, though, that forest recovery is not observed in the Laguna de Bay record; instead, grass and charcoal concentrations increase after 2500 BP. There is no palynological evidence from the Cagayan region, but increased human presence and activity in the lowlands are evidenced from several Neolithic shell midden sites of the valley from *ca.* 4000 BP (Hung 2005; Hung et al. 2011; Mijares 2005; Mijares and Lewis 2009). In Nagsabaran site, intensified settlement is further observed in the Late Neolithic occupation layers (*ca.* 2500 BP), with more than 60 postholes and several human burials (Amano et al. 2013). This increase in human population density in the Cagayan Valley is a potential extrinsic variable that affected lowland small mammal populations.

From the archaeological record of Luzon, it is still unclear whether direct predation and habitat loss may have directly diminished lowland cloud rat populations. These are factors that need to be explored in future studies. The available evidence points to the possible impact of translocated macaques and palm civets, which potentially acted as predators and habitat competitors for naïve, slow-breeding and arboreal cloud rats. The introduction of invasive rats and shrews also need to be studied and stratified remains from Callao Cave may soon provide fossil data on these introduced small mammals (Heaney pers. comm.).

7.5 Conclusion

The faunal records described and assembled here provide the first biostratigraphic sequences for the Philippines. These sequences supply the baseline means by which we can assess faunal changes through time in the vertebrate fossil record of the archipelago. The changes observed primarily come in the form of extinctions of native taxa without replacement (*vis a vis* faunal turnover with replacement) and human-facilitated introduction of invasive species. Furthermore, the evidence presented here provides the first archaeological substantiation for the introduction of invasive taxa into the Philippines. On the basis of current evidence from Late Holocene sites on Luzon, introduced taxa are not recorded before the presence of pottery in archaeological sequences. This indicates that macaques and palm civets were introduced in Luzon not earlier than the Neolithic. Direct dating on macaque teeth from Minori cave provides a t*erminus ante quem* for its introduction at 1827–1706 cal BP. The archaeofaunal evidence for translocation is important, since for a long time, biologists studying the Philippine fauna have categorized the macaque and palm civets occurring in the oceanic Philippines as native taxa. Substantiation of translocation (i.e. which species are native and which are non-native) is also important in understanding the evolution and modern assembly of Philippine faunal communities.

As has been shown in this chapter, the timing and trajectories of extinctions differ between the two faunal regions and among taxa. On Palawan, the last occurrence records of two extinct large mammals (tiger and *Rusa* deer) are in the Early Holocene. On the other hand, the hog deer (*Axis)* persists into the Late Holocene on Palawan but now only retains a relictual distribution in the small Calamianes Islands. On Luzon, lowland small mammal extinctions are identified in the Late Holocene. Early Holocene extinctions on Palawan were likely driven by island-wide environmental and climatic changes, possibly compounded by human predation. In the Late Holocene, palynological records on Luzon do not show indications of drastic climatic events that might have driven extinctions. Instead, it appears that a human extinction filter is in operation. As discussed above, the cloud rats appear to have evolved in the oceanic Philippines without native mammalian carnivores or arboreal primates, and this likely was an important factor in the evolutionary diversification of the Muridae. The introduction of non-native viverrids and macaques would have also initiated ecological interactions to which the native murids were naïve. As noted above, it is suspected that civets are the main mammalian predator of native small mammals on Luzon (Heaney et al. 2016a). Interactions between native small mammals, on the one hand, and viverrids and macaques, on the other hand, have not been given much attention by modern biologists especially since the latter were previously thought of as native inhabitants. The archaeological data presented suggests that the introduction of such invasive taxa possibly increased extinction risk for certain vulnerable native small mammals with *K*-selected life history strategies.

Chapter 8 Taphonomy and Subsistence in Philippine Faunal Records

8.1 Introduction

This chapter covers the taphonomic and human subsistence data for Pilanduk, Minori and Musang Caves. The chapter is divided into eight sections. The methods used in the taphonomic analyses are described in Section 8.2. The taphonomic analyses are presented sequentially for each assemblage (Sections 8.3 to 8.5). These analyses aim to draw out signatures of human behaviour and foraging practices as reflected in the archaeofaunal assemblages. A summary of taphonomic results is provided in Section 8.6. In Section 8.7, the three sites are compared with published zooarchaeological records in Luzon and Palawan in order to assess species representation and vertebrate subsistence data across time. Lastly, in Section 8.8, the taphonomic and subsistence data are contextualised within diachronic perspectives on indigenous ecological knowledge systems and tropical foraging histories.

8.2 Methods for Vertebrate Taphonomy

The taphonomic workflow (Figure 8.1) employed here follows a combination of the 'multivariate taphonomy' framework by Bar-Oz and Munro (2004) and the social zooarchaeology framework by Orton (2012). For each bone assemblage, a descriptive summary of taphonomic observations is provided, with a particular focus on bone surface modifications. This forms Stage 1, or the descriptive stage, as suggested by Bar-Oz and Munro (2004). The bone modifications are broadly categorised into two: abiotic processes and biotic processes. Examples of abiotic processes include weathering, water action, and mineral staining. Biotic processes include carnivore action, rodent gnawing and various imprints of human behaviour.

The zooarchaeological counting units (NISP, MNE, MAU) used here document frequencies of skeletal elements found in the assemblages (see Chapter 3). These frequencies provide information on two basic taphonomic questions: differential prey transport and differential survivorship of bone. Before drawing out any interpretations on potential transport decisions made by human (or other) agents, an assessment of the role of bone density-dependent attrition must be conducted. This form of attrition pertains to the degradation and loss of skeletal parts due to their structural density (Lyman 1994: 252). This analysis forms Stage 1 in Orton's (2012) framework and Stage 2.2 of the analytical phase in Bar-Oz and Munro (2004). To this end, the method used here involves analysing the correlation of bone volume density values with skeletal element survivorship. Estimation of bone mineral density (BMD) has been conducted for certain taxa using photon densitometry (PD) (e.g. Lyman 1984) or quantitative computed tomography (CT) (Lam et al. 1999). CT scanning is currently recognised as the most accurate estimator of BMD since it can represent the actual external shape of a skeletal element and the internal shape of voids through composite three-dimensional imaging (Lam and Pearson 2004, 2005; Lam et al. 1999). In this study, the taxon of interest is *Rusa* (sambar) deer. Ideally, deer taxa from lower latitudes or tropical environments should be used as local proxies due to the differing ecologies of lower- and higher- latitude species. However, BMD studies on Asian cervids or tropical cervids have not yet been conducted. The survivorship analysis thus opts for data available for confamilial taxa. The proxy primarily used here is BMD data for *Rangifer* from Lam et al. (1999). Data for the North American deer *Odocoileus* are also available from Lyman (1984); however, this PD study assumed a rectangular cross section for bone scan sites and consequently has less accuracy. The scan sites used from Lam et al. (1999) are the same as those from Lyman (1984). The assumption behind this type of analysis is that when skeletal part frequencies strongly correlate with BMD, the composition of the assemblage is influenced by density-mediated destruction. Bar-Oz and Munro (2004) advise that when such a correlation is found, further detailed taphonomic analysis should be carried out to determine the causes of attrition.

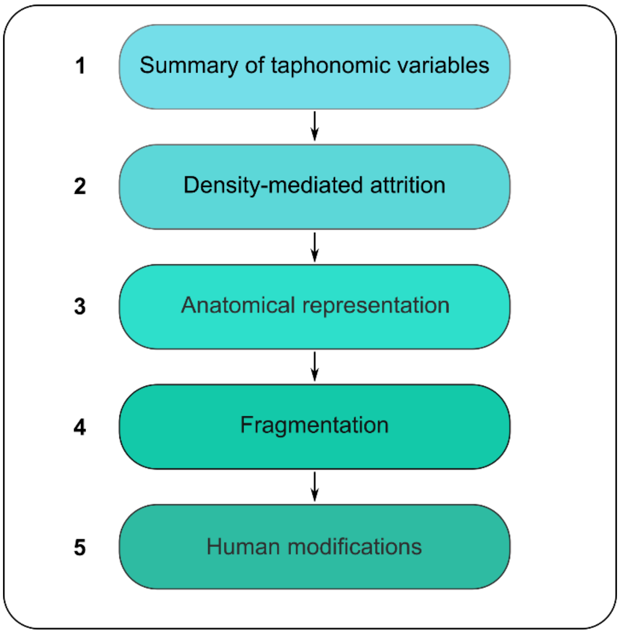


Figure 8.1 Taphonomic workflow showing the sequential stages of the analysis.

Once the variable of density-mediated attrition has been assessed, the analysis moves to the next stage, which involves anatomical representation. This is the suggested sequence in Bar-Oz and Munro (2004), falling under Stage 2.3, but it forms Stage 5 in Orton's framework. Stage 2 in Orton's framework involves the analysis of peri-depositional damage. However, in the taphonomic workflow implemented here, this is already covered under the summary of taphonomic variables. Following Bar-Oz and Munro (2004), I find that there is logical continuity in assessing skeletal part frequencies once density-mediated attrition is assessed per taxon. The analysis of skeletal part frequencies across a site is one of the standard ways to investigate human strategies of animal food resource use. Anatomical frequencies were assessed using NISP, MNE, MAU and %MAU. NISP and MNE values are not corrected for symmetry or for how often an element occurs in the skeleton. To account for these factors, MAU and %MAU are useful to show which body parts are present or absent in an assemblage.

The next stage of analysis involves breakage and fragmentation patterns. This forms Stage 3 in Orton's (2012) framework and falls under Stage 2.3 in the analytical phase proposed by Bar-Oz and Munro (2004). Fragment size class was recorded for each specimen, which were typically done in 10-mm increments (i.e. < 20 mm, 20-30 mm, 30-40 mm, etc.). The mode of fragmentation was documented primarily using the Freshness Fracture Index devised by Outram (2001, 2002) for long bone fragments. This index combines methods from two sources. The first is bone fracture criteria initially developed by (Johnson 1985). The second involves criteria developed by Villa and Mahieu (1991) to look at fracture angle, fracture outline and fracture edge texture. The FFI uses a scoring system of 0 to 2 for each of the three fracture criteria: angle, texture and outline. Each long bone is scored against these set of criteria. The combination of scores for each criterion can give a total score ranging from 0 to 6. Aggregated scores from 0 to 2 would suggest a pattern of fresh breakage while scores from 5 to 6 predominantly imply dry breakage. The method allows for taphonomic data to be generated from indeterminate fragments and allows for the consideration of what otherwise may be analytically absent specimens.

To further document patterns related to anatomical representation and fragmentation, analysis of animal body-part utility indices is also conducted. This draws from the pioneering work of Binford (1978) of developing indices based on measurements of food tissues (meat, marrow, fat and grease) associated with skeletal elements of caribou and sheep. These indices provide models about how different subsistence strategies and transport decisions would be reflected in the frequencies of skeletal parts. Among other authors, Metcalfe and Jones (1988) scrutinized the methodology of deriving utility indices, and it is their Food Utility Index (FUI) for caribou that is used as a proxy in this research.

The last stage in the analysis replicates Stage 4 in Orton's framework, which is the analysis of visible human modifications. These include modifications involved in butchery, cooking, and discard. Zooarchaeological investigations of anthropic modifications typically focus on postmortem processes of butchery. Lyman (1987: 252) defines butchery as "the reduction and modification of an animal carcass into consumable parts". Under this definition, Lyman also clarifies that 'consumable' refers to all forms of carcass products and that butchery incorporates a series of activities directed towards the extraction of all these consumable products. Butchery marks recorded include cutmarks, chop marks and impact scars, whenever applicable. Cutmark identification follows criteria set by Dominguez-Rodrigo et al. 2009, Fernandez-Jalvo and Andrews (2016), Olsen and Shipman (1988) and Shipman and Rose (1983).

Heat alteration of bones is another common human modification observed in assemblages. Burning of bones changes their colour in gradations, from shades of brown, to black, grey and white. Due to the ambiguity in identifying burnt brown-coloured bones, recording of burnt bones was limited to bones that were coloured black, grey and white. These correspond to carbonised and calcined bones. Recording of colour changes on bone due to heat alteration follows recommendations by Fernández-Jalvo and Andrews (2016), Schmidt and Uhlig (2012) and Stiner et al. (1995). An estimate of the percentage of bone surface burning (i.e. area of burnt bone surface per specimen) was also recorded in 25% intervals.

8.3 Pilanduk Cave Taphonomy

The taphonomic analysis for Pilanduk Cave focuses on the Trench 3 sequence from the 2016 excavations. Taphonomic data are aggregated and presented using the four major archaeological contexts in the site – contexts 111, 112, 117 and 118 (see Table 4.5). These contexts represent Layers II to IV. In terms of age, two charcoal samples from context 112 yielded dates of 20,468-20,034 and 22,004-21,540 cal BP (-46 and -52 cm from LDP, respectively). As discussed in Chapter 4, the stratigraphic compositions of 111 and 112 are very similar, with both consisting of dark greyish silt, extensive inclusions of ash, burnt bones and chert flakes. These two contexts comprise Layer II of the site. Context 111 represents the upper portion of Layer II, which contains intrusive earthenware pottery, while context 112 represents the lower portion of the layer. In context 117, one charcoal sample at the base of the layer yielded a ^{14}C age determination of 24,995-24,301 cal BP (-90 cm below LDP). However, in terms of its sediment and artefact composition, context 117 is actually very similar to context 111 and context 112. Because the sample for context 117 was at the base of the layer, this date may likely represent an age for context 118 (Layer IV). The age determination for the context 117 sample is actually an inversion, as its range slightly exceeds the dates from the underlying context 118; however, the ages do overlap. Three dates are available for context 118 and were taken at a depth of -98 to -113 cm below LDP: 23,785-23,140 cal BP, 23,875-23,295 cal BP and 24,440-23,933 cal BP. Context 118 has a markedly different composition from contexts 111, 112 and 117, with much less evidence for burning based on the sediments and the faunal remains, as well as fewer lithic tools.

Pilanduk Cave presents a highly fragmented but relatively well-preserved LGM assemblage in terms of anthropic bone surface modifications. As stated in Chapter 5, a total of 7826 bone fragments were analysed from the 2016 excavation. Eighteen percent of the assemblage were identifiable to taxon (family or lower). Nearly half of the indeterminate fragments (2258 out of 4583 fragments) consisted of large mammal long bone shaft fragments. The rest consisted of indeterminate cortical and spongy bone fragments that were mostly less than 20mm in size. Although not identifiable to actual element, the long bone fragments still yielded taphonomic information regarding butchery and fracturing patterns. In the succeeding sections for all three cave sites, NISP (number of identified specimens) counts are used for counts of bone fragments that were identified to taxon and/or element, whereas TNF (total number of fragments) is the abbreviation used for counts that include both indeterminate and identified fragments.

8.2.1 Abiotic Processes

Bone surface modifications caused by abiotic agents appear to have relatively reduced effects on the bone assemblage of Pilanduk Cave (Table 8.1). Only 4.6% of the total number of bone fragments displayed signs of weathering. Among weathered fragments, 94% of these were recorded with fine lines and spalling at Stage 1 (following the scheme of Behrensmeyer 1978). This suggests that for the LGM layers, there was relatively minimal sub-aerial exposure before burial of the bones in the cave.

Table 8.1 Summary of taphonomic data for Pilanduk Cave, expressed as percentages of TNF (total number of fragments) per layer. % $CaCO_3$ pertains to carbonate concretions and % Mn pertains to manganese oxide staining. % Helical refers to bone fragments with helical fractures and is computed based on total number of long bone fragments. See taphonomic data in Appendix C.

Context	TNF	% Weathered	% Abrasion	% CaCO3	% Mn	% Gnawed	% Burnt	% Cutmarks	% Helical
surface	261	0	0	46.0	0.8	0	13.4	<0.5	46.2
111	2174	12.1	8.7	<0.5	11.1	<0.5	45.8	0.7	67.4
112	2322	3.4	2.3	<0.5	4.8	<0.5	39.9	0.6	59.5
117	2561	0.5	0.1	<0.5	0.9	<0.5	46.2	1.5	17.0
118	506	1.2	0	0	0.4	<0.5	27.9	0	8.1

There is also minimal presence of carbonate concretions on the bones across the Trench 3 sequence. In comparison to other trenches in the cave site, there are also minimal concretions found in Trench 4 remains and from the 1979 excavations. These trenches are located in the centre and south portion of the cave. One section of the cave site does present bones with heavy concretions – the northern portion of the cave platform where a large speleothem pillar is located and surrounded by a flowstone. This is the area were the complete tiger metacarpal was found among redeposited surface remains. Manganese oxide staining, in the form of black coloration, is also observed in a small percentage of the remains.

The effects of sub-aerial weathering and mechanical abrasion across the Trench 3 sequence are relatively minimal, but amongst the layers, they are most prevalent in context 111 (Layer II). This is likely because for a long period of time after Pleistocene occupations, this level would have been the topmost layer of the cave platform. As described in Chapter 4, Layer I of the site constitutes a recently deposited level of sediment comprised of treasure hunters' backfill interspersed with remains from Metal Period burial activities.

8.2.2 Biotic Processes

The effects of biological agents, particularly humans, have left extensive evidence for bone surface modifications. These are mainly evident in the effects of burning and fragmentation patterns. The predominant surface colour of bones from these levels is medium to dark reddish brown, which is a possible indication of scorching. However, due to the ambiguity in recording heat-treated brown-coloured bones, this feature was not quantitatively recorded. Instead, evidence for charring and calcining was tallied. Burning is a significant process in the Pilanduk assemblage, especially in contexts 111, 112 and 117 (Layers II and III). Carbonized and calcined bones constitute 42% of the entire Pilanduk Cave assemblage. This taphonomic alteration is further discussed in Section 8.2.6. on human modifications.

There is very little evidence for gnawing in the Pilanduk Cave assemblage. Only 13 bone fragments across the sequence had signs of gnawing and carnivore tooth marks, accounting for only 0.16% of the analysed assemblage. Definitions for tooth marks (pits, punctures and furrowing) follow Binford (1981), Delaney Rivera et al. (2009), Dominguez-Rodrigo and Piqueras (2003), Haynes (1983), and Sala and Arsuaga (2018). Pits are tooth marks described as circular to oval depressions resembling the shape of a tooth crown or cusp. When a tooth mark penetrates the cortical bone, this is categorised as a puncture. Furrows are broad gouges that result from gnawing action and involves the extraction or absence of portions of the cancellous bone tissue.

Figure 8.2 Deer bones from Pilanduk Cave that show evidence for large carnivore gnawing: Pil-5371 proximal femur in anterior (a) and posterior (b) views, with a canine pit on the femoral neck; Pil-5823 proximal tibia in anterior (c) and posterior (d) views, with a canine pit on the antero-lateral end; and Pil-5392 metatarsal shaft in anterior (e) and posterior (f) views.

In the Pilanduk assemblage, of interest are three deer bone fragments from context 111, 112 and 117 that show distinct evidence of tooth marks and furrowing (Figure 8.2). A proximal femur fragment (Pil-5371; Figure 8.2 a and b) bears the following marks: a) pit on the anterior portion below the greater trochanter; b) furrowing on the proximal border resulting in the removal of the greater trochanter; c) furrowing on the posterior side below the neck; d) furrowing and gnawing damage on the distal-most end of the fragment that possibly contributed to the breakage and eventual detachment of the proximal end from the rest of the femoral shaft. A proximal tibia fragment (Pil-5823; Figure 8.2 c and d) bears gnawing damage and furrowing across the anterior portion of the epiphysis, as well as a pit on the proximo-lateral border of the epiphysis. A metatarsal fragment (Pil-5392, Figure 8.2 e and f) bears heavy gnawing damage that appears to have resulted in the removal of the proximal and distal ends and leaving only the shaft cylinder.

In Haynes' (1983: 169-170) neo-taphonomic description of large felid (lion, tiger and jaguar) gnawing, the main damage produced by large cats on the femur consists of the biting off of the greater trochanter and undercut biting of the femoral head. On the tibia, the proximal end or tibial crest is occasionally furrowed perpendicular to the element's long axis and the crest may also be bitten off. These descriptions are corroborated by the study of Parkinson et al. (2015) on tiger feeding and gnawing, where the greater trochanter of the femur is prone to destruction and the proximal end of the tibia is typically not well preserved. These descriptions are consistent with the gnawing damage found on the Pilanduk deer femur and tibia fragments described above. In certain cases, tooth mark dimensions in certain bone regions can also differentiate the taxon size of the carnivore, particularly for marks on long bone epiphyses (Delaney Rivera et al. 2009; Dominguez-Rodrigo and Piqueras 2003). At the time of secondary taphonomic analysis, only the femur fragment (Pil-5371) was available for measurement, although it was originally observed that the size of the tooth pit on the tibial fragment (Pil-5823) was of a similar size (Table 8.2). The length (major axis) of the pit on the femur fragment is 6.25 mm, while its breadth (minor axis) is 4.95 mm. Dominguez-Rodrigo and Piqueras (2003:1389-1390) conclude that pit lengths on epiphyseal sections of bone can be used to reliably establish three tooth-marking groups:

1.) marks under 4 mm are observed in all carnivores but lions,
2.) marks between 4-6 mm are made by middle-sized and large-sized carnivores, and
3.) marks above 6 mm are made by large carnivores.

For pantherines, comparative measurements for epiphyseal tooth pits are available only for lions, which is in the same taxon size range as the tiger (Table 8.2; Delaney Rivera et al. 2009: Table 3; Dominguez-Rodrigo and Piqueras 2003: Table 1). The tooth pit length measurement on the Pilanduk deer femur slightly exceeds 6 mm, suggesting that it was potentially made by a large carnivore. On Palawan, the only candidate for a large carnivore is the tiger. A canid has been recorded in the Terminal Pleistocene levels of Ille Cave, which would represent a middle-sized carnivore. However, this species was not identified in the Pilanduk assemblage and hence the LGM presence of a canid on Palawan cannot be confirmed. The only carnivore identified in Pilanduk is the tiger. The gnawing modifications and tooth pit dimensions on the femur and tibia specimens described above suggest that the gnawing damage was made by a large carnivore in the size range of the tiger. The gnawing damage displayed on the deer metatarsal is more typical of canid gnawing rather than large felid modifications (Parkinson et al. 2015). However, given the small sample and the absence of canid fossils in the LGM assemblage, canid gnawing cannot be confirmed.

Table 8.2 Measurements (in mm) for epiphyseal tooth pit dimensions for femur specimen (Pil-5371) and comparative pantherine and canid data from Dominguez-Rodrigo and Piqueras 2003 (Source A) and Delaney Rivera et al. 2009 (Source B). N = number of specimens measured, s.d. = standard deviation.

Element			Major axis (length)		Minor axis (breadth)	
proximal femur epiphysis		Pil-5371	6.25		4.95	
Comparative metrical data for tooth pits on epiphyses						
Taxon	Source	N	Major axis		Minor axis	
			mean	s.d.	mean	s.d.
Panthera leo	A	13	6.5	1.08	4.32	0.86
	B	5	4.94	1.71	3.95	1.58
Canis familiaris	A	23	4.93	2.02	3.34	1.71
Canis spp. *(jackals)*	A	40	3.5	0.7	3.55	0.56
Canis latrans	B	10	2.76	1.18	1.86	0.905

These fragments have clear evidence for carnivore-induced bone modification, although most of the assemblage does not show further evidence for tooth marks or other carnivore gnawing damage. The scarcity of gnawing occurrence indicates that tigers were not significant bone accumulators in the cave and nor did they scavenge substantially over human refuse left in the cave. The latter may be partly due to the fact that bone refuse was burned *in situ* in the cave. Porcupines also do not appear to have contributed to the bone accumulation given the lack of evidence for rodent gnawing.

8.2.3 Bone Density and Attrition

Before proceeding to further analysis of anthropic modifications, evidence of density-mediated attrition must first be assessed. Values for %MAU (= % survivorship) are plotted against published bone mineral density values. This method is taxon-specific, and in the Pilanduk Cave assemblage, the method is applicable only to the sample size of cervids. In the absence of bone density data for Asian or tropical deer species, the data for *Rangifer* and *Odocoileus* are used as proxies in this study. Both species are confamilial and represent the best proxies compared to using artiodactyls from lower latitudes that are non-cervids. Class D bone mineral density values for *Rangifer* from Lam et al. (1999, 2004) represent the most precise measures for the Cervidae. The only other published density data for cervids available are from the American taxa *Odocoileus* as published by Lyman (1984). This is potentially more appropriate as a proxy since it is a cervid that lives in lower latitudes compared to the circumpolar *Rangifer*. However, because the published data for *Odocoileus* consist of class A density data that have less accurate estimation of cross-sectional shape of bones, the Class D values for *Rangifer* are deemed more precise. The correlation coefficient used in the analysis is the non-parametric rank-order Spearman's rho (r_S). The analysis for density-mediated attrition was conducted two ways: using all available scan sites and using maximum density scan sites only. The latter refers to the maximum bone mineral density value recorded for a particular MAU category (see Lyman 1994:257). The analysis was conducted per context and with 111, 112 and 17 aggregated as one stratigraphic unit ('combined' in Table 8.3). When using class D values for *Rangifer*, a correlation is not observed between survivorship and bone mineral density in contexts 111, 112 and when all contexts are combined (Figure 8.3). In context 117, a moderate correlation is observed between the two variables. When using Class A bone density data from *Odocoileus*, non-significant correlations are observed in contexts 111, 112 and 117. When using 'combined' data, a weak correlation is observed (Figure 8.3). Caution is advised, nonetheless, when using Class A density values as proxies (Lam et al. 2004). In the analysis using maximum density scan sites, non-significant correlations appear across all categories.

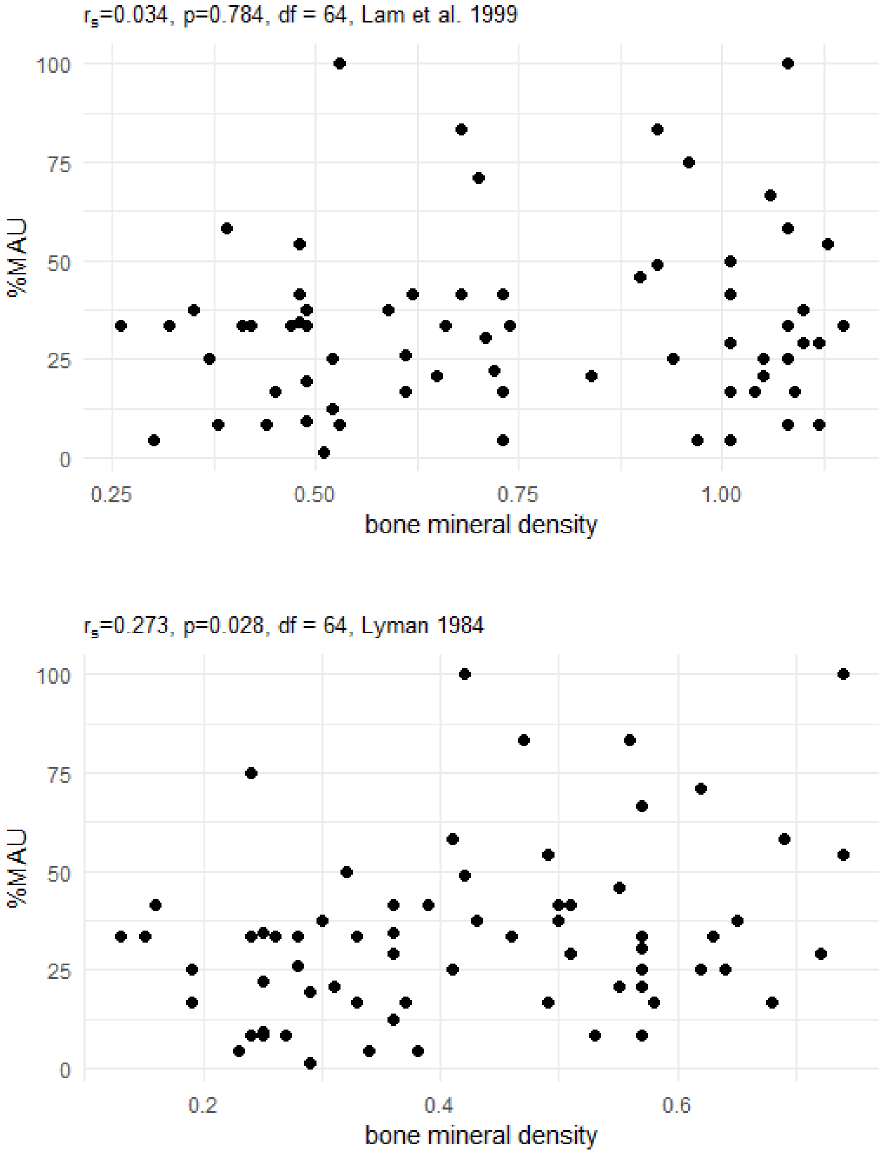


Figure 8.3 Bone survivorship (as %MAU) versus bone mineral density values for aggregated counts of cervid remains in Pilanduk Cave. The density values are derived from Class D data for *Rangifer* from Lam et al. (1999) (top) and Class A data for *Odocoileus* from Lyman (1984) (bottom). The correlation coefficient Spearman's rho (r_s) is shown with the p-value (p) and degrees of freedom (df). See Appendix D for data.

Table 8.3 Correlation coefficients (Spearman's rho, r_s) between published cervid bone density values (Lam et al. 1999 and Lyman 1984) and % survivorship (=%MAU) for cervids in Pilanduk cave. 'Combined' indicates aggregation of bone counts for contexts 111, 112 and 117. Analysis was conducted using all scan sites and using maximum density scan sites (see Lyman 1994: 257). See Appendix D for data.

context	all scan sites			
	Lam et al. 1999		Lyman 1984	
	r_s	p-value	r_s	p-value
111	-0.114	0.501	-0.017	0.923
112	0.018	0.906	0.137	0.354
117	0.474	0.022	0.457	0.282
combined	0.034	0.784	0.273	0.028

context	maximum density scan sites			
	Lam et al. 1999		Lyman 1984	
	r_s	p-value	r_s	p-value
111	0.080	0.795	-0.287	0.342
112	-0.022	0.934	0.181	0.473
117	-0.086	0.812	0.474	0.167
combined	-0.112	0.659	0.154	0.541

A note must be made regarding the taxonomic and analytical absence of elements such as vertebrae and ribs that are difficult to identify to taxon. This can possibly help to clarify the moderate correlation observed in context 117 (using Class D data from Lam et al. 1999) and in the 'combined' analysis (using Class A data from Lyman 1984). Across all levels, the % survivorship of low-density elements such as vertebrae and ribs is all relatively low due to the fact that such elements are difficult to identify to taxon, especially when fragmented. The MAU and %MAU values for such elements are actually underestimated. Because many of these specimens were not identifiable to taxon, these were not included in the bone density analysis. Density-mediated attrition is known to preferentially destroy these less dense, spongy axial elements. However, such elements are actually present in significant numbers, including in context 117. NISP counts are recorded for large mammal rib and vertebrae in contexts 111, 112 and 117 (see Table 8.5). Note that they are not recorded as cervids but are under the 'large mammal category'.

Overall, cervid skeletal abundance and survivorship are not significantly affected by density-mediated attrition in the whole stratigraphic unit, when using Class D deer data from *Rangifer* and when using maximum density scan sites. When broken down into contexts, density-mediated attrition is not significantly observed in contexts 111 and 112. In context 117, a moderate correlation is observed, although as will be shown in the next section, elements across the entire artiodactyl skeleton (including ribs and vertebrae) are also present in this context.

8.2.4 Anatomical Representation

As described in Chapters 5 and 7, cervids (n=1365) comprise the dominant taxon in Pilanduk Cave at 16% of total NISP. Wild pigs account for only 1% of the assemblage (n=91) and all other identified taxa account for less than 1%. Unidentified large mammal specimens account for 50% of the assemblage, and these remains are predominantly in the size range of the large cervid, *Rusa* sp. The succeeding taphonomic analyses will focus on the cervids and large mammal remains at the site.

Frequencies of cervid skeletal elements in contexts 111, 112 and 117 show that entire deer carcasses were brought into, processed, consumed and disposed of in the cave (Table 8.4, Figure 8.4). MNI counts show there are at least three individuals in context 111, seven individuals in context 112, five individuals in context 117 and at least two individuals in context 118. When 111, 112 and 117 are aggregated together, an MNI of 14 is recorded based on astragali counts. Appendicular elements appear to be well-represented (Figure 8.4), with forelimbs and hindlimbs equally represented in contexts 111, 112 and 117. Axial elements such as vertebrae and ribs appear to be underrepresented in the NISP and MNE counts for cervids in Table 8.4 and in Figure 8.4. However, these elements are actually well-represented in the large mammal counts for these three contexts, as shown in Table 8.5. Hence, these low-density, high meat-bearing elements are also present in the sequence.

Table 8.4 Cervid skeletal element representation by context (111, 112, 117, 118) in Pilanduk Cave. MNE, MAU and MNI are calculated for the whole element.

Element		111				112				117				118			
		NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI
antler		18	1	\	1	25	1	\	1	16	1		1	8	1	\	1
cranial		4			2	1			1	14			2	4			1
maxilla		2	1	0.5	1	1	1	0.5	1	2	2	1	2	5	2	1	2
mandible		7	3	1.5	3	11	9	4.5	5	16	7	3.5	4	1	1	0.5	1
vertebra	atlas					2	1	1	1	4	2		2	1	1		1
	axis	2	1	1	1	2	1	1	1	1	1	1	1				
	cervical	6	4	0.9	\	3	2			4	4						
	thoracic					2	2			4	4						
	lumbar	4	4	0.7	\	4	4			11	11						
innominate	ilium					3	2	1	1	3	2	1	2				
	ischium					1	1	0.5	1	1	1	0.5	1				
sacrum		2	2	2	2												
scapula	proximal									5	5	2.5	4	1	1	0.5	1
humerus	proximal	3				2				2							
	shaft		2	1	2	1	6	2.5	4	5	5	2.5	4		1	0.5	1
	distal	1				4				4				1			
radius	proximal	5				10				5				1			
	shaft	3	3	1.5	3	3	10	5	6	4	5	2	3		1	0.5	1
	distal	1				2				3							
ulna	proximal	1				11				3							
	shaft		2	1	2		11	5.5	6	2	3	1.5	2				
	distal	2								3							
metacarpal	proximal	5				7				5				1			
	shaft	1	5	2.5	3	1	7	3.5	4	5	5	2.5	3	1	2	1	2
	distal	1				7				1				1			

Table 8.4 continued.

Element		111				112				117				118			
		NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI	NISP	MNE	MAU	MNI
femur	proximal	2				8				10				5			
	shaft		3	1.5	3	2	5	2.5	5	4	10	2.5	5		3	1.5	2
	distal	3				1				4							
tibia	proximal					2				1							
	shaft	2	3	1.5	3	10	9	4.5	5	11	6	3	3	1	2	1	2
	distal	3				5				1				1			
metatarsal	proximal	4				4				4							
	shaft	6	5	2.5	3	5	4	2	3	14	4	2	2				
	distal	2															
metapodial	distal					7	4	\	\	8	3	\	\				
metapodial	shaft	1	1														
patella		2	2	1	2	2	2	1	2	1	1	0.5	1				
astragalus		6	5	2.5	3	10	10	5	7	0							
calcaneus		2	2	1	2	6	5	2.5	4	2	2	1	1				
cuboid		1	1	0.5	1	5	5	2	3	3	3	1.5	2	1	1	0.5	1
lunate		1	1	0.5	1	2	2	1	2	6	5	2.5	5				
magnum						2	2	1	1	3	3	1.5	2	1	1	0.5	1
scaphoid		2	2	1	2	5	5	2.5	3	3	3	1.5	2				
unciform										4	4	2	3				
phalanges	proximal	13	10	1.25	\	22	17	2.125	\	25	14	1.75		1	1	0.125	\
	intermediate	12	10	1.25	\	14	8	1	\	18	10	1.25		2	2	0.25	\
	distal	9	9	1.125	\	16	16	2	\	12	11	1.375		2	2	0.25	\

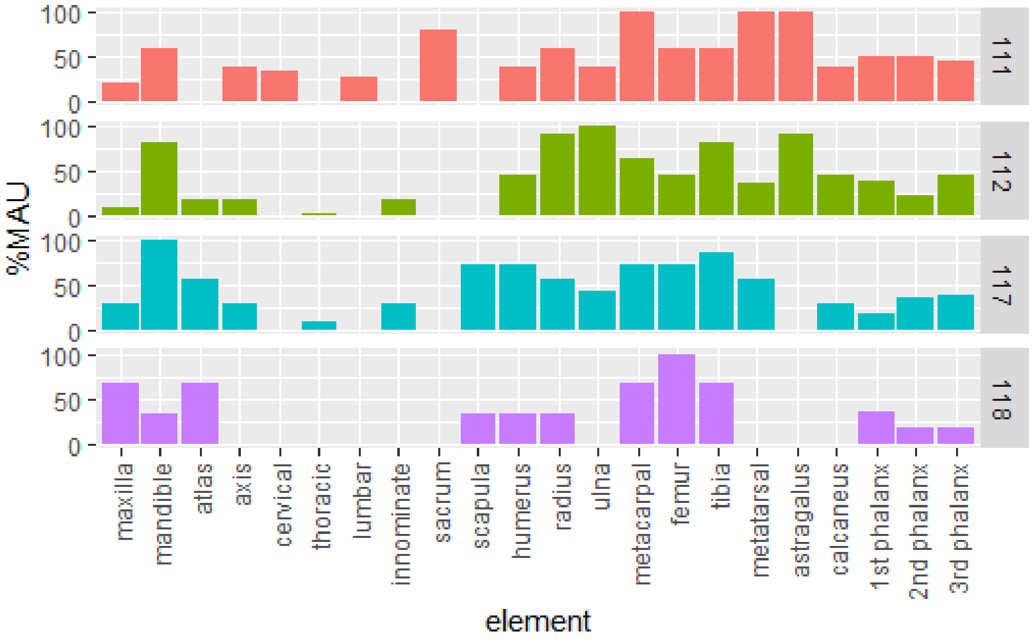


Figure 8.4 Skeletal element frequencies for cervids in Pilanduk Cave shown as %MAU for each context (111, 112, 117 and 118). See Table 8.4 and Appendix D for data.

Table 8.5 NISP counts for large mammal elements per context in Pilanduk Cave that are not identifiable to taxon.

Element	111	112	117	118	Total
cranial	41	11	69	7	128
maxilla			1		1
mandible	1		1		2
vertebra	117	187	245	72	621
rib	216	198	389	46	849
scapula		5	16	3	24
hum	3	2	3	2	10
radius	1	1	5		7
ulna				2	2
innominate		1	2		5
femur	4	7	2	1	14
tibia	2	1	1		4
diaphyses	563	583	979	133	2258
calcaneus	1	2			3
1st phalanx	1				1
3rd phalanx		1			1

To investigate selective transport of deer body parts, %MAU are compared against a Food Utility Index (FUI). This method was first developed by Binford (1978) to predict animal carcass transport decisions and subsequently refined by other authors (e.g. Metcalfe and Jones 1988). The FUI (also MGUI, or modified general utility index) is a combination of meat, marrow and grease indices. The analysis involves tallying counts per skeletal element portion against published FUI values per element for a particular taxon. The correlation between the two sets of values are then analysed, and a positive correlation potentially indicates transport decisions by human hunters. As a proxy for the Cervidae, FUI values produced by Metcalfe and Jones (1988) for caribou were used and correlation coefficients are shown in Table 8.6 (See Table 8.4 and Appendix E for data). There is presently no other cervid taxon available with published FUI data. Analysis of the two variables shows no significant correlation across contexts 111, 112 and 117. This indicates that differential transport of high-utility elements was not a significant factor in the bone accumulation across these levels.

Table 8.6 Correlation coefficients between published Food Utility Index values for caribou (Metcalfe and Jones 1988) and % survivorship (= %MAU) for cervids in Pilanduk cave. See Table 8.4 and Appendix E for data.

context	Spearman's rho	p-value	df
111	-0.3538	0.116	17
112	-0.1497	0.485	21
117	0.0358	0.871	21

8.2.5 Fracturing and Fragmentation

Patterns of bone fragmentation and fracturing provide insights into butchery processes in the site. Preservation of green breakage is evident across contexts 111, 112 and 117 based on unweathered, uneroded and sharp fracture edges of most long bone specimens (Figure 8.5). In contexts 111 and 112, a large percentage of helical (=spiral) fractures is observed on long bone fragments (Table 8.7). In context 111, 67% of long bone specimens show helical fractures, while 59% are observed for context 112. In context 117, only 17% of long bone fragments retained helical fractures. In the deepest cultural level, context 118, the presence of helical fractures is even more reduced at 8%. As described above, there is minimal evidence for carnivore gnawing. This suggests that the fresh fractures are more likely to be human-induced rather than due to carnivore ravaging. The fact that the bones are ubiquitously mixed with numerous chert flakes across contexts 111, 112 and 117 also implicates human action rather than other factors. Impact scars were also observed on many long bones, although these were unfortunately not consistently recorded during the analysis. Based on the minimal counts recorded, 2-3% of long bone fragments across contexts 111, 112 and 117 have impact scars. These are likely underestimations of actual occurrence of impact scars in these contexts. Fracture patterns and impact zones on the ends of long bones in Pilanduk Cave are very similar to those observed by Binford (1981) on bones that were derived from marrow-cracking activities (Figure 8.5).

Figure 8.5 Deer bones from Pilanduk Cave showing helical fractures and butchery marks in the form of cutmarks (cm) and chop marks: a) Pil-5413 proximal tibia (anterior) and midshaft with cm (context 112); b) Pil-6232 frontal bone fragment (dorsal) with chop marks on the base of pedicle (context 118); c) Pil-5645 distal humerus (medial) with cm on medial side (context 112); d) Pil-6156 distal humerus (anterior) with cm on medial side (context 117); e) Pil-5806a proximal metacarpal (anterior, context 112); f) Pil-5806b distal metacarpal (posterior, context 112).

The Freshness Fracture Index (Outram 2001; 2002) was used to further characterise green/fresh breakage and identify potential patterns of marrow and grease exploitation. Apart from the presence of helical fractures (under the fracture type criterion), fracture angle and fracture edge are also recorded under this method. These three criteria follow the methodological prescriptions of Villa and Mahieu (1991) for the assessment of fresh breakage. The FFI was recorded for long bone fragments in the assemblage, and FFI scores range from 0 to 6. Low FFI scores (0 to 2) indicate fresh fracturing, while high FFI scores (5 to 6) indicate predominantly post-depositional dry breakage. In contexts 111 and 112, at least 80% of long bone fragments had FFI scores less than or equal to 3. This potentially indicates the occurrence of fresh fracturing for the purpose of processing within-bone nutrients. The actual counts and proportion of FFI scores are shown in Table 8.8 and Figure 8.6, indicating that most scores in contexts 111 and 112 are at '3'. In context 117, most FFI scores lie at '4'. Outram (2001) notes that mid-range FFI scores (i.e. 3 and 4) suffers from a degree of equifinality. The FFI scores for these three contexts indicate that the phenomenon of fresh breakage is present, but other factors must be considered to substantiate marrow or grease processing in the site.

Table 8.7 Summary of long bone fracture data in Pilanduk Cave. TNF long bone = total number of long bone fragments, N helical = long bone fragments with helical fractures, % helical = percentage of long bone fragments with helical fractures, % FFI = percentage of long bone fragments with the range of FFI scores.

Context	TNF long bone	N helical	% helical	% FFI 0-2	% FFI 3-4	% FFI 5-6
surface	91	42	46.2	68.5	25.9	5.6
111	688	464	67.4	8.5	88.7	2.8
112	795	473	59.5	6.8	86.4	6.8
117	1183	201	17.0	4.9	87.7	7.4
118	221	18	8.1	0.7	93.8	5.5

Table 8.8 Freshness Fracture Index scores (Outram 2001, 2002) across the Pilanduk Cave levels.

	FFI Scores						
Context	0	1	2	3	4	5	6
surface	9	13	15	11	3	2	1
111	1	30	21	446	98	15	2
112	6	26	12	473	84	41	3
117	0	10	34	176	619	58	9
118	0	0	1	14	122	7	1

Figure 8.6 Bar plots of total number of fragments (TNF) for Freshness Fracture Index scores (0 to 6) in Pilanduk Cave. TNF counts are shown by context (111, 112, 117 and 118). See Table 8.8 for data.

Two factors to be considered for breakage patterns are burning and trampling. The patterns for burning, taxonomic representation and anatomical representation are very similar for contexts 111, 112 and 117. However, 117 differs from the other two contexts in terms of the lesser degree of preservation of green fractures and the higher prevalence of post-depositional dry breakage of bones. This can be partly attributed to this lower layer being trampled during later occupation represented by contexts 111 and 112, which immediately overlie context 117. The use of fire for burning waste and using hearths in the levels directly above context 117 would have also affected the bones at this level and led to further breakage. In the case of contexts 111 and 112, it appears that bone breakage due to burning of bone/carcass waste has also affected the preservation of fresh fractures such that we see a predominant FFI score of 3 in both levels. In other words, it appears that the fresh fractures in contexts 111 and 112 related to butchery have been mixed with dry fractures related to burning and trampling. This same pattern is observed in context 117, but to a higher degree of dry breakage, since FFI scores are mostly ‘4’ and there is a lesser proportion of helical fractures.

Fragmentation patterns are further shown in the division of fragment size classes (Figure 8.7). In all levels, fragments less than 20 mm in size dominate the assemblage (size class 1). However, there is variation in the element composition per size class for each context. In context 111, 73% of size class 1 consist of indeterminate cancellous bone fragments while 17% are shaft fragments. A similar pattern is replicated in context 112 where 64% of size class 1 consist of indeterminate cancellous bone and 19% are long bone fragments. In both contexts, the higher size classes (i.e. bigger fragment size) are dominated by long bone fragments. The high proportion of small cancellous bone relative to long bone fragments is said to be one potential line of evidence for comminution of bone for grease production (Outram 2001). This interpretation can be applied to contexts 111 and 112. As a matter of contrast, in context 117, size class 1 consists of 33% indeterminate cancellous bone and 36% long bone fragments. In context 118, size class 1 consists of 36% indeterminate cancellous bone and 31% long bone fragments. The low proportion of cancellous bone in contexts 117 and 118 does not support grease production.

To further investigate and quantify the exploitation of within-bone nutrients, NISP:MNE ratios for cervids were plotted against marrow and grease utility indices (Figure 8.8, Table 8.4, Appendix E). The method follows a similar principle as the analysis using the FUI (see Section 8.2.4); however, NISP:MNE ratios are used instead of MAU or %MAU. These counts are computed per skeletal portion and are plotted against published marrow index and grease index values (instead of FUI or MGUI values). In the absence of local data for Asian or tropical deer, the utility indices used here were those constructed by Binford (1978) for caribou, which serve as a confamilial proxy for the Cervidae. The assumption behind this analysis is that skeletal elements with high utility indices would be more fragmented and hence have a higher NISP:MNE ratio compared to elements with low utility (Lyman 1994: 281-282). NISP:MNE ratios in contexts 111 and 112 have strong positive correlations with the marrow utility index. This observation supports the interpretation that marrow processing was practised at these levels. In context 117,

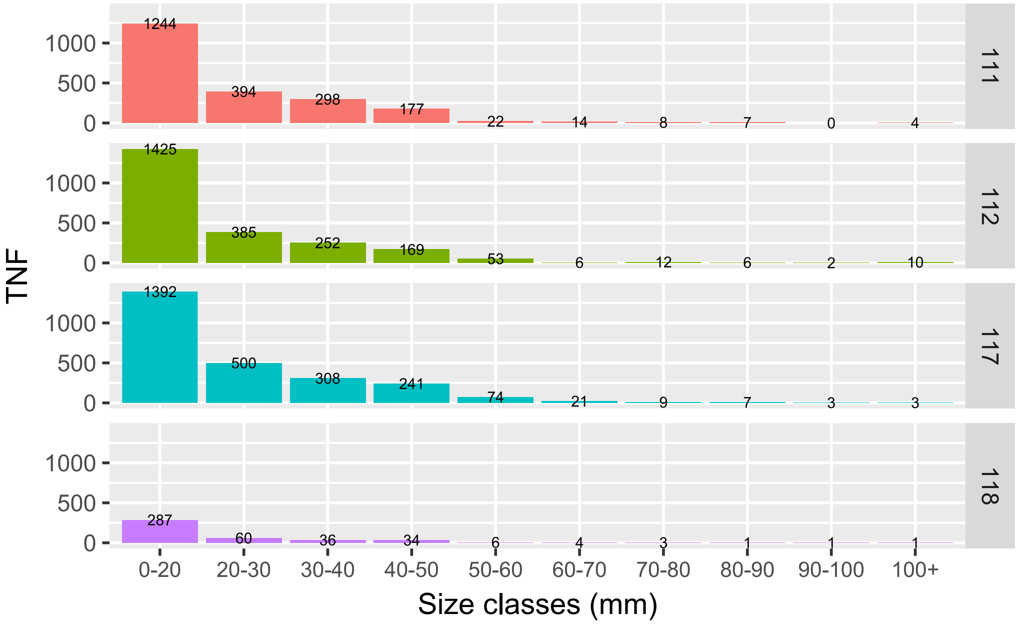


Figure 8.7 Bar plots of total number of fragments (TNF) per fragment size class (in mm) in Pilanduk Cave. TNF counts are shown by context (111, 112, 117 and 118). See Appendix C for tabulated counts.

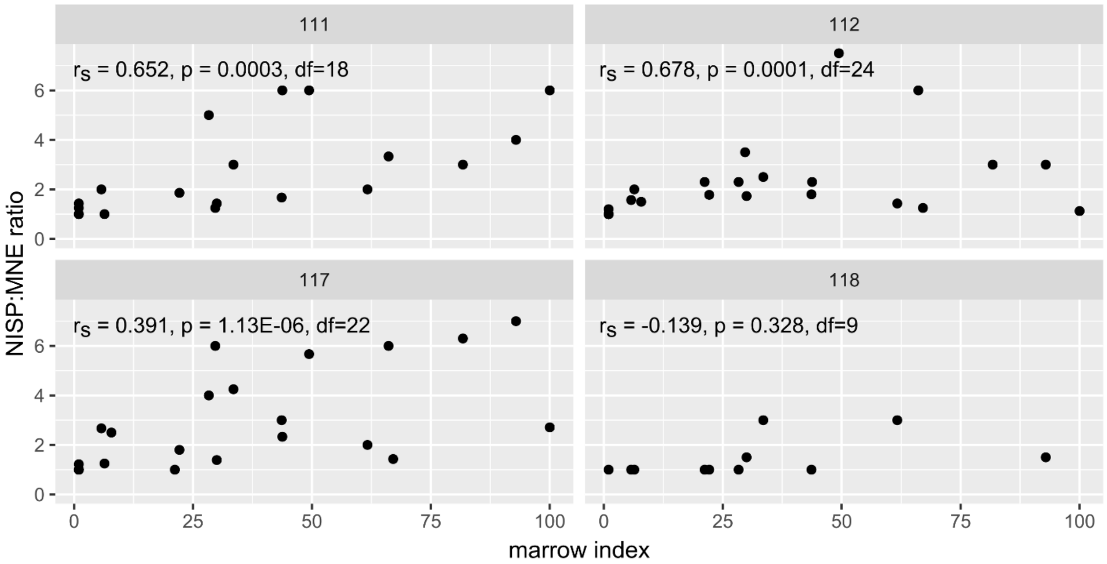


Figure 8.8 Cervid NISP:MNE ratios in Pilanduk Cave plotted against caribou marrow utility index from Binford (1978). The correlation coefficient Spearman's rho (r_S) is shown per context with the p-values (p) and degrees of freedom (df). See Table 8.4 and Appendix E for data.

there is a weak correlation observed. In context 118, there is no correlation observed. For the grease utility index, a significant positive correlation was found in context 112 ($r_S = 0.541$, $p = 0.004$), but not for contexts 111 and 118. For context 117, a weak correlation is once again observed ($r_S = 0.39$, $p = 0.048$) between the two variables.

Another interesting pattern related to marrow processing has to do with the fracturing of phalanges. Breakage patterns indicate that the first and second phalanges were being broken deliberately (Figure 8.9). Oblique fracture angles and smooth fracture edges on phalanges suggest green breakage. The phalanges do not bear evidence of gnawing, and hence we can rule out carnivore ravaging as the reason for breakage. Table 8.9 shows the percentage of phalanges that have been split or fractured. Longitudinal and transverse fractures were both observed for the first and second phalanges. The selection of phalanges for marrow extraction may relate to the kind and quality of marrow found in these elements. Although the first and second phalanges have lesser quantities of marrow and grease, the fats found in phalanges are said to be high in oleic acid (Morin 2007). Binford (1978) observed that in Nunamiut practices for processing caribou, they tended to prefer rich white grease over yellow grease. It is the white grease that is rich in oleic acid, a mono-unsaturated fat. Morin (2007) has noted that phalanges have high proportions of oleic acid in their total fat content, although the actual amounts are marginal compared to other elements such as the distal radio-ulna, distal tibia and metapodia. The dominant composition of unsaturated fatty acids (versus saturated fatty acids) in the distal bone marrows (i.e., metapodia and phalanges) has been observed in other Eurasian deer species (Sugár and Nagy 1992). Hence, it is possibly applicable in the case of Philippine cervids. In the case of Pilanduk Cave, the selection and splitting of phalanges may be related to the extraction of this kind of unsaturated marrow.

Table 8.9 Percentages of split phalanges in contexts 111, 112 and 117 out of total NISP per context (N). Context 118 was omitted due to small sample size. See also specimen counts in Table 8.4.

Element	111	112	117
1st phalanx	69.2 (13)	96.2 (22)	93.1 (25)
2nd phalanx	84.6 (12)	87.5 (14)	94.1 (18)
3rd phalanx	11.1 (9)	6.3 (16)	8.3 (12)

Figure 8.9 Deer phalanges from Pilanduk Cave showing transverse and longitudinal splits: a) Pil-4511 proximal phalanges in plantar view from Kress' excavation; b) Pil-5349 proximal (left) and intermediate phalanges (middle and right) in plantar view from context 111; c) Pil-5806 proximal and intermediate (rightmost) phalanges in transverse aspect from context 112.

8.2.6 Human Modifications

8.2.6.1 Burning

Frequencies of burnt bones in the entire assemblage show that 40% have evidence of charring and 2% have evidence of calcination (Table 8.10). Heat alteration leads to the loss of organic compounds and a reorganisation of inorganic material (Mayne Correia 1997; Thompson 2004; 2005). This process significantly affected the organic composition of bones in the LGM layers, such that there was insufficient collagen retrieved from bone and teeth samples submitted for radiocarbon dating. Heat alteration is particularly extensive across contexts 111, 112 and 117 (Layers II – IV, Table 8.10). In these levels, 40-46% of bones showed evidence of charring and calcination, whereas only 28% of bones in context 118 showed burning traces. Discrete accumulations of ash in Layer II and III, as well as a few cases of articulated burnt bones in Layer II, possibly indicate *in situ* burning of bone in these levels; however, this part of the cave may also been used to dump hearth remains. Of the recorded burnt bone fragments, 80-89% of these exhibit evidence for burning that covers 90-100% of the external bone surface. This means that many bone fragments were uniformly burnt, rather than having patches of burning traces on bone surface. It was also observed that among these fragments, traces of charring were evident in the cross section and internal surface of the fragments, indicating burning occurring after breakage/fracturing. The presence of calcined bones, although small, indicates direct heat exposure (Stiner et al. 1995) in all four LGM contexts/levels. Proportions of burnt cancellous (37-43%) and burnt compact bone (57-63%) are similar across the levels, with no preference showing for cancellous bone. The latter is said to be expected if the burning is due to usage of bones as fuel for fires (Costamagno et al. 2005). However, this was not the case in Pilanduk Cave.

Table 8.10 Number and proportion of burnt bones in Pilanduk Cave. TNF refers to the total number of fragments per context/layer. % >40mm = percentage of burnt bones that are less than 40mm in size, % burnt 90% - percentage of burnt bones showing evidence of burning on 90-100% of bone surface.

Layer	Context	TNF	charred	calcined	total burnt	% burnt	% > 40mm	% burnt 90%
I	surface	261	32	3	35	13.4	3.4	80.0
II	111	2174	964	32	996	45.8	41.4	80.3
II	112	2322	879	48	927	39.9	41.8	86.0
III	117	2561	1117	66	1183	46.2	36.4	89.5
IV	118	506	126	15	141	27.9	23.5	88.7
Total		7824	3118	164	3282	41.9	37.4	85.6

Among the bones from the 1970 excavation of Kress, about 37% showed evidence for burning, indicating a close pattern of heat alteration with the 2016 assemblage. The squares excavated by Kress were in the middle of the cave platform, whereas those from the 2016 excavation were predominantly from the south section of the cave.

Bosch et al. (2012) outline eight models to infer the role of fire in a bone accumulation's formation. Using their compiled criteria, it appears that the evidence for heat alteration in Pilanduk Cave assemblage follows a pattern for waste removal. Specific evidence and criteria for burning of waste in order to clean a living space are provided by Cain (2005). Charring and non-charring for cancellous and compact bones show the same proportions (see Appendix C), indicating that there was no selection between bone types and that all bones for discarding were affected by fire in a similar manner. Nonetheless, the ubiquity of hearth remains across the LGM levels of Pilanduk Cave and evidence for burning of bone in contexts 111, 112 and 117 possibly indicate that bones were also used as fuel. Fernandez and Jalvo (2016:157) suggest that bones associated with hearth remains provide a good fuel to keep the hearth hot for longer and with almost no smoke, and that this usage better explains the presence of burnt fragments in hearths as opposed to the simple aim of cleaning the area.

The pattern for burning in Pilanduk Cave also possibly shows a signature for bone marrow procurement. Binford (1981) provides one ethnographic example from the Nunamiut for bone marrow extraction that involves the use of fire. Defleshed bones are exposed to fire for a short duration and are turned frequently to prevent charring. As Bosch et al. (2012:117) explain, three main factors are expected in this scenario: a high percentage of marrow-rich bones among the burned elements, a high fragmentation rate among the burned bones (breakage to access the marrow), and limited burning damage (mostly scorching and not charring). In the Pilanduk Cave assemblage, there is an abundance of fractured and burned marrow-rich bones and an abundance of small-sized fragments. The typical colour of non-charred and non-calcined bones in the site grades from reddish to dark brown, possibly indicating scorching. These three lines of evidence follow the criteria for bone marrow procurement using fire. Nonetheless, the criterion of scorching needs further substantiation, and the possible evidence for *in situ* burning and extensive charring does not follow bone marrow procurement. The evidence for *in situ* burning possibly relates to the overprint of waste removal or using bone as fuel; hence, it is not possible to clearly determine if fire was used in bone marrow processing. Other instances of the use of fire for consumption (e.g. roasting, grease manufacture) can also be obscured if the terminal process of fire use is for waste removal, and such is the case for the Pilanduk cave assemblage.

8.2.6.2 Butchery Marks

Butchery marks in the form of cutmarks, chop marks or scraping marks are observed in less than 2% of the bone assemblage (Figure 8.5). The recording of cutmarks ideally should include axial elements, but due to time constraints, the focus was on long bone fragments that were greater than 20mm in size. Hand lenses with up to 10x magnification and a Dinolite were primarily used. The relatively low incidence of cutmarks may be an artefact of analytical effort, and the assemblage can certainly benefit from a more intensive cutmark study in the future.

With this caveat, cutmarks observed on bone fragments still provide clear evidence for human modifications in the accumulated bone assemblage (Table 8.11). As can be expected, nearly all cutmarks are found on deer bones, and these provide information into carcass processing of deer. Local ethnographic and ethnoarchaeological work on butchery practices and butchery marks are not yet available. In this case, Binford's (1981) ethnoarchaeological study among the Nunamiut is used as a proxy comparative dataset that provides an inventory of cutmark placement and function. The only other published cutmark inventory coding system derives from the experimental butchery study of Soulier and Costamagno (2017) on red deer carcass processing using replicas of Middle Palaeolithic stone tools.

The placement and configuration of cutmarks in various deer bones in Pilanduk Cave are consistent with butchery marks derived from the skinning, dismemberment and filleting of a cervid carcass based on comparisons with Binford (1981) and Soulier and Costamagno's (2017) work. Regarding butchery marks on the distal tibia and the metapodia, Binford (1981) notes that what may be interpreted as filleting marks on these bones can possibly be marks from cleaning bones for marrow cracking, especially since these elements are not meaty body portions. Cutmarks on certain diaphyses from Pilanduk Cave may also be related to marrow processing. Soulier and Costamagno (2017) further caution that certain cutmarks interpreted as resulting from disarticulation (using Binford's system) can also be produced during defleshing. Certain butchery marks on metapodia interpreted as filleting may be related to tendon removal instead.

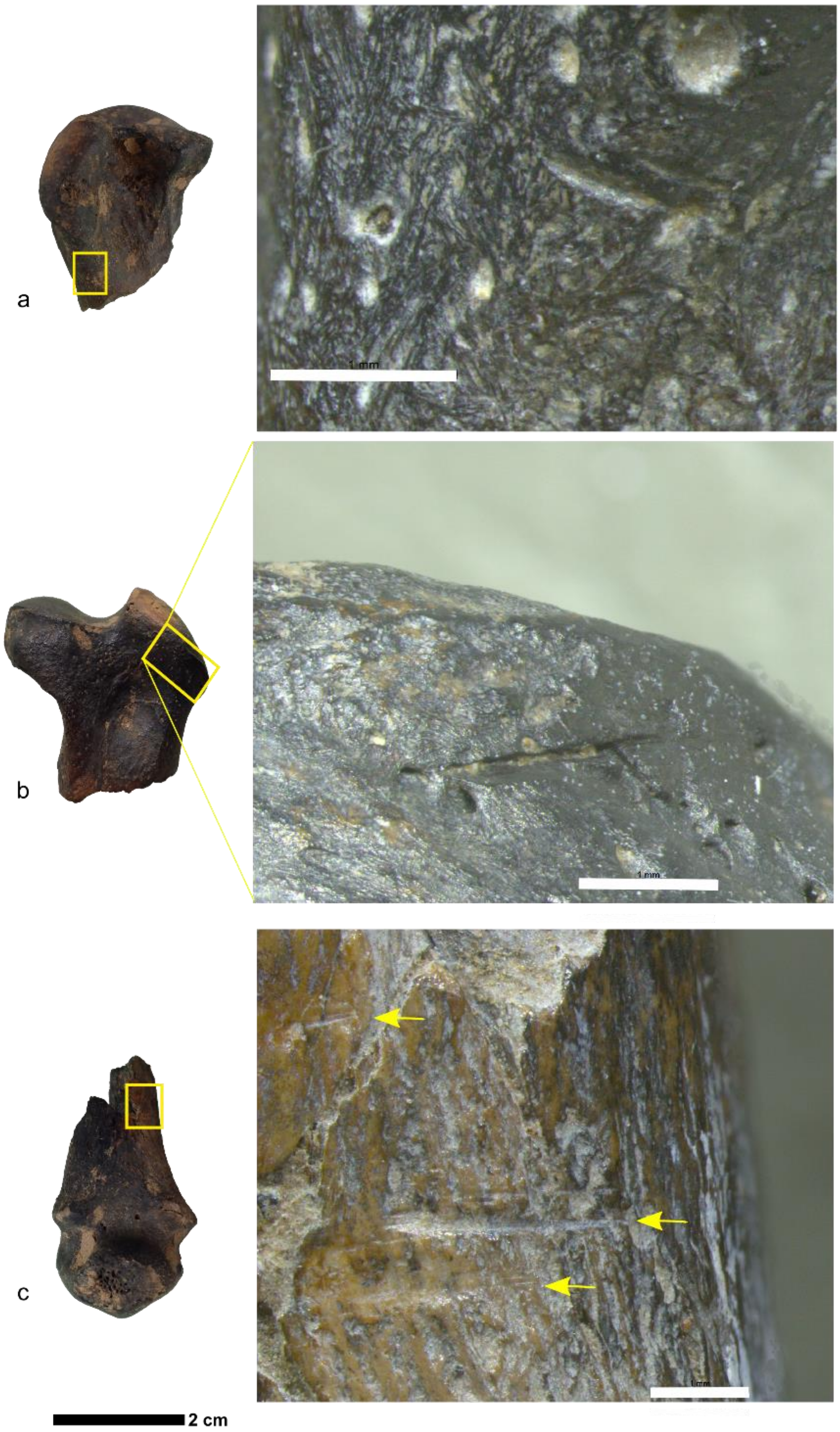
Table 8.11 Summary of butchery mark data for deer and large mammals in Pilanduk Cave showing specimen counts for identified butchery marks for each archaeological context. The interpretation of the activity (skinning, dismembering or filleting) from which the marks derive is based on the placement and configuration of butchery marks (after Binford 1981: Table 4.04). P = proximal, D = distal, ? = uncertain. According to Soulier and Costamagno (2017): *may be defleshing, ^may be tendon removal.

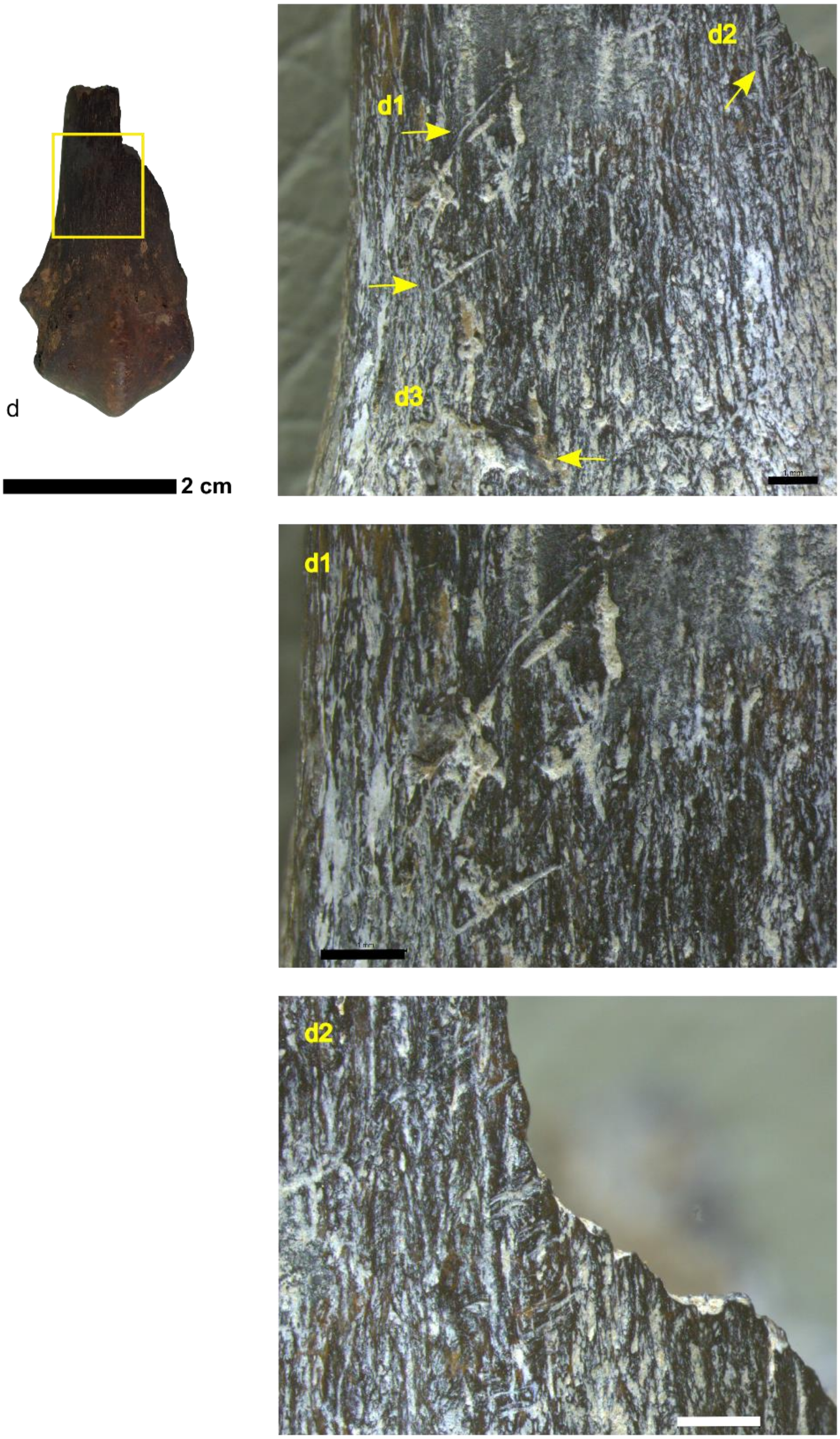
Element	skinning	dismembering	filleting
Context 111			
P radius		1	
P metacarpal		1	
P femur			1
D femur			
diaphysis			9?
Context 112			
D humerus		3*	2
P ulna		1	
P metacarpal		1	
D metacarpal	1^		
P tibia			3
D tibia			1
diaphysis			2?
Context 117			
frontal	1		
parietal	1		
mandible		1	
rib		1	
D humerus		2	
P radius	1	1	
P metacarpal			1
ilium		1	
P femur		1*	
P metatarsal			1
diaphysis			20?

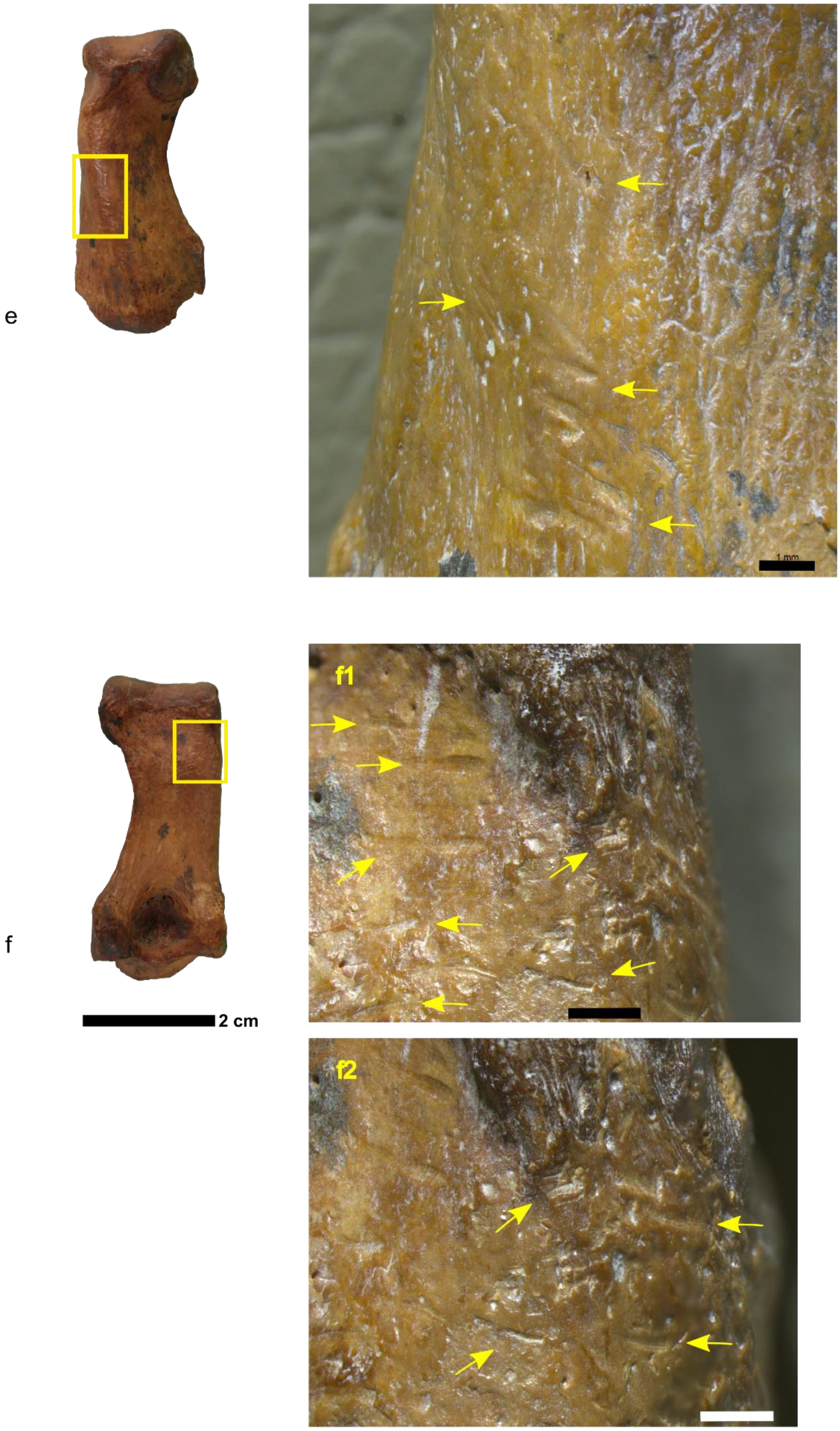
Of further interest are butchery marks found on three out of the nine tiger specimens in the assemblage (Figure 8.10). As described in Chapter 5, only tiger metapodia and phalanges were recovered. The main butchery marks observed are cutmarks and a few possible scrape marks (see notes on tiger bone taphonomy in Appendix C). Cutmarks were diagnosed as linear incisions that have a V-shaped cross-section, internal microstriations (Potts and Shipman 1981) and thinner linear marks parallel to the main incision (or 'shoulder effect' after Shipman and Rose 1983). Placement, distribution and orientation (relative to long axis of the bone) of the butchery marks were also noted. Hertzian fracture cones (Bromage and Boyd 1984) were also used a criterion, but these were not found in the tiger specimens described here. Scrape marks are broader areas of linear marks that may have V- or U-shaped profiles; marks potentially produced by humans typically have some reference to muscle attachments (Fernandez-Jalvo and Andrews 2016:27).

The proximal third metacarpal fragment (Pilanduk-7365) presents cutmarks on the lateral and anterior sides of the proximal articular end (Figure 8.10 a and b). On the lateral side, there are two parallel cutmarks, and on the proximal side, there is one isolated cutmark. Both sets of cutmarks surround the bulbous proximo-lateral articulation of the metacarpal. The right fourth metacarpal fragment (Pilanduk-8803) has several sets of cutmarks and a possible scrape mark on both the dorsal and plantar aspects of the distal shaft (Figure 8.10 c and d). The sub-terminal phalanx (Pil-5393) has possible scrape marks along the dorsal shaft and on the plantar side of the distal articulation (Figure 8.10 e and f). On the plantar side, they are placed around the distal ligament attachment site. The possible scrape marks have a U-shaped profile and have internal microstriations. They appear to be irregularly spaced compared to gnawing marks. In contrast to trampling marks, the marks on the plantar side are placed on the protected concave area of the ligament attachment whereas the borders and angles of the bone do not appear to have damage (as to be expected if they were trampled; see Fernandez-Jalvo and Andrews 2016:29). The placement of the butchery marks at the ends of the metapodia and on the dorsal and distal sections of the phalanx (where ligaments and muscle attach) suggests that these marks possibly derive from skinning the forefoot of a tiger, one likely objective of which is to obtain tiger fur.

Figure 8.10 Butchery marks on tiger bones from Pilanduk Cave. a) Two parallel cutmarks on the neck of the proximo-lateral articulation of Pil-7365 (proximal R third metacarpal fragment) seen in lateral view; b) Cutmark on the edge of the proximal articulation of Pil-7365 seen in anterior (dorsal) view; c) Three cutmarks on the anterior (dorsal) aspect of the distal shaft of Pil-8803 (distal R fourth metacarpal fragment) d) cutmarks (d1 and d2) and possible scrape mark (d3) on the posterior (palmar) aspect of Pil-8803; e) possible scrape marks on the dorsal shaft of Pil-5393 (sub-terminal phalanx); f) possible scrape marks on the plantar side of Pil-5393 shown in two views, plantar (f1) and medioplantar (f2). Scale bar in all cut mark microphotographs are 1 mm.




d
2 cm
d1
d2
d3
d1
d2


e
1 mm
f
f1
f2
2 cm

8.2.7 Summary of Taphonomic Evidence for Pilanduk Cave

The combination of taphonomic evidence from Pilanduk Cave reveals an occupation record for a primary butchery and consumption site for deer. Artefact associations (lithics), butchery marks on bones, and minimal evidence for carnivore gnawing indicate that the bone accumulation is largely human-derived. In addition, the complete representation of skeletal elements for cervids and cervid-sized large mammals suggests that whole carcasses were brought into the cave as opposed to preferential transport of particular body parts.

Marrow processing also appears to be an important activity on-site. As detailed above, the evidence derives from the combination of the following data: helical fractures on long bones, FFI scores, the correlation of the NISP:MNE ratio and marrow index, and splitting of phalanges. Taken together, these indicate strong evidence for marrow extraction in contexts 111, 112 and 117. The evidence from impact scars and cutmarks, albeit in very small proportion, also lends some support to this. There is partial evidence for grease production in the form of fragmentation patterns and the significant correlation of NISP:MNE ratio and the grease utility index in context 112. However, the morphological pattern of fracturing observed in the assemblage – wherein cancellous ends of certain high utility long bones are still left intact – is inconsistent with bone grease production (Morin and Soulier 2017). It may have been that grease production was practised to some extent in the cave, but marrow extraction was the more predominant activity.

Body part representation (as %MAU) and its lack of correlation to the Food Utility Index further demonstrate that selective transport – either of low utility or high utility body parts – was not evident in these LGM levels. The cutmark data suggest that all stages of processing (skinning, dismembering and filleting) for the cervids were also conducted on-site. This further supports the conclusion that entire carcasses were brought in and that consumption also occurred on site.

Lastly, the evidence for heat alteration across contexts 111, 112, and 117 shows that the bones may have been used as fuel in hearths. The evidence also suggests that the eventual discard of food refuse involved burning of bone waste presumably to clean the cave area. Well-defined hearth features were not observed in Trench 3, but the heterogeneous distribution of burnt bones across contexts 111, 112 and 117 and the ubiquity of ash deposits indicate that areas of frequent hearth rebuilding occurred during this part of the occupation sequence.

8.4 Minori Cave Taphonomy

The taphonomic data for Minori Cave focus on the two excavation units with the longest sequences and largest number of vertebrate remains: Square 27 (TNF = 1404) in Chamber D and Square 37 (TNF = 411) in Chamber A. Due to insufficient stratigraphic information on the specimen records, the aggregation of counts was based on the presence and absence of pottery (see Chapter 4). Ceramic-bearing levels are grouped together based on the deepest occurrence of pottery in the trench. Below these 'cut-off' depths, the levels are aggregated as aceramic levels.

8.3.1 Abiotic Processes

The Minori Cave bone assemblage displays a varied set of bone surface modifications, albeit observed in small proportions (Table 8.12, Appendix F). Across Squares 27 and 37, there are bone modifications evident from weathering in the form of fine lines (4.9% of TNF summed from both squares) and spalling (7.9%), abrasion (2.1%), water erosion (2.4%) and root action (1.1%). This indicates that there are various post-depositional and diagenetic changes that have affected the preservation of the animal remains. Such processes also appear to have resulted in high fragmentation rates and high percentages of dry fractures. Mineral staining is minimal across the sequence at ~3%.

8.3.1.1 Weathering

In Square 27, 18.6% of the total assemblage show signs of weathering, predominantly under Stage 1. In the ceramic levels, 27.9% of bone fragments show weathering marks, compared with 15.3% in the aceramic levels. In Square 37, the inverse is observed: there are more weathered bones in the aceramic levels (32.3%) compared to the ceramic levels (4.8%). Nearly all of weathered bone fragments in Square 37 are in weathering stage 1. Certain bone fragments in Square 27 were in weathering stage 2 (n=29) and stage 3 (n=5), indicating longer surface exposure for a small number of bones.

Table 8.12 Summary of taphonomic data for Minori Cave, expressed as percentages of TNF (total number of fragments) per layer. Ceramic-bearing and aceramic layers are divided for each square. $CaCO_3$ = carbonate concretions, $CaCO_3$ ≥50% = fragments covered 50% or more of the bone surface by carbonate concretions, Mn = manganese oxide staining, Cm = cutmarks, Helical = long bone fragments with helical fractures. See Appendix F for taphonomic data.

Layer	TNF	% weathered	% CaCO3	% CaCO3 ≥50%	% Mn	% Gnawed	% Burnt	% Cm	% Helical
Square 27									
Ceramic	369	27.9	20.9	79.2	3.8	2.2	11.3	2.7	27.6
Aceramic	1035	15.3	15.5	70.0	3.3	0.0	8.4	0.2	8.3
Total	1404	18.6	16.9	73.0	3.4	0.6	9.3	0.9	12.3
Square 37									
Ceramic	126	4.8	7.9	60.0	0.0	0.8	0.8	5.6	48.7
Aceramic	285	32.3	22.8	73.8	3.9	0.0	2.5	0.7	28.0
Total	411	23.8	18.2	72.0	2.7	0.2	1.9	2.2	33.6

8.3.1.2 Carbonate Concretions

A small percentage of Minori Cave bones have carbonate concretions: 16.9% for Square 27 and 18.2% for Square 37. It is notable that amongst the bones with concretion, 72% of them have concretions covering 50% or more of the bone surface. The picture drawn here is that most of the bones across the sequence have no concretions, but the small proportion of bones with them presents heavy concretion. This indicates that precipitation of carbonates and their subsequent concretion to bones do not happen uniformly across the cave sequence. Instead, there is a patchy distribution of bones with heavy concretion found commingled with bones without concretion. Such a pattern may indicate small and discrete precipitation events due to water action within small areas of the cave. Alternatively, it might be indicative of post-depositional disturbance and mixing of archaeological remains, wherein remains from a separate area of the cave where precipitation and concretion occur have become mixed with bones where the excavation squares are located.

8.3.2 Biotic Processes

Gnawing is also minimal in the Minori Cave assemblage. Only the ceramic levels of Square 27 show minimally significant numbers at 2.2% and all are from carnivore gnawing. As previously noted, there are no known native carnivores on Luzon. Hence, evidence for carnivore gnawing is further indication of the introduction of invasive carnivores (see Chapter 7). The domestic dog is the likely candidate, as dog remains also appear in these upper levels, although palm civets are also possible bone ravagers. The absence of rodent gnawing also indicates that murids were not significant bone accumulators or modifiers in the site.

8.3.2.1 Burning

A small proportion of bones in Square 27 shows evidence of burning (Table 8.13). Roughly the same proportion of bones was burnt in the ceramic and aceramic levels, at 11% and 8% respectively. Most of these consist of charred long bone shaft (diaphysis) fragments. Although site reports did not indicate whether there were hearth or ash remains in any of the levels, the presence of calcination in Square 27 specimens indicates the exposure to direct fire. In Square 37, only a very few bones (n=8) displayed evidence of burning.

Table 8.13 Number and proportion of burnt bones in Minori Cave. TNF refers to the total number of fragments per layer.

Layer	TNF	charred	calcined	total burnt	% burnt
Square 27					
Ceramic	434	42	7	49	11.3
Aceramic	970	55	26	81	8.4
Total	1404	97	33	130	9.3
Square 37					
Ceramic	126	1		1	0.8
Aceramic	285	4	3	7	2.5
Total	411	5	3	8	1.9

8.3.3 Anatomical Representation and Survivorship

In Minori Cave, the sample size of cervids in the aceramic levels of Square 27 permitted the analysis of survivorship (= %MAU) as related to bone mineral density (Figure 8.11; see Appendix D for data). All the other levels and taxa did not have sufficient sample size. The bone density values used in the analysis derive from Class D data for *Rangifer* from Lam et al. (1999) and Class A data for Odocoileus from Lyman (1984). The correlation coefficients for the respective sets of bone density values (r_s= 0.401, p= 0.047 using Lam et al. 1999; r_s= 0.463, p= 0.0197 using Lyman 1984) demonstrates a moderate correlation between the two variables. This indicates that density-mediated attrition has influenced the preservation of bones in the assemblage. The high survivorship of teeth relative to bone (Figure 8.12) also suggests preservation bias. Anatomical representation for both cervids and suids (Figure 8.12, Tables 8.14 and 8.15) indicates small numbers for elements across the skeleton. Large mammal counts (Table 8.16) indicate that low-density elements such as cranial bones, ribs and vertebrae were also present. The larger proportion of identifiable teeth relative to bones can possibly be indicative of recovery bias (i.e., teeth were being selectively retrieved and recorded). However, the presence of various other specimens that include indeterminate long bone shaft fragments (n=951) runs contrary to this. It appears that differential preservation related to structural density is the most significant factor shaping the pattern of anatomical representation in the assemblage.

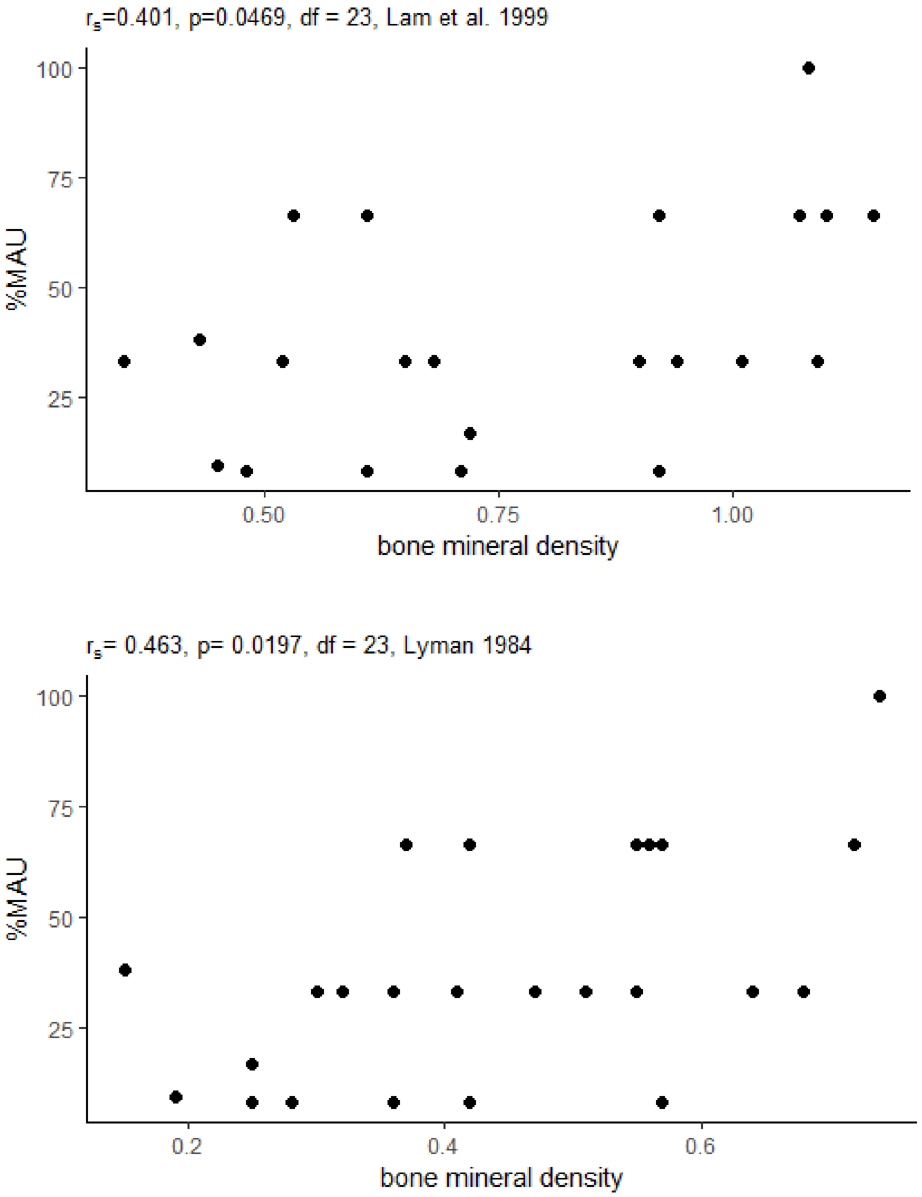


Figure 8.11 Bone survivorship (as %MAU) versus bone mineral density values for cervid remains in the aceramic levels of Square 27 in Minori Cave. The density values are derived from Class D data for *Rangifer* from Lam et al. (1999) (top) and from Odocoileus from Lyman (1984) (bottom). The correlation coefficient Spearman's rho (r_s) is shown with the p-value (p) and degrees of freedom (df). See Appendix D for data.

Table 8.14 Cervid skeletal element representation in Squares 27 and 37 of Minori Cave. NISP = number of identified specimens; MNE = minimum number of elements.

Element		Square 27				Square 37			
		ceramic		aceramic		ceramic		aceramic	
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
antler				11		3			
cranial						2	2		
mandible		1	1						
m1	upper	1	1	1	1	5	5	2	2
	lower	1	1	2	2			3	3
m2	upper			1	1	10	10	4	4
	lower	2	2			6	6	2	2
m3	upper					12	12	1	1
	lower	2	2	2	2	2	2	1	1
incisor		4	4			3	3	7	7
premolar		6	6	6	6	19	19	17	17
vertebra	axis	1	1						
	cervical			5	3				
innominate	ilium			2	2				
humerus	proximal	1	1						
radius	proximal			3	2				
	shaft			1	1				
metacarpal	proximal			2	2				
	shaft			2	2	2	2	3	3
femur	proximal							1	1
	shaft	1	1	4	3				
tibia	proximal			2	2				
	shaft	2	1						
	distal					1	1		
metatarsal	proximal	3	3			1	1		
	shaft			2	2				
metapodial	distal			1	1				
	shaft					1	1		
astragalus		1	1	1	1				
calcaneus						1	1		
phalanges	proximal	1	1			3	3		
	intermediate	1	1			3	2		

Table 8.15 Suid skeletal element representation in Squares 27 and 37 of Minori Cave. NISP = number of identified specimens; MNE = minimum number of elements.

Element		Square 27				Square 37			
		ceramic		aceramic		ceramic		aceramic	
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
cranial		3	3	4	4				
mandible								1	1
maxilla		4	4						
m1	upper	3	3						
	lower	2	2	1	1	3	3		
m2	upper	1	1					3	3
m3	upper	3	3					1	1
	lower							3	1
canine		9	9	1	1	2	2	1	1
incisor		18	17	1	1	9	8		
premolar		13	13	1	1	3	3	3	3
dm		3	3			1	1		
dp4		1	1			2	2	1	1
vertebra	lumbar			1	1				
sacrum		1	1						
ulna	proximal	1	1	3	2				
femur	proximal			1	1				
	shaft			2	1				
metapodial	proximal			2	2				
metapodial	distal	2							
astragalus			1	1					
magnum				1	1				
phalanges	proximal	2	2						
	distal	1	1						

Table 8.16 Minori Cave NISP (number of identified specimens) counts for large mammal skeletal elements that were not identifiable to taxon.

Element	Square 27		Square 37		
	ceramic	aceramic	ceramic	aceramic	Total
cranial	10	9	4	2	25
mandible				1	1
vertebra	7	15			22
rib	8	28	2	3	41
scapula	4	1			5
humerus	3	1	2	2	8
radius				3	3
ulna		1	1	1	3
innominate	2	1		2	5
femur	2	3	1		6
tibia	3	1	1	3	8
shafts	164	681	27	79	951
phalanx				2	2

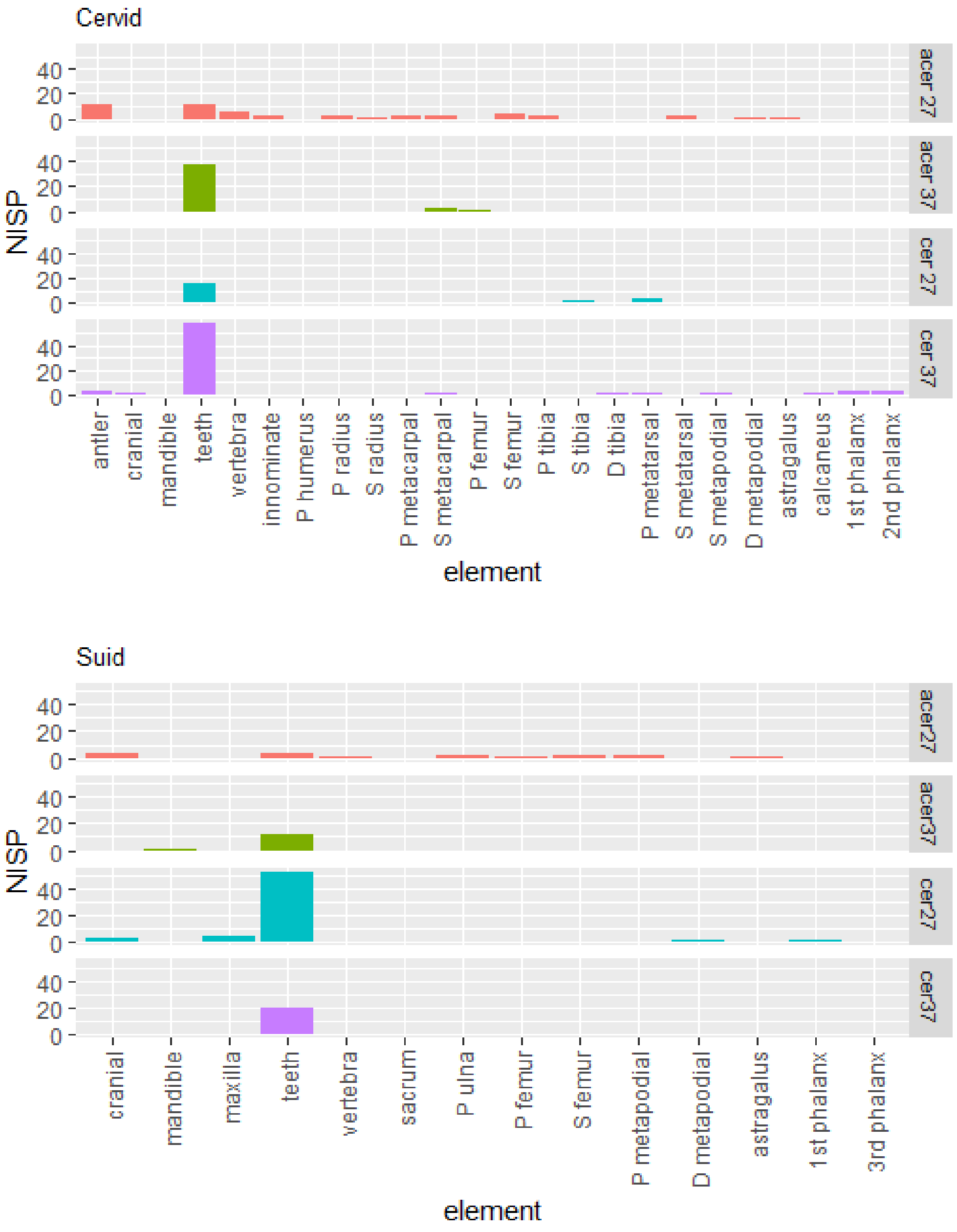


Figure 8.12 Skeletal element representation for cervids and suids in Minori Cave. NISP counts are segregated for the aceramic (acer) and ceramic-bearing (cer) levels of Squares 27 and 37. See Table 8.14 for NISP counts.

8.3.4 Fracturing, Fragmentation and Butchery Marks

Taphonomic data on fracturing and fragmentation are derived from proportions of fracture types and recording of the Freshness Fracture Index for long bone fragments (Table 8.17). The predominance of green fractures in Pilanduk Cave contrasts with the pattern of dry bone breakage observed in the Minori Cave assemblage. In Square 27, less than a quarter of the specimens showed the presence of helical fractures. Across the sequence, most fracture types observed were longitudinal (n=283), transverse (n=360) or diagonal (n=130). In Square 37, there is a higher percentage of helical fractures in the ceramic levels (48%) and the aceramic levels (28%). However, there is a significantly smaller sample size for long bone fragments in Square 37 than in Square 27.

In terms of FFI scores, over 75% of long bone fragments in Square 27 had FFI scores greater than or equal to 4. In Square 37, over 60% of the FFI scores are greater than or equal to 4. This pattern largely indicates dry breakage and that the assemblage has suffered from other forms of fragmentation apart from fresh fracturing (Outram 2001). Fragments size data also indicate high fragmentation (Figure 8.13). In Square 27, 48% (n=636) of the assemblage are in size class category 1 (≤ 20mm) and, 32% (n=431) are in category 2 (20-30 mm). In Square 37, 65% (n=269) of the assemblage are in size category 1.

Table 8.17 Summary of long bone fracture data in the ceramic-bearing and aceramic levels of Squares 27 and 37 in Minori Cave. TNF = total number of fragments, TNF long bone = total number of long bone fragments, N helical = long bone fragments with helical fractures, % helical = percentage of long bone fragments with helical fractures, N FFI ≥ 4 = long bone fragments with a Freshness Fracture Index (FFI) greater than or equal to 4, % FFI ≥ 4 = percentage of fragments with an FFI ≥ 4 among fragments for which FFI was recorded.

Square 27	TNF	TNF long bone	N helical	% helical	N FFI ≥ 4	% FFI ≥ 4
Ceramic	434	203	56	27.58621	137	78.735632
Aceramic	970	774	64	8.268734	170	74.889868
Total	1404	977	120	12.2825	307	76.558603
Square 37						
Ceramic	126	39	19	48.71795	23	60.526316
Aceramic	285	107	30	28.03738	72	75.789474
Total	411	146	49	33.56164	95	71.428571

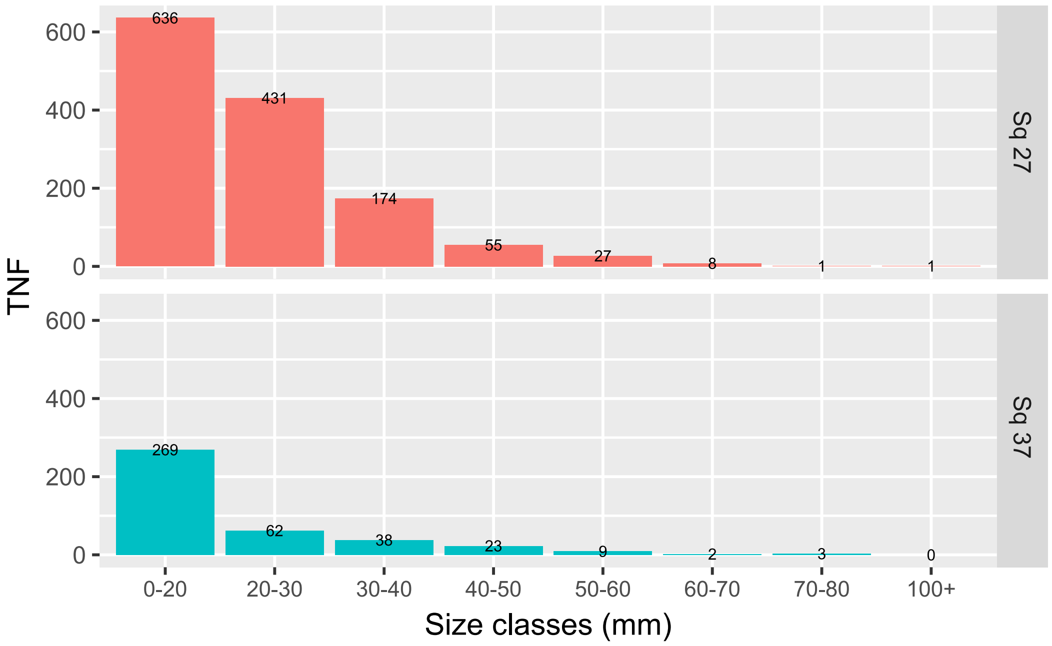


Figure 8.13 Bar plots of total number of fragments (TNF) per fragment size class (in mm) in Squares 27 and 37 of Minori Cave. See Appendix F for fragment counts.

Although there is a large overprint of dry breakage based on the fragmentation data, there is some direct evidence of human modifications. A small percentage of remains in both squares shows butchery marks that are predominantly in the form of cutmarks (Table 8.12). Cutmark diagnosis and criteria are similar to those presented in Section 8.2.6. Most of the bones with cutmarks are in the ceramic-bearing levels: 2.6% in Square 27 and 5.6% in Square 37.

In summary, the taphonomy of the Minori Cave assemblage presents a faunal record with a large overprint of diagenetic processes. It is a highly fragmented assemblage influenced by density-mediated attrition and dominated by dry breakage patterns. Nonetheless, the minimal incidence of gnawing and the presence of cutmarks on some bones indicate that the assemblage is a largely human-derived bone accumulation. The patterns of species representation observed in Minori Cave appear to show the most informative subsistence data for this site, and this will be discussed in Section 8.5.

8.5 Musang Cave Taphonomy

In Musang Cave, the two excavation units with the longest sequences and largest sample sizes are G4 (N= 845) and G5 se1m (N = 131). The sample size for G5 se1m is actually very small, but this is shown to compare the taphonomic observations across the levels/layers of the G4 stratigraphic sequence. These two trenches are adjacent to each other. As noted previously, there appears to be some intrusive material in Levels 4 - 7, wherein 'younger' bone and bones with different preservation states are mixed with other bones. There are also several levels in G4 (Level 1, 3 and 4) that contain human remains. These human bones are likely intrusive since they have a different preservation state from the animal remains. It is not certain whether bovid and macaque remains in Levels 4-7 are part of the original strata or if they are also intrusive like the human remains. These observations have implications for how bones are grouped together into ceramic-bearing and aceramic levels. Because of these uncertainties, bones are aggregated in two ways. The first version of aggregating counts follows Thiel's (1988) stratigraphic reconstruction wherein levels 4a, 5a, 6a, 7a, 8, 9 , 10 and 11 are considered as aceramic levels (see Tables 8.20 and 8.21). The second way of aggregating is to treat all finds from levels 1-7 as ceramic-bearing levels. This means that bones from Levels 4 - 7 are grouped together with bones from Levels 4a, 5a, 6a and 7a. Only bones from Levels 8-11 are considered aceramic in this second version.

The small sample sizes for Musang Cave is partially due to the loss of specimens since the time Thiel analysed the assemblage. As mentioned, the bone counts in Thiel's (1988: Table 1) analysis do not match the number of bones found in museum storage. The surviving number of bones is greatly reduced. With these caveats and limitations in mind, the taphonomic data for Musang Cave are described in the following sections.

8.4.1 Abiotic Processes

Bone surface modifications caused by abiotic agents have varying distribution across both trenches (Table 8.18, Appendix G). In Level 2 of G4 trench, 84% of the specimens show signs of weathering, indicating that bones from these levels were exposed sub-aerially for a longer extent compared to the rest of the assemblage. This contrasts with specimens from Level 1, the topmost layer, where only 1.7% of specimens is weathered. Level 11, the deepest level, also shows a notable percentage of weathered specimens, at 43%. The weathering stage for nearly all of these specimens is at Stage 1.

Carbonate concretions are also present across the sequence. When concretions are present, they are recorded as covering ≥50% of the bone surface. The presence of these concretions has limited the observation of bone surface modifications on many bones. Because of this, the percentages shown for gnawing, manganese staining, burning and cutmarks are likely reduced estimates.

Table 8.18 Summary of taphonomic data for Squares G4 and G5se1m of Musang Cave, expressed as percentages of TNF (total number of fragments) per level. Division of levels follows Thiel's (1988) stratigraphy. $CaCO_3$ = carbonate concretions, Mn = manganese oxide staining, Cm = cutmarks, Helical = long bone fragments with helical fractures, FFI ≤ 3 = long bone fragments with a Freshness Fracture Index less than or equal to 3. See taphonomic data in Appendix G.

Layer	Level	TNF	% weathered	% CaCO3	% Mn	% Gnawed	% Burnt	% Cm	% Helical	% FFI ≤ 3
G4										
II	1	299	1.7	45.5			2.0		20.3	28.7
II	2	72	84.7	81.9		1.4			4.3	4.8
II	3	35		48.6			31.4		3.6	23.8
II	4	15		13.3						
II	5	1								
I	4a	116	30.2		0.9	0.9		6.0	14.9	32.2
I	5a	15								
I	6a	21		47.6						
I	7a	149	0.7	35.6	1.3	0.7	2.7		41.7	48.9
I	8	75	4.0	25.3	9.3		4.0		50.0	52.7
I	9	9	22.2	11.1	11.1					
I	11	7	42.9	28.6	28.6					
no layer	no level	39	25.6	61.5	23.1		2.6		43.8	55.6
Total		853	14.1	37.9	2.6	0.4	0.0	0.8	25.3	34.2
G5se1m										
II	1	7	57.1						20.0	20.0
I	4a	29		72.4					5.6	7.7
I	5a	48		52.1			10.4		50.0	80.0
I	6a	14		71.4					85.7	66.7
I	7a	22	22.7	45.5					28.6	40.0
I	8	12		25.0	8.3				12.5	33.3
I	9	1								
Total		133	6.8	51.9	0.8				30.5	40.5

8.4.2 Biotic Processes

On specimens where bone surfaces are not covered by concretion, a very few gnawing marks were observed (Table 8.18). Only three fragments across the sequence show evidence of gnawing and all are from carnivore gnawing. To reiterate, the presence of carnivore gnawing is indirect evidence for the presence of introduced carnivores, since native carnivores are not known in the Late Quaternary fauna of Luzon.

A small number of bones (n=25) across the Musang Cave sequence shows evidence of burning (Table 8.19). The highest number of burnt fragments is in Level 3 (n=11), with seven fragments showing calcination. It is only at this level where calcination is observed and hence it is only at this level where there is indication that bones were directly exposed to fire.

Table 8.19 Number and proportion of burnt bones in Squares G4 and G5se1m of Musang Cave. TNF refers to the total number of fragments per level. Only levels with burnt bones are presented.

Level	TNF	charred	calcined	total burnt	% burnt
G4					
1	299	6		6	2.0
3	35	4	7	11	31.4
7a	149	4		4	2.7
8	75	3		3	4.0
no level	39	1		1	2.6
Total	597	18	7	25	4.2
G5se1m					
5a	48	5		5	10.4

8.4.3 Anatomical Representation

Anatomical representation of cervid and suid remains is shown in Tables 8.20 and 8.21, using NISP and MNE counts. The specimen counts in these tables are aggregated in two versions, as explained above. Very small sample sizes for both cervids and suid skeletal elements prohibited running survivorship analysis and other taphonomic analyses. Similar to the pattern observed in Minori Cave, isolated teeth are the most common identifiable elements in the assemblage. This likely attests to preservation bias wherein teeth are better preserved than bone specimens due to their structural density. Large mammal counts (Table 8.22) are also presented, and they show that low-density elements such as ribs and vertebrae are also present in small numbers. Indeterminate shaft fragments have the highest counts for large mammal specimens. Regardless of aggregation method, cervid specimens are more abundant than pig specimens across the sequence. One notable effect of the aggregation method is the reduction of counts for the aceramic levels in the second version (Table 8.21) compared to the first version (Table 8.20) of bone counts.

8.4.4 Fracturing, Fragmentation and Butchery

Taphonomic data on fracturing and fragmentation are summarized in Table 8.23. In Level 7a and 8 of G4 trench, there is a higher number of specimens with helical fractures compared to other levels. Around 50% of the long bone fragments in Levels 7a and 8 also have FFI scores ≤3. This indicates the possible occurrence of fresh fracturing in these two levels. According to Thiel's sequence, these two levels are designated as aceramic levels. Only four other levels in G4 trench have a significant amount of fracturing data, Levels 1-3 and 4a. In these levels, 32% or less of the long bones have FFI scores ≤3, indicating that dry breakage is predominant in these levels rather than green fractures. Over 50% of fragments across the sequence are in size class 1 and 2 (0-20 and 20-30 mm) (Figure 8.14). The observation of butchery marks was limited by the presence of concretions on many fragments. It was only in Level 4a that specimens with cutmarks were identified (n=7). Six fragments were from cervid or large mammal remains. One specimen was from a macaque femur shaft, with two cutmarks possibly produced by a metal implement. This is based on the sharp and steep V-shaped profile and relatively even and uniform morphology of the two marks; however, further microscopic analysis is needed to confirm this (see Greenfield 1999, 2013 for metal cutmark criteria). Two of the large mammal specimens appear to be intrusive 'younger' bone fragments, based on their colour (natural colour of fresh bone) and unweathered appearance. Therefore, these two fragments cannot be attributed as coming from that level. Note that in Thiel's stratigraphy, Level 4a is supposedly an aceramic level.

Table 8.20 Cervid and suid skeletal element representation in G4 trench of Musang Cave, aggregated according to the stratigraphic order presented by Thiel (1988) for the division of ceramic and aceramic levels. NISP = number of identified specimens; MNE = minimum number of elements, \ = not applicable.

Element		Cervid				Suid			
		G4 1-7		G4 4a-11		G4 1-7		G4 4a-11	
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
antler		5	\	2	\	\	\	\	\
cranial		3	3	2	2	2	2		
mandible		4	2	4	2	2	1		
teeth		5	5	10	10				
vertebra	atlas							1	1
	axis			1	1				
	cervical	1	1						
innominate	ilium			1	1				
humerus	proximal							1	1
radius	proximal			1	1				
	shaft	1	1						
	distal					1	1		
ulna	proximal	3	3	1	1	1	1		
metacarpal	shaft	1	1	3	2				
femur	proximal			1	1				
	shaft	1	1	2	2				
tibia	proximal	1	1						
	shaft			2	1				
	distal			5	3				
metatarsal	proximal	1	1						
	shaft			1	1				
	distal			1	1				
metapodial	complete					1	1	2	2
	proximal					1	1		
	shaft	1	1	2	2				
	distal	1	1	2	1	1	1	4	4
astragalus				2	2	1	1		
calcaneus		1	1			2	2		
cuboid		1	1						
cuneiform						1	1		
phalanges	proximal	1	1	3	3				
	intermediate	1	1			2	2	1	1
	distal	1	1	2	2			2	2
Total		33	26	48	39	15	14	11	11

Table 8.21 Cervid and suid skeletal element representation in G4 trench of Musang Cave, wherein levels 1-7 and 4a-7a are aggregated together as ceramic-bearing levels. NISP = number of identified specimens; MNE = minimum number of elements, \ = not applicable.

Element		Cervid				Suid			
		G4 1-7, 4a-7a		G4 8-11		G4 1-7, 4a-7a		G4 8-11	
		NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
antler		6	\	1	\	\	\	\	\
cranial		5	5			2	2		
mandible		5	3	3	2	2	1		
teeth		5	5	10	10				
vertebra	atlas							1	1
	axis	1	1						
	cervical	1	1						
innominate	ilium			1	1				
humerus	proximal							1	1
radius	proximal			1	1				
	shaft	1	1						
	distal					1	1		
ulna	proximal	3	3	1	1	1	1		
metacarpal	shaft	1	1	3	2				
femur	proximal	1	1						
	shaft	1	1	2	2				
tibia	proximal	1	1						
	shaft	2	1						
	distal	3	3	2	2				
metatarsal	proximal	1	1						
	shaft	1	1						
	distal	1	1						
metapodial	complete					1	1	2	2
	proximal					1	1		
	shaft	1	1	2	2				
	distal	3	3			4	4	1	1
astragalus		3	3						
calcaneus		1	1			2	2		
cuboid		1	1						
carpal/tarsal						1	1		
phalanges	proximal	2	2	2	1				
	intermediate	1	1			3	3		
	distal	2	2	1	1	2	2		
Total		53	44	29	25	20	19	5	5

Table 8.22 NISP (number of identified specimens) counts for large mammal elements in G4 trench of Musang Cave that were not identifiable to taxon. Counts are aggregated in two versions (see text), the first version following Thiel (1988).

	Thiel (1988)		Second version	
Element	G4 1-7	G4 4a-11	G4 1-7, 4a-7a	G4 8-11
cranial	3		4	
mandible	1	1	3	
vertebra	12	5	16	2
rib	17	2	27	
scapula		1	2	
hum	3	3	4	2
radius		8	3	6
innominate	2		3	
femur	4	2	6	1
tibia	1	3	3	1
shafts	234	109	368	34
phalanx	1		1	

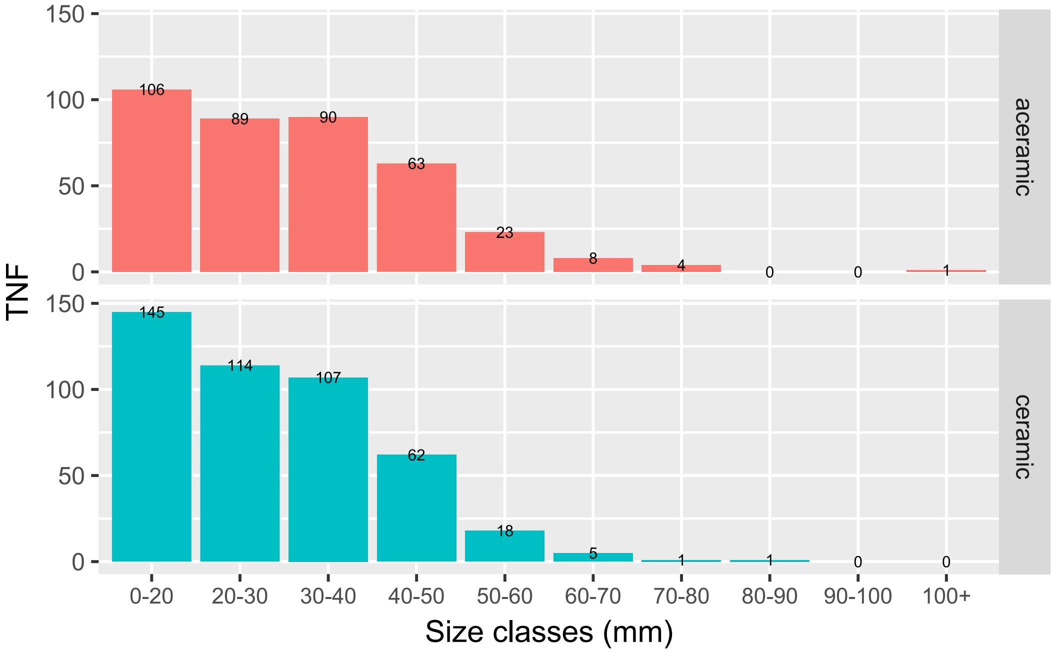


Figure 8.14 Bar plots of total number of fragments (TNF) per fragment size class (in mm) in G4 trench of Musang Cave. Counts are segregated for the aceramic and ceramic-bearing levels. See Appendix G for fragment counts.

Table 8.23 Summary of long bone fracture data in Musang Cave. TNF = total number of fragments, TNF long bone = total number of long bone fragments, N helical = long bone fragments with helical fractures, % helical = percentage of long bone fragments with helical fractures, N FFI ≤ 3 = long bone fragments with a Freshness Fracture Index (FFI) less than or equal to 3, % FFI ≤ 3 = percentage of fragments with an FFI ≤ 3 among fragments for which FFI was recorded.

Level	TNF	TNF long bone	N helical	% helical	N FFI ≤ 3	% FFI ≤ 3
G4						
1	299	182	37	20.3	37	28.7
2	72	70	3	4.3	3	4.8
3	35	28	1	3.6	5	23.8
4	15	2	0	0	0	0
5	1	0	0	0	0	0
4a	116	67	10	14.9	19	32.2
5a	15	0	0	0	0	0
6a	21	1	0	0	0	0
7a	149	108	45	41.7	44	48.9
8	75	60	30	50	29	52.7
9	9	4	0	0	0	0
11	7	0	0	0	0	0
no level	39	32	14	43.8	15	55.6
Total	853	554	140	25.3	152	34.2
G5se1m						
1	7	5	1	20	1	20
4a	29	18	1	5.6	1	7.7
5a	48	14	7	50	8	80
6a	14	7	6	85.7	4	66.7
7a	22	7	2	28.6	2	40
8	12	8	1	12.5	1	33.3
9	1	0	0	0	0	0
Total	133	59	18	30.5	17	40.5

The taphonomy of Musang Cave is quite similar to the Minori Cave assemblage, with its considerable overprint of diagenetic processes. The Musang Cave record shows a highly fragmented assemblage that has been significantly influenced by post-depositional dry breakage and assemblage loss related to trephic (curatorial) events. Nonetheless, the evidence for fresh fracturing in certain levels (Levels 7a and 8) and the presence of cutmarks on a small number of bones (Level 4a) provide indications of the anthropic origin of the bone accumulation.

8.6 Summary of Taphonomic Evidence

Pilanduk Cave presents a well-preserved LGM bone assemblage for Palawan Island that shows many taphonomic signatures for human activities and decisions. The evidence points to preferential hunting and consumption of deer on the site. Anthropic taphonomic evidence includes fracturing, fragmentation, cut marks, skeletal part representation and extensive heat alteration. Minimal carnivore gnawing marks across the assemblage also indicate that humans were the primary accumulators of the animal remains. Data from anatomical representation suggest transport decisions for bringing in whole deer carcasses up into Magmisi Peak and into the cave (at 165 masl). The deer individuals were likely caught from the lowland vicinities of the Iwahig River plain. Apart from meat consumption, marrow extraction is also evident based on fracturing and fragmentation patterns of bones. The ubiquity of burnt bones, ash and charcoal across Layer II and Layer III suggest frequent hearth rebuilding across this LGM occupation sequence. Bone refuse may also have been incorporated into hearths to clean the living space.

Minori and Musang Caves present Holocene sequences for the island of Luzon. In contrast to Pilanduk Cave, these two assemblages have smaller sample sizes and relatively poor bone preservation. Both Luzon assemblages show a large overprint of diagenetic processes that obscure anthropic bone modifications or that cannot be resolved due to equifinality. Recording protocols, post-excavation and curatorial decisions have also affected assemblage sizes. Nonetheless, the taphonomic evidence available points to human-derived bone accumulations. Based on this, further inferences can be derived from taxonomic profiles of the assemblages, which in turn provide meaningful insights into subsistence practices across time.

8.7 Species Representation and Vertebrate Subsistence Patterns in Palawan and Luzon

In this section, the archaeofaunal records of Pilanduk, Minori and Musang caves are once again assembled and compared with published faunal records for each island. The aims are to assess diachronic patterns of human subsistence based on the vertebrate record and examine human responses to ecological changes from the LGM to the Late Holocene. The Pilanduk Cave record is combined with the Ille and Pasimbahan Cave sequences to present zooarchaeological data from the LGM to the Late Holocene. These are the only vertebrate records for Palawan that have sufficient taphonomic information to infer human accumulation and modification of bone assemblages. For Luzon, the records of Callao Cave, Nagsabaran open site and Pintu Rockshelter are once again joined with those of Minori and Musang Caves.

8.5.1 Subsistence Patterns on Palawan Island

Palawan Island assemblages are subdivided into temporal periods and the faunal counts (NISP) per period are presented in Table 8.24. The Late Pleistocene is subdivided into the LGM of Pilanduk Cave and the Terminal Pleistocene levels of Ille Cave. The phases of the Holocene (Early, Middle and Late) are covered by Ille and Pasimbahan Caves (Ochoa 2009; Ochoa et al. 2014). The relative abundances of large mammals and medium-sized vertebrates are illustrated in Figure 8.15. Large mammals typically dominate these assemblages, but there is variation recorded for deer and wild pig abundances across time. This variation relates to diminishing deer populations on the island and eventual local extinction. Macaques are the most common medium-sized vertebrate and are treated separately from the other taxa in Figure 8.15 due to their relative abundance. The medium-sized vertebrate category (Med_Vert) in these figures is an aggregation of counts for other medium-sized tropical forest species that include mammals (e.g. pangolin, porcupine and small carnivores) and herpetiles (turtles and monitor lizard). The counts for macaques and medium vertebrates are used to further investigate diet breadth and site use across time.

The LGM assemblage comes from the archaeological layers of Pilanduk Cave dated to 21,000–20,000 cal BP in Trench 3 (see also Table 5.1). These correspond to context numbers 111, 112, and 117. The deepest layer from context 118 (ca. 25,000 cal BP) is not included in the plots here due to the very small sample size for prey taxa (NISP = 58, excludes murids and bats). However, as recorded in Table 5.1, the rusine deer is the most abundant taxon in this layer and the wild pig is absent.

In the Late Pleistocene assemblages from Pilanduk and Ille Caves, deer is the dominant prey (Figure 8.15). Of the two deer species, it is the *Rusa* cervid, the larger taxon, that is the most abundant in the Late Pleistocene assemblages. Although many cervid remains cannot be definitively separated between *Rusa* and *Axis*, most of the cervid and large mammal remains are actually in the size range of the *Rusa* deer. In contrast to other large mammal taxa, the wild pig is considerably smaller than the rusine deer, as it is a dwarf island endemic, and the tiger is notably larger than the rusine deer.

Good surface preservation of bones and similar recovery methods across the three cave sites (hand-collection, sieving and flotation) indicate that low species richness in Pilanduk Cave is not just an artifact of preservation and archaeological recovery. Wet-sieving and flotation did not yield many micro- and medium-sized vertebrate remains within Layers I-IV. This indicates that bats did not have considerable presence during these periods of human occupation, and that bats were also not hunted for food. Cervid remains comprise 90% of the LGM assemblage. Only a very small number of macaque, squirrel and porcupine remains were identified. In the Terminal Pleistocene record of Ille, nearly 75% of the assemblage consist of deer. As referred to in Table 7.1 on the taxonomic structure of vertebrate assemblages (Palawan B), these two Pleistocene assemblages are less speciose than the Holocene assemblages on the island. Note that in the linear regression analysis in Chapter 7, it was shown that sample size is not significantly driving species richness, and that there are factors other than sample size influencing richness across the sites. One such factor is human prey choice. Based on comparisons with other Palawan assemblages, the LGM levels of Pilanduk Cave present an occupation site that was focused on large-game hunting and processing of deer. This is further demonstrated in Table 8.25, where NISP counts are aggregated to assess prey size choices. These counts vary from those in Figure 8.15 in that they combine counts identified to taxon with counts of elements only identified to size category (large mammal, medium-sized mammal and medium-sized reptile). In Pilanduk, nearly 99% of the bone assemblage belong to the large mammal category. The Terminal Pleistocene levels of Ille Cave also show a very high proportion of large mammal remains (82%) compared to other medium-sized vertebrates.

Table 8.24 Number of identified specimens (NISP) in Palawan vertebrate assemblages aggregated by temporal period and archaeological site. LGM = Last Glacial Maximum, TP = Terminal Pleistocene, EH = Early Holocene, MH = Middle Holocene, LH = Late Holocene, † locally extinct.

TAXON	**LGM**	**TP**	**EH**		**MH**		**LH**	
	Pilanduk	Ille	Ille	Pasimbahan	Ille	Pasimbahan	Ille	Pasimbahan
Axis calamianensis†	75					8		4
Rusa sp.†	175							
Cervidae	796	288	43		8		3	
Sus ahoenobarbus	62	14	58	35	231	192	179	191
Canid		2	6					
Panthera tigris†	9	2						
Prionailurus bengalensis			2		3			
Arctictis binturong					1		1	
Paradoxurus philippinensis			12		5		4	
Viverrid		1	2	5	1	9		16
Amblonyx cinereus			1					
Herpestes brachyotis		1	1				1	
Mydaus marchei			6	4	3	2	3	
Macaca fascicularis	4	13	57	28	51	75	40	65
Hylopetes nigripes			3		1			
Sundasciurus sp.		5	6		1			
Sciurid	1			3		1		2
Hystrix pumila	2	1	15	2	3	5	2	6
Manis culionensis			8	2	4		1	1
Cyclemys dentata	5	7	14		3		3	
Cuora amboinensis		1	1					
Geoemydid	29	59	171	16	29	8	25	7
Varanus palawensis	2	7	76	27	51	13	45	12
Serpentes		6	46	38	39	26	39	25
Total NISP	1160	407	528	160	434	339	346	329

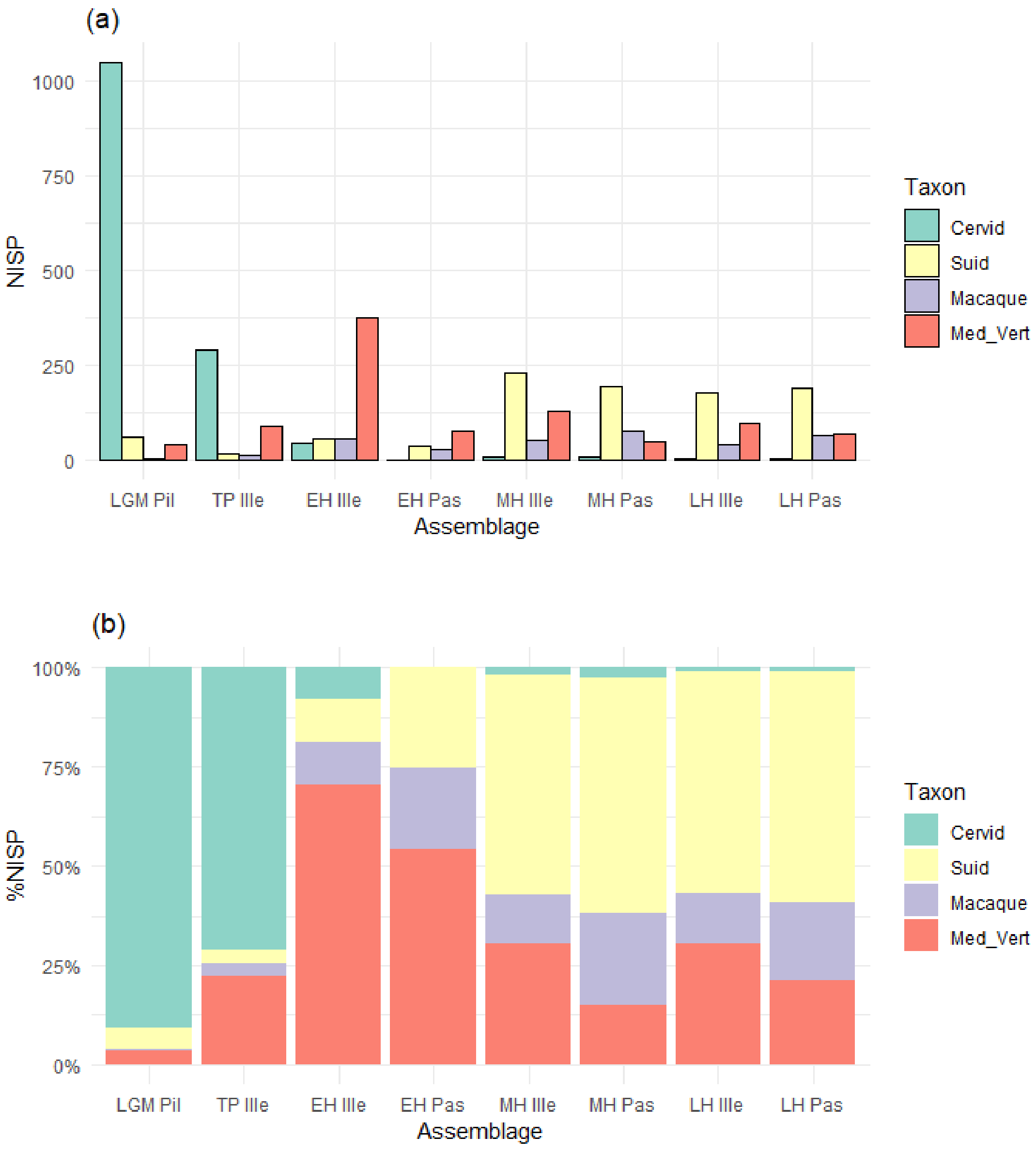


Figure 8.15 Bar plot (a) and stacked percentage plot (b) of NISP counts for large mammals, macaques and medium-sized vertebrates (Med_Vert) in the Palawan record aggregated by temporal period. The 'Med_Vert' category includes terrestrial and arboreal rainforest taxa. LGM = Last Glacial Maximum, TP = Terminal Pleistocene, EH = Early Holocene, MH = Middle Holocene, LH = Late Holocene, Pil = Pilanduk, Pas = Pasimbahan.

In the Early Holocene, it is notable that a higher proportion for medium-sized vertebrates is evident in both Ille and Pasimbahan Caves (Figure 8.15). This is the only phase when large mammal counts notably decrease, accounting for ≤50% in the assemblages. When considering data in Table 8.24 and Figure 8.15 for the Early Holocene, large mammal remains (cervid and suid) account for 25% or less of all macrovertebrates. When considering data in Table 8.25, large mammals account for 26% and 50% for Ille and Pasimbahan Caves, respectively. There is a sharp drop in the relative abundance of deer remains during the Early Holocene, and the large mammal remains consist mainly of wild pig remains. In Ille Cave, the Early Holocene levels contain a number of human cremation burials dated to ca. 9000 cal BP (Lara et al. 2015; Lewis et al. 2008). In Pasimbahan Cave, similar cremation burials were also uncovered in later excavations of the site (M. Lara, pers. comm.). In this case, the use of these two cave sites during this phase appears to have been more focused on human interment practices rather than on large-game hunting.

Table 8.25 NISP and %NISP counts for aggregated large mammal, medium mammal and reptile bone counts in Palawan assemblages. LGM = Last Glacial Maximum, TP = Terminal Pleistocene, EH = Early Holocene, MH = Middle Holocene, LH = Late Holocene, Pil = Pilanduk, Pas = Pasimbahan.

Prey category	LGM	TP	EH		MH		LH	
	Pil	Ille	Ille	Pas	Ille	Pas	Ille	Pas
NISP								
large mammal	4843	517	166	192	350	736	336	706
medium mammal	20	38	201	148	109	374	98	286
reptiles	41	73	263	43	83	21	73	19
Total NISP	4904	628	630	383	542	1131	507	1011
% NISP								
large mammal	98.8	82.3	26.3	50.1	64.6	65.1	66.3	69.8
medium mammal	0.4	6.1	31.9	38.6	20.1	33.1	19.3	28.3
reptiles	0.8	11.6	41.7	11.2	15.3	1.9	14.4	1.9

By the Mid-Holocene, the pattern of deer rarity continues. It has been previously observed in the Ille and Pasimbahan records that a resource shift from deer to wild pig occurs during the Mid-Holocene (Ochoa and Piper 2017; Ochoa et al. 2014; Figure 8.15) . In the Late Pleistocene, deer appears to be the preferred prey over wild pig when they were present in the landscape. This was first observed in the Terminal Pleistocene record of Ille Cave (Ochoa 2009; Philip J. Piper et al. 2011a), and is now further corroborated by the LGM record of Pilanduk

Cave. It appears that the rarity and eventual demise of cervids in the Holocene prompted the resource switch to wild pig as the main large game.

A similar pattern for relative abundances of wild pig and medium-sized vertebrates continues into the Late Holocene. Deer is exceedingly rare, and only the smaller cervid species (*Axis*) is recorded. The contribution of medium-sized vertebrates to the subsistence record is also of importance. They occur in much higher proportions across the Holocene compared to the Late Pleistocene records. These include arboreal and semi-arboreal forest taxa such as macaques, viverrids and squirrels. Turtles and monitor lizards are also commonly found in the Holocene assemblages. Post-Pleistocene ecological changes across the island may have prompted the broadening of the foraging repertoire to include more forest taxa. Expansion of closed forests is reported at the onset of the Holocene based on cave guano stable isotope records from Gangub and Makangit Caves (Bird et al. 2007; Wurster et al. 2010). O'Donnell (2016) suggests on the basis of palynological records that more open environments persisted in the vicinities of the Dewil Valley contrary to the isotopic records. Regardless, it is evident from the vertebrate record that a wider variety of forest habitats was increasingly utilised by human foragers at the onset of the Holocene.

8.5.2 Subsistence Patterns on Luzon Island

Faunal counts (NISP) for Luzon Island assemblages are presented in Table 8.26, wherein cave assemblages are subdivided into temporal periods. Callao Cave is the only Late Pleistocene record and the subsistence data is for *Homo luzonensis*. The Holocene phases of the Luzon record are ascribed to *Homo sapiens*. The Early and Middle Holocene phases are combined ('EMH') due to the paucity of radiometric dates and are represented by the aceramic levels of Minori and Musang Caves. The ceramic-bearing levels of both caves are assigned to the Late Holocene. This assignation is based on the earliest records of pottery in the Cagayan Valley region at ca. 4000 cal BP (Hung 2005; Mijares 2008). As discussed in previous chapters, Nagsabaran site and Pintu Rockshelter are both Late Holocene sites. Nagsabaran is a well-dated site, with the earliest ceramic-bearing levels dating to ca. 4000 cal BP. The younger cultural layer is ascribed to the Late Neolithic/Metal Age and dated to ca. 2500 cal BP.

The relative abundances of large mammals, murids and medium-sized mammals are shown in Table 8.26 and illustrated in Figures 8.16 and 8.17. The murid category combines large and small murids. The large arboreal cloud rats were potentially human prey, but other murids are likely products of natural death occurrences. Although they might not have been human prey, the murid category is included to further illustrate the pattern that native murids and artiodactyls occur across the temporal sequence, whereas introduced taxa appear later in the Holocene sequence. The medium mammal (Med_Mammal) category includes only introduced taxa: macaques, viverrids and domestic dogs. There are no known native mammals of this size category in the Luzon fauna. The counts for these taxa are aggregated due to the small number of specimens. The murid category only includes native murids, as introduced rats have not been reported in these sites.

As noted in Section 8.4, Musang Cave bone counts are aggregated in two ways. Hence, the plots in Figures 8.16 and 8.17 have two versions, owing to two different ways by which NISP counts are aggregated in Musang Cave. All other counts from the four sites are the same in all figures. The first version of aggregating counts follows Thiel's (1988) stratigraphic reconstruction, whereas the second versions combines Levels 1-7 with Levels 4a - 7a.

Large mammals expectedly dominate these assemblages across all periods. Once again, there are differences observed for deer and wild pig abundances across time. This variation is due to the process of introduction of domesticates. In Palawan Island, the variation was due to the extinction of native fauna. Deer is the dominant prey in the Late Pleistocene record of Callao Cave, as well as in the Early to Mid-Holocene records of Minori and Musang Caves. In Callao Cave, 82% of the Late Pleistocene assemblage consist of large mammal counts, predominantly deer. This pattern appears to parallel the Late Pleistocene record of Palawan, and this is of interest since two human species are involved (*H. luzonensis* for Luzon and *H. sapiens* for Palawan). It appears that when cervids are present, they are the preferred human prey in both Luzon and Palawan Islands, for both species of human.

Table 8.26 Number of identified specimens (NISP) in Minori and Musang Caves aggregated by temporal period and archaeological site. EMH = Early to Middle Holocene, LH = Late Holocene.

Taxon			Version 1 (Thiel 1988)		Version 2	
	EMH	LH	EMH	LH	EMH	LH
	Minori aceramic	Minori ceramic	Musang aceramic	Musang ceramic	Musang aceramic	Musang ceramic
Rusa marianna	212	88	96	24	38	82
Sus philippensis	45	98	20	35	3	52
Sus scrofa				2		2
Bubalus bubalis			3	1		4
large mammal I	589	505	259	307	49	517
large mammal II			10	1		11
Phloeomys pallidus						
Crateromys sp.	2					
Carpomys undescr. sp.	6			1		1
Bullimus/Rattus sp.	1	1	1			1
Batomys sp.						
Apomys microdon						
phloeomyine	2		3	2		5
murid	33	13	7	1	3	5
Paradoxurus philippinensis						
Canis lupus familiaris		3				
Macaca fascicularis		18	4	1		5
intermediate mammal		14	3	1		3
Microchiroptera	1					
small mammal	9	1	1	3	1	3
Varanus sp.	3		2	5	1	6
turtle	1		6	1	1	6
snake	4	5	4	4		8
fish		1	31	11		42
bird	2	1	3	3		6
macrovertebrate	113	10	60	57	6	112
microvertebrate	24	8	5		2	3
Total	1047	766	518	460	104	874

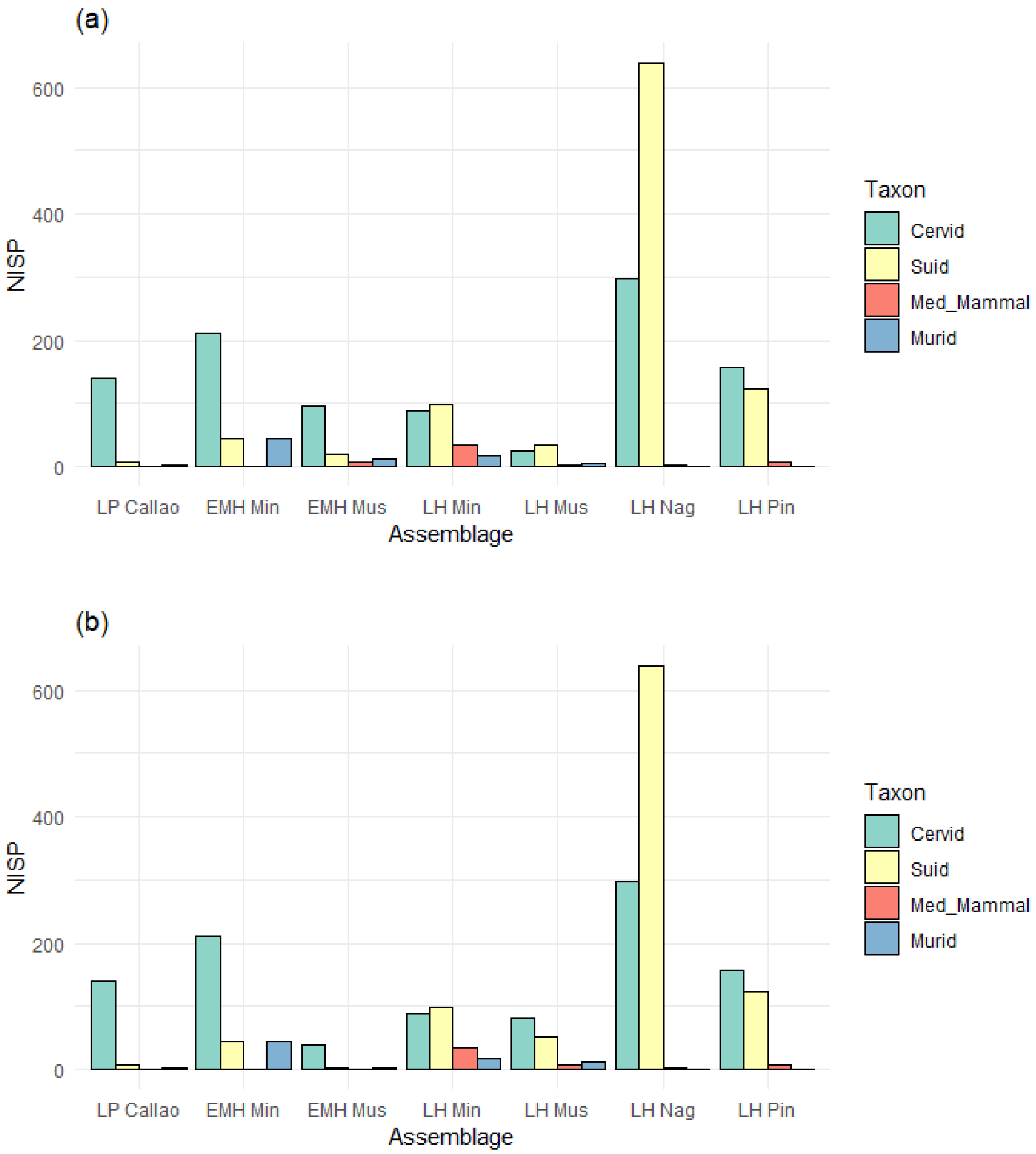


Figure 8.16 Barplots of NISP counts for large mammals, medium-sized mammals (Med_Mammal), and native murids in the Luzon record aggregated by temporal period. (a) and (b) vary only with regards to Musang Cave counts. (a) shows Musang Cave bone counts aggregated following Thiel (1988), (b) shows Musang Cave bone counts aggregated differently by this author (see text).

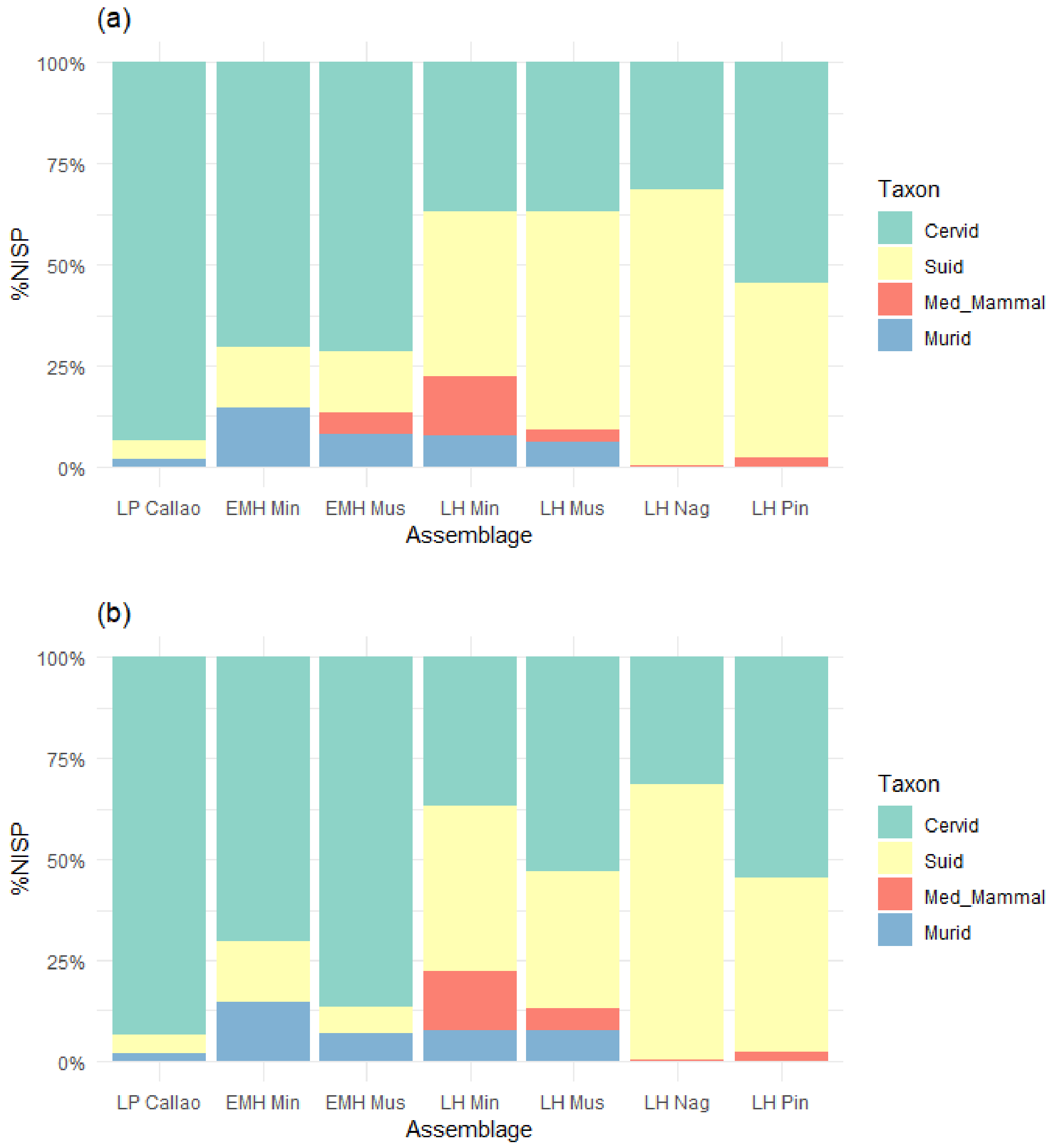


Figure 8.17 Stacked percentage plots of NISP counts for large mammals, medium-sized mammals (Med_Mammal), and native murids and in the Luzon record aggregated by temporal period. Versions (a) and (b) vary only with regards to Musang Cave counts. (a) shows Musang Cave bone counts aggregated following Thiel (1988), (b) shows Musang Cave bone counts aggregated differently by this author (see text).

In the case of Musang Cave, cervid abundance contrasts with Thiel's (1988) assertion that pig is the dominant taxon in the cave sequence. As noted previously in Chapter 6, this relates to the misidentification of certain bone fragments ascribed as pigs. These time-averaged records may be reflective of general trends; however, future work must also look into possible seasonality of hunting practices in the tropics. At present, the scarcity of ecological data on the endemic fauna of the Philippines (e.g. reproduction, seasonal movement, antler shedding, etc.) set limits on speculating about seasonality patterns (see Section 8.8).

Suid counts increase in the Late Holocene, likely due to the introduction of the domestic pig. In two Late Holocene sites where domestic pig is identified (Musang Cave and Nagsabaran), suid remains outnumber cervid remains. However, the wild pig is still more abundant than the domestic pig in both sites and is not replaced by the latter. Based on dental remains, Amano (2013:323) notes that there is one domestic pig for every three or four wild pigs in Nagsabaran.

Regarding introduced taxa in Musang Cave, the patterns vary depending on the version of bone count aggregation. As discussed in Chapter 4, Thiel (1988) divided Levels 4 to 7 in G4 trench into ceramic bearing sections (4, 5, 6 and 7), and non-ceramic bearing sections (4a, 5a, 6a, and 7a). In the first version shown in Table 8.26 and illustrated in Figures 8.16b and 8.17b, we find that bovid and macaque remains are found in the Early to Middle Holocene levels (EMH). I have reservations over the Early to Mid-Holocene ascription of bovid and macaque remains in Musang Cave based on comparison with the well-dated and well-stratified record of Nagsabaran site and due to the various stratigraphic uncertainties in Musang Cave. In Nagsabaran, domestic bovids and dogs are only found in the Late Neolithic levels. When using the second version of aggregation (joining counts from 4 -7 with 4a-7a), all the introduced taxa in Musang are grouped with the Late Holocene levels. My own interpretation of the stratigraphic data is augmented by the taphonomic data, wherein in different preservation states up to Levels 7 and 7a indicate intrusive material or mixing of remains. In this sense, the macaque and bovid remains may be intrusive to 4a to 7a like the pottery, or these levels may all be ceramic-bearing levels (4 to 7 and 4a to 7a).

8.8 Subsistence Patterns in the Philippines: Historicising IEK Systems

The taphonomic histories and vertebrate subsistence records presented here also serve as a window into ecological practices and ecological knowledge systems of past human groups. They provide long temporal records by which we can historicize various aspects of indigenous lifeways of foragers that have inhabited and continue to inhabit these landscapes. These subsistence histories can potentially be linked to IEK systems recorded in ethnohistorical and ethnographic accounts. In the following ethnographic and archaeological accounts presented here, the aim is to historicize IEK systems. In the ethnographic synopsis, I highlight aspects that can be potentially linked to the zooarchaeological data. I further relate such data to diachronic perspectives on the utilisation and modification of local landscapes.

A case in point is for the modern-day Agta, which are the most documented foragers in Philippine ethnography. I briefly discuss the literature on the Agta here to serve as an introduction to the complex histories of foragers in the Philippine archipelago. Nonetheless, the Agta of Luzon is only one among many indigenous groups in the Philippines that traditionally practice foraging (among a suite of other economic strategies). On Palawan Island, for instance, the Batak, Tagbanua and Pala'wan groups also present important histories of changing economies along the foraging-farming spectrum (Eder 1987; Novellino 2007, 2010). Furthermore, ethnographic studies among the Agta and other ethnoarchaeological work during the 1980s aimed at using contemporary foragers to aid reconstruction of prehistoric foraging societies in the Philippines (Griffin and Solheim 1988; Headland and Reid 1989). It has been recognised that ethnographic analogy for the service of archaeology is fraught with difficulties; nonetheless, the economies of modern foragers do need to be taken into account in order to adequately model aspects of past foraging societies (e.g. Binford 2001; Kelly 2013).

As briefly described in Chapter 3, Agta groups inhabit northeastern Luzon, particularly the forests of the Sierra Madre and the Pacific coastline. They engage in hunting, fishing and gathering wild foods, as well as swiddening, wage labour and commercial foraging and trading (Estioko and Griffin 1975; Griffin and Griffin 2000; Headland 1987; Minter 2010; Peterson 1990; Rai 1990). The mix and scheduling of economic strategies are partly based on variability of seasons brought about by environmental perturbations such as typhoons, as well as influx of and shifting economic relations with non-Agta. The Agta live in extended family residential clusters, with some distinction held between communities living primarily near the coast, or those living inland. The latter usually live along rivers, and these waterways serve as principle foci of Agta social identity (Estioko and Griffin 1975; Griffin 1984). During the wet season (approximately October to February in northeastern Luzon), nucleation of related people usually occurs (Griffin 1984). Wet-season camps usually last for several months in adjacent locales of a particular river year after year (Griffin 1989). During the dry season, residency becomes more dispersed and there is greater mobility and diversification of subsistence activities. River terraces in the lowland forest are said to be favoured campsites; these are chosen for their proximity to hunting, forest collecting, and fishing locales, as well as to swidden fields for those Agta groups with a heavier reliance on horticulture (Allen 1985; Griffin 1989). Fishing is an important dry-season activity, in both freshwater and marine littoral habitats.

With regards to hunting, ethnographers document that in the 1970s and 1980s, the Agta considered wild pigs to be more abundant than deer, and they killed more pigs than deer (Griffin 1998; Headland 1991; Peterson 1990; Rai 1990). This is said to be partly for their preference for wild pig meat and possibly due to the environmental idiosyncracies during the period of ethnographic observation (Griffin 1984). Hunting is a year-round activity but is particularly favoured during the wet season when wild pigs have more stored fat and they can be stalked quietly on the wet forest floor (Griffin 1984; Minter 2010). Protein and fat from wild game is particularly important during the wet season, when swollen rivers are unsafe for fishing (Mudar 1985). In the dry season, prey often to retreat to higher elevation areas, which make them more difficult to track (Minter 2010). Dry season hunting is often done with dogs, which can stalk prey more silently. Dogs are said to be trained to drive startled game to hunters waiting in ambush, and hunting with dogs enable Agta to specialize in hunting and de-emphasize cultivation (Griffin 1998). Hunting with dogs is also said to be favoured by women hunters (Estioko-Griffin 1981).

An ethnoarchaeological study by Mudar (1985) on Agta hunting of wild pigs presents the only data of its kind so far in Philippine literature. The data is based on the collection of wild pig crania and mandibles from the Nanadukan Agta, which were kept by them as trophies of their hunting forays. The pig cranial materials were aged using tooth eruption and wear methods. The resulting mortality profiles indicate a bimodal pattern, wherein the youngest and oldest members of the wild pig population were harvested. This pattern is said to be reflective of active pursuit hunting, whereby the most vulnerable members of the wild pig population (immature and older individuals) fall prey to the Agta hunters, while many of the mature adults are able to escape the bows and dogs of the hunters.

As discussed in Chapter 2, tropical rainforests have been stereotypically characterised as either lush paradises, on one hand, to green deserts on the other. It has long been argued that most of the biomass in tropical rainforests are in plant growth, many of which are inedible for humans (Bailey et al 1989; Headland and Bailey 1991). Griffin (1984) has previously suggested that even with its dispersed resources, the rainforests of Luzon are game-rich environments for the Agta foragers. This may hypothetically be applicable to periods prior to defaunation during the Anthropocene. However, the 'empty forest syndrome' (Redford 1992) is presently observed across many regions, including the Philippines, wherein rainforests appear to be depleted of wildlife. Biological surveys suggest a declining trend for many native mammal species on Luzon and across the archipelago (Heaney et al. 1998; 2016a). There are limited ecological data about distribution of wild game populations traditionally hunted by indigenous groups in the Philippines. Ethnographic data from Agta communities suggest game scarcity in northern Luzon in the past few decades (Griffin and Griffin 2000; Minter 2010); consequently, several Agta communities in the past decade engage in fewer hunting trips due to lower rates of hunting success. This contrasts with previous data (Estioko and Griffin 1975; 1981) from at least two decades before, wherein certain Agta groups had higher hunting success rates. The latter led Griffin (1984) to suggest the idea that the tropical rainforests of Luzon were game-rich habitats that could sustain foragers, even as these forests are relatively carbohydrate-poor.

Socio-economic changes and increasing influx of non-Agta into traditional Agta territories has brought about much transformation in Agta economies. Overhunting and deforestation by non-Agta colonists has contributed to the game scarcity described above (Griffin and Griffin 2000; Headland 1991; Minter 2010). Another example of transformation relates to female hunting. Ethnographic work by Estioko-Griffin (1981, 1984) famously documented women hunters among the Cagayan Agta in the early 1980s. However, later studies show that women hunters were increasingly rare by 1985 (Griffin and Griffin 2000) and were no longer documented in later communities studied in the 2000s (Minter 2010; Dyble 2016). Hunting tools have also shifted, from the predominant use of bows and arrows to an increase in the use of shotguns in the last few decades (Griffin and Griffin 2000; Headland 1991; Minter 2010; Rai 1990).

Moving back in time, historical records document forager exchange relations with lowland and coastal complex polities engaged in the maritime luxury goods trade by at least the first millennium AD (Jocano 1975; Junker 2002a; Scott 1983, 1984). Early Spanish sources note that lowland chiefs, whose polities were located in major river valleys and coastal areas, relied on foragers of the interior for forest products and raw materials such as gold ore, iron ore, beeswax, hardwood, animal hides and civet (see Hutterer 1974; Junker 1999, 2002b). Historical archaeological research in the Visayas region further support this. Based on the archaeology of the Basey region of Samar Island, Hutterer (1974; 1976) has proposed a model of internal trade between coastal port communities and foragers and/or swiddeners living in the interior that had territorial access to the forest products that circulated in maritime trade. Such inter-ethnic exchanges are said to be related to intra-regional diversity and availability of forest resources. In the Tanjay region on Negros Island, archaeological data also demonstrate the presence of a maritime trading chiefdom in the central Philippines as early as the twelfth century, even though Chinese historical records make no mention of this polity (Junker 1999; 2002). Pottery and other artefacts traded into and found in hunter-gatherer camps around Tanjay document at least a millennium of exchange between foragers and agriculturalists.

These archaeological data from the Visayas Islands from the first millennium to the onset of European contact could not resolve the 'wild yam question' posed by Headland (1987). This pertains to the issue of whether tropical rainforest foragers could live independently of starch staples sourced from agriculturalists. As discussed in Chapter 2, the antiquity of rainforest foraging across the Indo-Pacific has been pushed back to at least 40,000 years based on archaeological data from Borneo, Sri Lanka and New Guinea. This puts to rest the wild yam question and shifts the discourse to understanding the behavioural flexibility and adaptations of tropical rainforest foragers from the beginnings of modern human colonisation of these environments. As archaeological and palaeoenvironmental data from the Philippine archipelago has increased this past decade, we can now add considerable time depth to the long-term dynamics of forager lifeways on Luzon and Palawan.

8.8.1 Island-specific Adaptations and Tropical Rainforest Foraging

The archaeological patterns described in Section 8.7 provide insights into tropical rainforest foraging practices and island-specific adaptations across time. These adaptations are likely reflective of the existing ecology of the area at a particular period. During the LGM, the evidence from Pilanduk Cave shows a focus on large game hunting and freshwater foraging in this site. The vertebrate assemblage is clearly dominated by deer, with only a minimal input from other species, whether of large taxa (like wild pigs and tiger) or medium and smaller sized taxa (such as macaques, monitor lizards and turtles). The predominance of deer hunting is potentially reflective of the more open environments posited for Palawan during the LGM (Bird et al. 2007; Wurster et al. 2010). The data on freshwater foraging derives from the molluscan record reported by Kress (1990), wherein a large percentage of the Pilanduk shell remains come from freshwater and terrestrial species, rather than brackish or marine species.

This LGM subsistence record provide insights into inland foraging strategies, since Pilanduk would have been around 40 km away from the coast during this period. The focus on large game hunting and freshwater foraging may be reflective of seasonal subsistence strategies of inland foragers. Alternatively, it may also reflect the strategies of foragers that have broader territorial ranges and that move seasonally between inland and coastal locales. In the Terminal Pleistocene levels of Ille Cave in northern Palawan, the predominance of deer among human prey species is still observed. Similar to Pilanduk, Ille Cave would have been further inland during the Terminal Pleistocene.

The seasonality and scheduling of subsistence activities is difficult to assess given the available data and requires further consideration in future work. To date, we still do not have detailed ecological data for many of the endemic animals of the archipelago, including those for wild pigs and deer. The ethnographic data from the Agta presents some insights about Luzon warty pigs. Information from hunters and hunters' kills (e.g. Griffin 1984; Mudar 1985; Minter 2010) indicate that wild pigs start to give birth at the end of the rainy season and into the middle of the dry season (Mudar 1985; Peterson 1981). However, the gestation period is not known. Wild pigs are also said to put on fat before the wet season. These data partly explain the seasonal preference for pig hunting in the wet season. In contrast to the bearded pigs of Borneo, which undergo large-scale population movements, seasonal migrations for Philippine pigs have not been reported (see Oliver 1993).

Behavioural biological data for endemic Philippine deer species are also scarce. As a point of comparison, the males of the congeneric sambar (*Rusa unicolor)* of South and Southeast Asia are said to be found in various stages of antler growth throughout the year (Leslie 2011). Such data precludes inferring seasonality patterns using archaeological antler remains, as is typically done for deer species from higher latitudes. The gestation period for the sambar is said to be eight months, but some reports it could be longer. For the Visayan spotted deer (*R. alfredi*), it is reported that in captivity, calving occurs year-round and that young animals are reported to be captured in the wild at all times of the year (Blouch et al. 1998; Cox 1987).

Despite these limitations, some further observations may be noted regarding hunting practices on Palawan and Luzon across the Holocene. Some authors have remarked that broad-spectrum foraging strategies are characteristic of the adaptive repertoire in tropical rainforest environments in Southeast Asia (O'Connor and Bulbeck 2014). On Luzon and Palawan, there is variation observed between foraging strategies, which reflects the differing ecologies and distribution of resources on the two islands. On Palawan, palaeoenvironmental proxies suggest the expansion of closed tropical rainforests by the onset of the Holocene (Bird et al 2007; Wurster et al. 2010). The Holocene vertebrate records from Ille and Pasimbahan Caves show a higher diversity of targeted species. The assemblages are still highly uneven and dominated by large game, but arboreal taxa (macaques and civets) and other medium-sized vertebrates appear in greater numbers across the Holocene sequence. This stands in contrast to the LGM record of Pilanduk.

The variability in hunting strategies is also connected with the changing palaeogeographic configuration of Palawan Island. This shift from deer to pig hunting and the broadening of the prey base relates to island-wide ecological changes on Palawan during the Holocene. This is evident from the palaeogeographic data discussed in Chapters 2 and 7, wherein much of Greater Palawan was inundated due to post-LGM sea-level rise. This led to a drastic decrease in exposed land area and habitat. The molluscan data also present striking changes in the relative abundances of particular species across time. The Late Pleistocene record of Pilanduk Cave shows a predominance of freshwater and terrestrial species (Kress 2000). The period of occupation occurs during a time of lowered sea levels, and the coast was at least 40 km away from the site. The Early Holocene record of Pasimbahan Cave shows a similar trend of mollusc abundances (Ochoa et al. 2014). By the Middle Holocene, characteristic dense shell midden deposits are documented across the island. In contrast to the earlier shell middens, the Mid-Holocene middens consist mainly of mangrove and marine species. This has been observed in Ille, Pasimbahan and Sa'gung Caves (Kress 2000; Ochoa et al. 2014; Szabo et al. 2004). The timing of appearance of these middens is said to be related to the proximity of sites to mangrove areas during the Mid-Holocene sea-level high-stand and the stabilization and expansion of mangrove systems during this period (Robles et al. 2015). During the Terminal Pleistocene, Ille and Pasimbahan Caves would have been over 50km inland, whereas at present they are less than 5 km away from the coast.

On Luzon, the focus on large game is reflective of the local ecology of the island, wherein deer and pigs form the bulk of the animal resource. There is a more limited array of human prey species on Luzon compared to Palawan; nonetheless, deer and pigs may have been sufficient to supplement the protein and nutritional needs of Holocene foragers in the Callao area, alongside freshwater resources. In the Minori and Musang record, fish remains are relatively low, but it is uncertain whether this is an artefact of preservation. Thiel (1990) also reports the presence of molluscs across the Musang Cave sequence, which primarily consists of the freshwater snail *Thiara scabra*. Along with Callao Cave, the sites are strategically located beside a major tributary of the Cagayan River, and *T. scabra* is still observed in the river today.

There is a contrast to note between the Holocene distribution of deer remains in Minori and Musang Caves compared to the reported preference of the Agta for wild pig in recent decades. This may partly have to do with the decreasing population trend of the Philippine deer across its modern range. Seasonality of hunting practices and the effects of environmental perturbations may also be at play in the archaeological record, and this should be explored in future work. As described above, deer is the dominant taxon in the non-ceramic bearing layers in these two sites, whereas pig remains become equally abundant or more abundant than deer remains in the Late Holocene sites of northeastern Luzon (including for Nagsabaran and Pintu Rockshelter). These archaeological records differ with ethnographic records, which shows that wild pig is the preferred and most hunted wild game. These diachronic records demonstrate the variability in hunting patterns in this part of Luzon.

8.8.2 Hunting Practices and Landscape Use

The zooarchaeological data can also be linked to long-term patterns of landscape use. The archaeological data across Palawan Island lends itself useful for such an exploration. As described in Section 8.3, the well-preserved bone assemblage of Pilanduk Cave shows an LGM record of residential cave occupation that is specialised towards hunting of large game. The archaeological evidence from the site allows us to explore the interpretation of it as a central place wherein highly valued food resources were consumed and shared. Taphonomic evidence shows the transport, butchery and discard of entire deer carcasses on site. This implies that the consumption of high-quality meaty parts occurred in the cave, and that entire animals would have likely been shared among several individuals. Meat of large animals is said to be widely shared among human foraging societies and food sharing to be integral to forager social interactions (see e.g. Hawkes et al. 2001; Kelly 2013). In Pilanduk Cave, the targeted deer taxon falls between the size range of *Rusa marianna* (40-96 kg) and *Rusa unicolor* (109-260 kg). It is highly likely that deer of this size range were shared among several human individuals or even family units. Marrow consumption is also evident from butchery evidence and this accounts for an important fat and nutritional resource. Together, meat and marrow constitute high quality dietary sources and also likely represent highly valued resources, given the universally high social valuation of meat among foragers (e.g. Binford 2001; Hawkes et al. 1991; Kelly 2013; Marlowe 2010; Minter 2010; Widlok and Tadesse 2005).

The ubiquitous evidence for hearth remains across the LGM sequence of Pilanduk Cave also draws attention to the role of cave hearths as food processing and social hubs. Fire and hearths have deep human evolutionary significance, providing various advantages such as cooked food, warmth, light and protection from predators (Brown et al. 2009; Shimelmitz et al. 2014: 197; Wrangham and Carmody 2010; Wrangham et al. 1999). All of these advantages appear applicable in the Pilanduk case, including protection against predatory tigers. Indeed, the strategic location of the cave and the configuration of its steep cave platform may have lent security advantages that accounted for its choice as residential camp. Fire was also used for the maintenance of the site, as is evident from the use of fire on bone discard. Stiner and colleagues' (2011; see also Blasco et al. 2014) further extend the argument for 'hearth-side socioeconomics', wherein hearths provide forums for complex social manoeuvres and cooperation as early as the Lower Palaeolithic. Campfires are also known ethnographically as settings for complex social interactions among foragers, including for story-telling (e.g. Dunbar 2014; Wiessner 2014). Recent work with the Agta of Luzon, for instance, documents the importance of campfire tales and their implication for evolutionary models for social cooperation (Smith et al. 2017). Minter (2010) also documents the centrality of game animals and animals in general among the Agta, and how animal tales are shared over evening campfires. In addition, the ubiquity of flake tools and lithic debitage across the LGM sequence also present Pilanduk as a site for tool manufacture. Preliminary aggregate analysis of the lithic remains during this phase appears to indicate the presence of all stages of the lithic manufacturing sequence (Manipon 2017). Although we can only speculate about the nature of social interactions occurring on the site, the archaeological and faunal data mark Pilanduk Cave (and Magmisi Peak) as an important central place in the landscape where people assembled to consume valuable food resources and where campfires provided a conspicuous setting for social interactions. Within such a setting, food resources were likely shared and the attendant skills involved in the processing of such resources (e.g. hunting, butchery, tool manufacture, etc.) may have also been performed and shared.

Moving into the Holocene, the symbolic marking of caves and karst formations in the landscape has been explored by Paz (2012) for the Dewil Valley record of El Nido, northern Palawan. Several cave sites in this karstic valley have been used as burial grounds for millennia, including for highly complex cremation burials in the Early Holocene phase of Ille Cave (Lara et al. 2015). These human cremations at Ille represent the oldest of their kind in Southeast Asia. In the Mid to Late Holocene levels, flexed and extended human burials are also observed. These burials cut into shell and bone middens across the sequence. This shows the continuous and intermittent usage of Ille cave as both burial ground and campsite in the last few thousand years. In modern times, Paz (2012) also notes that caves in the El Nido area are labelled by the local Tagbanua and Cuyonon as 'Pasimbahan', which roughly translates to 'place of worship'. Various kinds of votive artefacts are found across the Holocene sequence in these cave sites, and ritual offerings have continued into modern times. In central Palawan, an outcrop called *Linaminan* (house/place of *Linamin*) has also produced archaeological evidence that dates back to the 9th-10th centuries AD and is hypothesised to have been used as a ritual space based on the votive artefacts on-site (Szabo et al. 2007). *Linamin* is a female natural deity and the site is perceived as a sacred space by the indigenous Pala'wan.

8.8.3 Anthropogenic Modification of Environments

A final example drawn here pertains to instances of landscape modification, which clearly involve ecological know-how and changing ecological relationships of humans to their environments. An example that stands out from the archaeology of the Indo-Pacific region relates to early vegeculture and forest management practices (Barton and Denham 2018). In the case of Palawan, preliminary evidence for plant management strategies is found in Ille and Pasimbahan Caves (Barker et al. 2011; Lewis et al. 2008; Ochoa et al. 2014). More extensive data are evident from the archaeology of Borneo (Barker et al. 2017) and the New Guinea highlands (Denham et al. 2003; Summerhayes et al. 2017). These data demonstrate how the 'cultured forests' of SEA and Oceania have long histories of human management. Within the faunal data presented here, an example that can be drawn for ecological modification involves animal translocations.

The introduction of taxa on Luzon in the Late Holocene presents pervasive ecological changes that were previously not recognised. Translocation events have the impact of changing the local ecology and initiating trophic cascades that often leads to biodiversity loss (Doherty et al. 2016; Lambertini et al. 2011). As archaeological evidence from Luzon shows, macaques and palm civets were introduced by humans during the Late Holocene. These species are considered economically and culturally favoured animals and have been translocated widely across Wallacea (Heinsohn 2003). Although there are possible earlier instances of translocations across ISEA, the emerging picture seems to be that most translocations occurred *after* the earliest introductions of pottery and domestic animals (Piper 2017). Macaques and palm civets are now naturalised across Luzon and the oceanic Philippines. They are viewed as native wild species by local inhabitants and are hunted up to the present for their meat, skins, and other body parts.

The introduction of non-native wild species is a form of ecological intervention that represents a changing logic of engagement of local inhabitants who released (whether through migration or trade) new animals in the landscape. Such practices appear to stand in contrast to past practices of local foragers that have occupied the islands prior to these translocations. These translocations may have partly benefited Neolithic or Late Neolithic human communities for the addition of wild game into the landscape that served various purposes. Nonetheless, as discussed in Chapter 7, these introductions have also negatively impacted island faunas.

8.9 Conclusion

This chapter has provided the taphonomic evidence for the three study sites of the research. Data on various biostratinomic and anthropic variables have provided taphonomic histories of the assemblages. The well-preserved bone assemblage of Pilanduk Cave presents various lines of evidence for the preferential selection and consumption of *Rusa* deer (large deer). Carnivore ravaging is very minimal, which suggests that humans were the main accumulators of the assemblage. Of the rare evidence for carnivore ravaging, the evidence points to tiger gnawing, which in turn lends further support to the hypothesis of their natural distribution on Palawan Island. Butchery marks on three tiger foot bones also suggest possible skinning for tiger fur. The predominance of deer in Pilanduk Cave contrasts with the Holocene subsistence record of Ille and Pasimbahan Caves, wherein medium-sized mammals and reptiles are increasingly well-represented. This broadening of the prey base is possibly connected to the expansion of lowland rainforest at the onset of the Holocene.

In the case of Minori and Musang Caves, the imprint of various biostratinomic and diagenetic processes has limited the inferences on prey processing and consumption. Nonetheless, species representation in these sites provide a valuable dataset to assess subsistence patterns across time and compare hunting practices between the two islands. Similar to the Palawan record, deer is the dominant prey choice in the Late Pleistocene of Luzon. However, the Holocene assemblages differ between the islands. Deer is still a dominant prey choice on Luzon up to the Mid Holocene, whereas on Palawan, deer are increasingly rare by this time. Deer become extinct on Palawan, whereas deer remains extant on Luzon up to the present. The contribution of pig remains on Luzon is increased by the Late Holocene due to the incorporation of domestic pigs. However, as discussed above, domesticates do not replace wild taxa in the Neolithic as the base of the diet. Medium-sized mammals are abundant across the

Holocene sequence of Palawan, owing to their natural distribution on the island. On Luzon, medium-sized mammals in the form of macaques and palm civets only appear in the Late Holocene record, suggesting their invasive status and human introduction during this period. The Late Holocene record of Luzon also documents the introduction of domestic pig, dog and carabao.

Lastly, this chapter has contextualised the subsistence data within long-term perspectives on foraging lifeways. The chapter has presented an initial attempt to link ethnographic and archaeological studies of Philippine foraging economies to the zooarchaeological analysis. This exploratory narrative has shown that taphonomic histories and subsistence records from Luzon and Palawan can be re-framed as aspects of IEK systems of human groups that have inhabited these landscapes.

Chapter 9 Late Quaternary Biodiversity Changes and Human Palaeoecology in ISEA: Summary and Conclusions

9.1 Introduction

This concluding chapter presents a summary of the major results of the thesis and addresses the two research questions laid out at the beginning of this work. The first question relates to biodiversity changes in tropical island faunas, while the second question involves human ecological responses and behavioural adaptations in tropical island environments. I relate these discussions to broader thematic issues in archaeology, biogeography and conservation, as well as to new archaeological findings in ISEA. To end, some avenues for future work are suggested.

9.2 Biodiversity Changes Across the Holocene

This thesis has laid down groundwork to build robust faunal sequences and archaeological chronologies that document palaeoecological changes across the Late Quaternary. The construction of faunal sequences for the Philippines has been hampered by large gaps in chronologies from the Late Pleistocene to the near-present. The sequences assembled here were made possible by directed efforts to fill in some of the chronological gaps in the Late Pleistocene and Holocene. For Palawan, it was necessary to provide a Late Pleistocene faunal record to connect to existing Holocene assemblages. This has been realised with the re-excavation and re-dating of Pilanduk Cave in southern Palawan. Re-dating of the archaeological sequence confirms two Late Pleistocene occupation phases: an older phase at 25,000 cal BP and a younger phase at the Last Glacial Maximum (21,000-20,000 cal BP). The excavation yielded a well-preserved faunal assemblage. Morphological and taphonomic studies of the remains confirm the LGM presence of the tiger (*Panthera tigris*) on Palawan. The inventory for tiger bones total to nine specimens and taphonomic evidence also point to tiger gnawing on a few deer bones. The study also provides a taxonomic diagnosis for two cervid taxa (*Rusa* sp. and *Axis calamianensis*) based on antler and post-cranial remains. All three large mammals are locally extinct.

In the case of Luzon, it was necessary to provide well-described Holocene archaeofaunas that can be connected to existing Pleistocene and Late Holocene sequences. The Minori and Musang Cave assemblages serve to fill in the Holocene gaps and have provided records for several native and non-native taxa of Luzon. Included among records of native taxa are those for previously unknown and extinct giant cloud rat species from the genera *Carpomys* and *Crateromys*. *Carpomys* sp. represents a *de novo* species discovery, and the fossil *Crateromys* likely also represents a new species. These fossil discoveries add to the latest neobiological inventory of previously unsuspected mammalian diversity on Luzon. The very high species discovery rate works towards augmenting what biologists label as the 'Linnaean shortfall'. This refers to the fact that only a small fraction of species globally are known to science (Lomolino et al. 2016; Whittaker et al. 2005). The fossil record tends to produce records of new species, especially in the Pleistocene or older geological periods. Given that the modern mammalian fauna of Luzon is now relatively well-described (Heaney et al. 2016a), what is surprising about the new fossil murid records is that these taxa are of Holocene-age that persist into the Late Holocene. Of the four murid taxa identified in Minori and Musang Caves, two of them are previously unknown extinct species.

The *in situ* speciation and diversification of vertebrate lineages on Luzon also weigh upon human evolutionary dynamics, due to the announcement of a new endemic and small-statured human – *Homo luzonensis* – from Callao Cave in Luzon (Détroit et al. 2019). Signs of hominin presence have been reported for the Middle Pleistocene of Luzon (Ingicco et al. 2018) and Flores (Brumm et al. 2010), which come in the form of lithic tools found in association with megafauna. Hominins were also present in Sulawesi by at least 118,000 years ago (van den Bergh et al. 2016). These findings show that the evolution of *Homo floresiensis* in ISEA was not just a one-off process of hominin evolution in an oceanic island. Instead, human diversification occurred not only in the African and Asian continents, but also in the oceanic islands of Southeast Asia. Investigating the evolution of *H. luzonensis* requires understanding its biogeographic context, and the faunal sequences and diagnoses of native and non-native taxa presented here contributes towards understanding the faunal community in which this human species evolved.

The fossil records analysed and assembled here have also worked towards understanding the sequence and timing of biodiversity changes. As described in Chapter 7, two major changes and processes are observed across the Holocene: extinctions without replacement and the human introduction of invasive species. On Palawan, last occurrence records for the tiger and rusine deer indicate Early Holocene extinction events. Last occurrence records for the Calamian hog deer indicate a Late Holocene extirpation event.

Currently, all known Holocene extinction records on Palawan are of large mammals. In contrast, Holocene extinction records for Luzon are only of small mammals, and they occur in the Late Holocene.

The asynchronous timing of Holocene extinctions underlines the observations by Turvey and Fritz (2011) that different processes are responsible for past and present extinction processes. Large mammal extinctions on Palawan during the Early Holocene appear to be largely driven by environmental changes during the Pleistocene-Holocene transition. Human hunting cannot be discounted, nonetheless, as deer were evidently intensively hunted across the island. The eventual disappearance of the species may have been compounded by human hunting of a species that was becoming increasingly rare. The case of the hog deer differs from the rusine deer in that the former persists into the Late Holocene. In the absence of evidence for extensive environmental change during this period that parallels that of the Pleistocene-Holocene transition, anthropogenic factors appear to be the main driver of extirpation for the Calamian hog deer.

Late Holocene faunal disappearances on Luzon also appear to implicate human impacts. An important factor that has been discussed in this thesis is that of the introduction of invasive species. The Luzon record provides the first archaeological confirmation for the introduction of macaques and palm civets into the oceanic Philippines. This contrasts with the case of Palawan, where there are Late Pleistocene (for macaques) and Early Holocene (for civets) records for these taxa on the island. Archaeological records on Luzon indicate that both species are present only in ceramic-bearing archaeological levels, indicating human introduction not earlier than the Neolithic. A direct date on a macaque tooth from Minori Cave provides a minimum age for its introduction at 1827–1706 cal BP.

In a global summary of the biogeography of extinctions of island mammals, Kouvari and van der Geer (2018) observe the anomalously low records of extinction for the Philippines. This observation calls attention to how little we know still about past extinction dynamics in the archipelago, and the same is true for many parts of ISEA. On Luzon, the fossil records presented in this thesis only cover one out of eight recognised centres of endemism ('sky islands'). Each of these centres supports endemic taxa found only within its restricted area. According to historical records, the Cagayan Valley is one of the areas of Luzon that was heavily deforested during the colonial era (Bankoff 2007). Other areas that have historical records for high human population density are the Ilocos region and the area surrounding Manila and Laguna de Bay. These lowland areas were the first to be deforested in the last four centuries. The records of three extinct lowland species in the Cagayan area raises the question of what lowland species might have been previously supported by these other areas of Luzon.

Anthropogenic activities have been shown to profoundly impact patterns of species diversity on islands by rendering native assemblages depauperate and inflating species richness with introduced taxa (van der Geer et al. 2017). The Luzon fauna remains incredibly speciose unlike that of other oceanic islands around the globe. One primary reason for this is that many living non-volant species are montane taxa or elevational generalists (Heaney et al 2016a). The extinction records presented here are those of lowland species, and it is in the lowlands where human activities have been most intensive. The Luzon fauna is exceptionally biodiverse and remains so in the Anthropocene, but the extinction records of native small mammals raise the question of how much lowland species diversity has been reduced by the human extinction filter phenomenon across the Holocene. As discussed in Chapter 7, Holocene extinction records have also come to light in the Wallacean islands of Flores, Timor, Sumba and Alor (e.g. Aplin and Helgen 2010; Locatelli et al. 2015; Louys et al. 2018; Meijer et al. 2010, 2019; van den Bergh et al. 2009). Among the documented extinctions are various murid rats, and the proposed extinction drivers for these species are increased aridity and deforestation of the islands (Louys et al. 2018). Unlike Luzon, the faunas of these islands have not been as extensively surveyed by neobiologists, but it is argued that certain fossil murid species identified in Timor, Sumba and Alor are likely presently extinct. On Luzon, living giant cloud rats are well-documented, and hence the fossil cloud rats belonging to *Carpomys* and *Crateromys* described from Musang and Minori Caves are deemed presently extinct.

These new extinction records lead our attention to neobiological estimations of species diversity. As observed by Helmus et al. (2014) and van der Geer et al. (2017), long-standing models of island biogeography can prove inadequate unless they take into account the impact of human activities on the processes of immigration, speciation and extinction. In many oceanic islands across the globe, species introductions appear to have artificially inflated mammalian richness, particularly on small islands with relatively depauperate faunas. However, on an exceptionally biodiverse and large oceanic island such as Luzon, eleven non-native mammal species are dwarfed by the current count of 56 native species (Heaney et al. 2016a). With the extinction records of at least three native species (*Carpomys* sp. and *Crateromys* sp. reported here and *Batomys* sp. reported by Heaney et al. 2011), the question arises whether introduced taxa replaced more vulnerable native taxa upon initial introduction. In this regard, species introduction may superficially inflate mammalian species richness in the present day, but invasive taxa may also be involved in an extinction filter that has reduced native species richness in the Late Holocene of ISEA. In Oceania, avian extinctions are relatively well-documented, with the Holocene arrival of humans resulting in rapid biodiversity loss (Steadman 2006).

In the case of Luzon, what is of interest is the underestimation of *lowland* species richness. It has been observed in several Philippine islands that mammalian species richness reaches its peak in montane elevations (Heaney 2001, Heaney et al. 2016b, Hutterer et al. 2018). However, when extinction records of lowland mammals are considered, it appears that lowland species richness is underestimated by models that are based solely on modern biotas.

Moreover, the extinct cloud rats recorded for northeastern Luzon represent an expanded array of body sizes of cloud rats. This is further testament to the morphological and ecological diversity of this particular clade and to the extraordinary evolutionary laboratory that the Philippine archipelago represents. The two Old Endemic murid lineages – cloud rats (Phloeomyini) and earthworm mice (Chrotomyini) – are said to be most abundant and diverse at medium to high elevations (Heaney et al. 2010, 2016b). The records for extinct cloud rats in the Cagayan Valley indicate that there was also diversification occurring for lowland taxa. The clarification of the status of macaques and civet cats as non-natives also implies that the diversification of murids in the oceanic Philippines occurred without the presence of these taxa. This may partly elucidate the evolutionary radiation of the Muridae on Luzon.

These observations also raise the issue of mammalian extinction risk in the past and the present. As noted in Chapter 7, the resiliency of the living endemic fauna must be re-assessed in light of fossil extinction records. The latter suggests that there were vulnerable taxa that became extinct in the Late Holocene. What we can presently characterise as resilient taxa among lowland species are elevational generalists – i.e., species that occur across elevational gradients of the 'sky islands' of Luzon and this contributes to their survival amidst intensive human disturbance of lowland habitats. There is also a need to study ecological interactions of macaques and palm civets with endemic species and to assess whether these are ecologically benign or harmful. These interactions have been overlooked in the past, partly due to the perceived native status of macaques and palm civets. This recommendation follows previous suggestions that further research is required to investigate whether mammal faunas that have survived past extinction filters are now threatened by different anthropogenic threats (Turvey 2009; Turvey and Fritz 2011: 2573).

The palaeobiological data presented in this thesis aim to contribute to conservationist aims to protect and preserve modern biodiversity in this recognised hotspot. Palaeobiological data across the globe have been increasingly refined by archaeological efforts and these have significant potential to inform present-day conservation decisions (Lyman 2012; 2015). In the biodiversity hotspots of ISEA, an important goal is to create baselines and benchmarks by which we can describe and model biodiversity patterns before and after the colonisation of humans. Both modern and fossil faunas for many of these islands remain poorly known.

Documentation of fossil faunas can have direct contributions to conservation assessments. For instance, previous data for the identification of the Calamian hog deer on Palawan Island (Ochoa 2009; Piper et al. 2011b) have led to conservation recommendations for its reintroduction to Palawan (Widmann and Lastica 2015). This recommendation comes from a broader discourse regarding the potential of Pleistocene re-wilding for the conservation of endangered taxa (e.g. Donlan et al. 2006; Louys et al. 2014). As the thesis also shows, the fossil record provides direct evidence for the identification of invasive taxa versus long-term residents of a faunal community. Fossil records can also facilitate the identification of susceptible taxa, and these can have implications for understanding extinction risk in the present. Invasive taxa are known to be major drivers of recent extinctions and endemic island faunas are most vulnerable to invasive predators (Bellard et al. 2016; Doherty et al. 2016; Tershy et al. 2015). In this light, recent calls have been made to gradually eradicate invasive mammals on islands in order to protect threatened native taxa (Holmes et al. 2019).

Taken together, the zooarchaeological records presented here provide greater insight into the exceptional biodiversity of the Philippine archipelago. The records for extinct taxa and invasive taxa have considerable implications for understanding mammalian biodiversity dynamics. These records also contribute pertinent data that are beneficial for conservation strategies.

9.3 The Philippine Faunal Subsistence Record Across Time

The faunal records assembled here document not only biodiversity changes in the archipelago but also human adaptations in the tropical island environments of ISEA. In particular, they provide complex detail to island-specific adaptations that humans have tailored to local environments and that reflect the changing ecology of the area from the Late Pleistocene to the Late Holocene. In the Holocene, there is also growing evidence for human environmental impacts on faunal communities.

As Rabett (2012) has previously observed, previous simplistic portrayals of tropical hunter-gatherers have masked the complex archaeological evidence for behavioural variability of *Homo sapiens* across the region. Although the focus of this section is on subsistence strategies, it is worth mentioning that localised adaptations are clearly reflected in lithic, bone and shell technological traditions of ISEA. These are evident, for instance, in the Toalean tradition of Sulawesi (Bulbeck et al. 2000; Glover 1976), scraper and side-scraper assemblages from East Timor (Glover 1986), bifacially flaked points from Eastern Java assemblages (Simanjuntak and Asikin 2004) and the bone industry at the Niah Caves of Borneo (Rabett 2016; Rabett and Piper 2012). Furthermore, with the recent announcement of *Homo luzonensis* (Détroit et al. 2019), our attention is drawn not only to the behavioural variability within our species, but to the evolutionary diversity of the genus *Homo* within ISEA. The investigation of 'rainforest prehistories' (Mercader 2002b) is also brought into the forefront, whereas previously these environments have been viewed as prehistoric backwaters. The presence of at least four human species now known in ISEA suggests that tropical rainforest and other tropical island environments appear to be part and parcel of human diversification and *in situ* speciation. Past characterisations of behavioural patterns have predominantly relied on descriptions of flake-based lithic traditions that are widespread in the region. One thing that can be surmised from this body of evidence is that lithic reduction sequences cannot be taken as a wholesale representation of human populations' technological complexity (Rabett 2012:184). Instead, other technological and symbolic media in the form of bone artefacts, shell tools, and cave 'art' require further attention (Aubert et al. 2014; Brumm et al. 2017; O'Connor et al. 2014; Szabo et al. 2007). In this regard, the growing tropical subsistence record of the region is now providing a wealth of evidence for human behavioural variability from the Late Pleistocene to the Holocene. It is within this context that I summarise the evidence from Philippine vertebrate faunas.

9.3.1 Foraging Patterns and Human Environmental Impacts

The synthesis of archaeofaunal records from various Philippine sites documents particular aspects of foraging lifeways – in this case, that of hunting patterns and procurement of vertebrate resources across time (Figure 9.1). Deer is central to many human cultures (Baker et al. 2015), and this pattern is replicated in the Philippine faunal record. Deer appears to be a consistent resource that humans relied on in the archipelago across time. More generally, large herbivores appear to be a regular subsistence target of hominin populations in Southeast Asia from its earliest occupation (Rabett 2017). On both islands of Luzon and Palawan, deer is the largest human prey in the Late Pleistocene. It is worth noting here the available large game on both islands to show a picture of varying local ecology. On Palawan, the tiger would have been the largest wild animal in the landscape in the last 21,000 years followed by the rusine deer, whereas on Luzon, deer would have been the largest vertebrate after the extinction of the Middle Pleistocene megafauna. This contrasts with other Sundaic islands and the Southeast Asian Mainland that have a wider variety of large mammals, and with some Wallacean islands where giant rats would have been the largest mammal that Holocene human inhabitants would have encountered. It must be noted, though, that the Late Pleistocene record for Callao Cave (Figure 9.1) now represents subsistence behaviour for *Homo luzonensis*, and not *H. sapiens.* During this period from 67,000–50,000 BP, at least one member of the Middle Pleistocene megafauna was still extant, a large bovid possibly similar to the tamaraw (*Bubalus mindorensis*) of Mindoro Island. There is no evidence yet on the timing of extinctions of the Luzon megafauna, but the identification for *H. luzonensis* raises the question of possible long-term impacts of a different kind of human on the faunal community of Luzon. The presence of *H. sapiens* on Luzon is surmised for the Holocene based on proxy evidence from Palawan and other islands in ISEA, although human remains have not been reported from the MIS-2 or the Early Holocene assemblages of Luzon. In the case of Palawan, *H. sapiens* fossils are recorded from the Late Pleistocene levels of Tabon Cave (Détroit et al. 2004) and Early Holocene levels of Ille Cave (Lara et al. 2015).

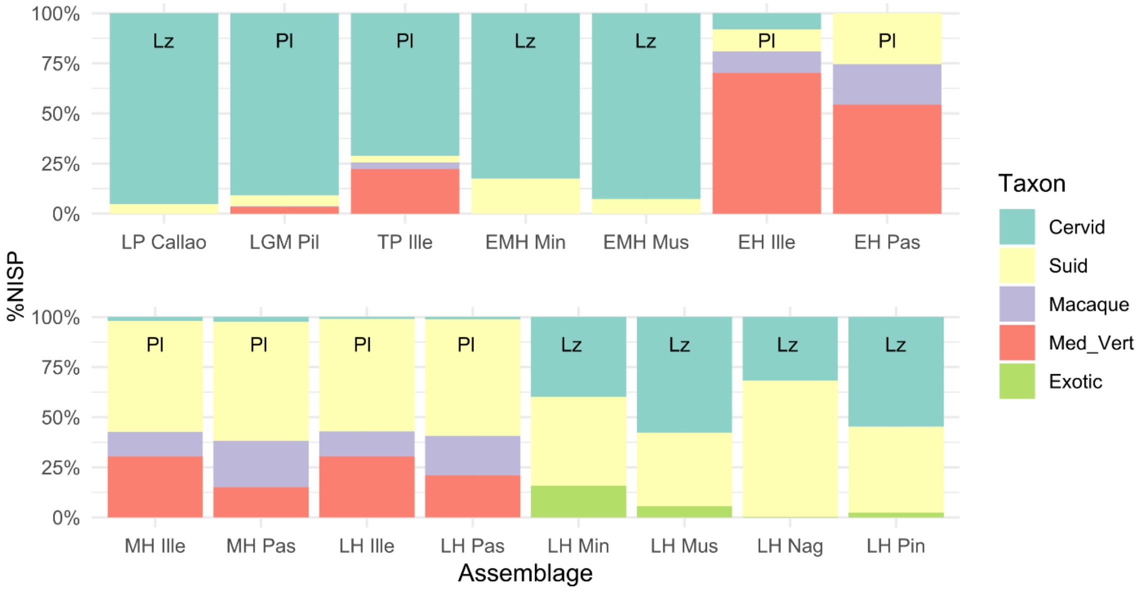


Figure 9.1 Summary of human prey distribution (as %NISP) in Luzon and Palawan across time. Lz = Luzon assemblage, Pl = Palawan assemblage. Temporal markers: LP = Late Pleistocene, LGM = Last Glacial Maximum, TP = Terminal Pleistocene, EMH = Early to Mid Holocene (for Luzon), EH = Early Holocene (for Palawan), MH = Mid Holocene, LH = Late Holocene. Sites: Pil = Pilanduk, Min = Minori, Mus = Musang, Pas = Pasimbahan, Nag = Nagsabaran, Pin = Pintu. Pilanduk, Ille and Pasimbahan are from Palawan Island, whereas the rest are from Luzon. Med_Vert = medium sized vertebrates (includes mammals and reptiles), Exotic = non-native taxa.

The LGM levels (~21,000 cal BP) of Pilanduk Cave present an occupation site that was focused on large-game hunting and consumption of deer. The predominance of deer and the low abundance of other forest species may be in support of postulated drier and more open environments on the island during the Last Glacial Period (Bird et al. 2007; Wurster et al. 2010). A similar pattern continues into the Terminal Pleistocene (14,000 cal BP) record of Ille Cave, where deer is still the dominant taxon and other rainforest taxa are more limited. In other parts of Southeast Asia, a reduction in the faunal base is also evident in some sites during the Terminal Pleistocene (Rabett 2012), as well as site abandonment in arid locales during the LGM (O'Connor and Bulbeck 2014).

At the onset of the Holocene, a broadening of the vertebrate resource base is evident in the Palawan record, with the incorporation of various arboreal, semi-arboreal and other medium-sized vertebrates. This appears to be consistent with the broad-spectrum tropical forest subsistence observed in other parts of SEA. In sites where there is palaeoenvironmental evidence for the presence of tropical rainforests, there appears to be a broad range of taxa and habitats that humans utilised. The earliest evidence for tropical rainforest reliance in South (Sri Lanka) and Southeast Asia (Sumatra and Borneo) shows utilisation of a broad range of rainforest taxa, with local variations on the targeting of small and large game, as well as mollusc and aquatic resources (Barker and Farr 2016; Roberts et al. 2015; Wedage et al. 2019; Westaway et al. 2017). The pattern observed on Palawan partly chimes with the evidence from Song Terus and Braholo Cave in Java (Amano et al. 2015). A reliance on taxa adapted to open environments is observed during the LGM, and a subsequent reliance on arboreal and semi-arboreal taxa becomes evident at the onset of the Holocene.

By the Mid Holocene, a resource switch for large game is also observed in Palawan where the wild pig becomes the main large prey instead of deer (Ochoa and Piper 2017). This is in response to the scarcity and eventual extirpation of deer on the island. As discussed in Chapter 7, this phenomenon is related to island-wide environmental and palaeogeographic changes related to sea-level rise, inundation of land area, and vegetation shifts indicating the expansion of tropical rainforests (Piper et al. 2011, Robles et al. 2015). This appears to be a relatively rare pre-Neolithic record in the region wherein a resource switch involves the local extinction of previously intensively hunted native fauna. By the Late Holocene, evidence for extinctions increase across the Indo-Pacific.

The Luzon record presents a different pattern. Here, deer is the dominant prey in the Late Pleistocene record of Callao (Mijares et al. 2011) and this continues into the Holocene. Note that the reliance on deer as an animal staple is evident for both *H. luzonensis* and *H. sapiens*. By the Late Holocene, pig remains appear to increase (Figure 9.1). Pig counts are mainly attributed to the wild pig but are also augmented by the introduction of domestic pig. As noted previously, domestic pigs and other domestic taxa do not replace wild taxa in the subsistence base even by the Late Neolithic (Amano et al. 2013). Ethnographic records among the Agta of Luzon also show the continued importance of large wild game (Estioko-Griffin and Griffin 1981; Griffin 2013; Peterson 1990). Deer were regularly hunted by Agta inhabiting certain locales where it was still abundant. Certain Agta groups also show seasonal preference for deer during the drier months of the year and for wild pig during the wet season.

On Luzon, evidence for the introduction of non-native mammals is also evident during the Late Holocene. This contrasts with the Palawan record, in which macaques and civets are interpreted as native inhabitants. The introduction of exotic taxa can be contextualised within the broader picture of the introduction of Neolithic artefacts and animal translocations in the region. From ca. 4500-4000 cal BP, earthenware pottery is recorded in the Batanes Islands and in northern Luzon (Bellwood and Dizon 2013; Hung 2005). On Philippine and Wallacean sites, the introduction of non-native species has been typically or incidentally lumped into the Austronesian 'Neolithic package'. This is largely due to the lack of chronological resolution in the Late Holocene, such that the timing of these introductions for different taxa is unknown. The data presented for Luzon indicate that the timing and directionality of introductions vary. The Nagsabaran site provides radiometric dates for these events. Among animal domesticates, the domestic pig was introduced earliest at 4000 cal BP, possibly contemporaneous with the introduction of pottery (Hung 2005; Piper et al. 2009). In the same site, domestic dogs and bovids were introduced over a millennium later (Amano et al. 2013).

The introduction of macaques and palm civets outside of their native range across the Wallacean region is hypothesized to be due to release for wild game hunting and for pest rat control, respectively (Heinsohn 2003). These are instances of landscape and ecological interventions and human impacts during the Late Holocene that have been rarely documented in earlier periods in SEA. Macaques and viverrids are native to Sundaic islands such as Borneo, Palawan, Java and Sumatra, as well as mainland SEA. As discussed in Chapter 7, current genetic data suggest that the likely population source of modern macaques and palm civets in the oceanic Philippines is Borneo. This implies a south-to-north route for the introduction of these taxa into the Philippines. This contrasts with the north-to-south route posited for the Neolithic introduction of pottery and domestic pig from Taiwan to the northern Philippines (Bellwood 2004; Mijares 2005; Piper et al. 2009). An earlier instance of animal introductions with an eastward trajectory involves the 'Pacific Clade' of domestic pigs. It has been suggested that the translocation of these domesticated pigs into Island SEA and Oceania passed through Sumatra and Java, reaching the Lesser Sunda Chain between 4000 BP and 3500 BP (Cucchi et al. 2008;

Dobney et al. 2008; Piper et al. 2009). The emergent picture is that of variable timing and trajectories for translocations of different taxa and complex circulation of artefact types across the region.

Invasive taxa are related to loss of native species in the Late Holocene. In modern times, defaunation constitutes a major driver of global environmental change, with over 300 terrestrial vertebrate species recorded to have gone extinct globally since CE 1500 (Dirzo et al. 2014; Turvey 2009). Ecologists have also referred to this as the 'empty forest syndrome' (Redford 1992). As discussed in Chapter 7, there is a growing archaeological record for anthropogenic biodiversity loss during the Late Holocene in ISEA and new extinction records are coming to light (e.g. Louys et al. 2018; Meijer et al. 2019). This trend points towards an earlier wave of anthropogenic extinctions across ISEA prior to the Anthropocene and demonstrates one of the pervasive and long-standing impacts of modern humans in these island environments. The human extinction filter phenomenon must be further appraised in the context of long-term hominin presence in the oceanic Philippines. The announcement of the endemic human *Homo luzonensis* (Detroit et al. 2019) and the proxy record for human presence in the Middle Pleistocene of Luzon (Ingicco et al. 2018) indicates that humans/hominins were present on Luzon for at least 700,000 years from present. Apart from hunting megafauna, we do not yet have evidence for the magnitude of environmental impact of *H. luzonensis* and this is an avenue requiring consideration in the future. In the case of modern humans, the archaeological record for the Philippines now provides initial evidence for the direct and indirect means by which defaunation has occurred across the Holocene.

9.3.2 Subsistence Records and IEK Systems

The subsistence data documented by zooarchaeological records also reflect indigenous ecological knowledge (IEK) systems of local human populations. Typically, data on human behavioural ecology or subsistence may be seen as an end in themselves. However, these data and other forms of archaeological data can also be viewed as components of indigenous knowledge forms. These knowledge systems are partly manifested in the diachronic record of procurement of local resources, of which the zooarchaeological record has much to contribute. Although there are inherent ontological problems with translating and interpreting indigenous knowledge, archaeological methodologies do provide practicable means by which we can attempt to uncover local knowledge systems in the past. As narrated in the previous section, these records provide long temporal views by which we can contextualise local adaptations and historicize indigenous lifeways. Recalling the discussion in Chapter 3, indigenous translates to *katutubo* in Filipino, and the root word *tubo* translates to 'root' or 'to be rooted in'. I underscore here that the historicizing is rooted to *place*; hence, the emphasis on local adaptations and local environments in these tropical islands. *Place* and *landscape* present a shared local context for past and present human societies, and in turn, this context provides continuity and connection by which we can attempt to comprehend indigenous ecological knowledge systems across time. This exploration does not intend to present a monolithic notion of indigeneity or a static view of place (or environments), but instead recognises that places and human populations change. Investigating these transformations is crucial to our understanding of the dynamic ecology and diverse lifeways of human groups across time. The Southeast Asian subsistence and technological record presents a wide array of localised strategies and practices from which examples can be drawn. In Niah Caves of Borneo, for instance, Piper and Rabett (2016) suggest that the butchery patterns for different arboreal species of primates and viverrids may be indicative of ethno-taxonomic categorisations different from modern scientific Linnaean categories. In Braholo Cave of Java, Amano et al. (2015) document hunting and butchery strategies of arboreal species at the onset of the Holocene, which intuit the intimate knowledge of forest habitats by human hunters and their manufacture of projectile technologies.

The zooarchaeological data presented in this thesis allow us to assess localised strategies embedded in past IEK systems through examining foraging practices at specific locales and specific points in time. In this thesis, I have attempted to re-frame the data within this narrative and I summarise these here. As noted above, we are presented with island-specific adaptations on Palawan and Luzon, which reflect the differing ecologies of the islands and the hunting practices tailored to variable ecological settings from the Late Pleistocene to the Late Holocene. Admittedly, these time-averaged faunal assemblages only afford us palimpsests; however, they do present valuable means by which we can add considerable time depth to studies of indigenous foraging lifeways.

On Palawan, resource acquisition in an inland setting is documented by the LGM levels of Pilanduk Cave, where there is a specialised focus on deer hunting. The specialisation observed in this site is reflective of its LGM location and ecology, wherein the cave was at least 40 km away from the coast and environmental proxies suggest a more open environment during this period. In the Holocene, there is much change and contrast recorded. As discussed, the vertebrate and molluscan data from Ille and Pasimbahan Caves indicate the acquisition of a broader range of terrestrial, arboreal, freshwater and marine taxa. These previously inland sites have been transformed into near-coastal sites by the Mid Holocene. Note that Ille has a

Terminal Pleistocene layer that parallels the Pilanduk record of specialised deer hunting. Across the Holocene, the assemblages are still dominated by the largest prey species available, but there is also a considerable diversity of taxa observed. As reviewed above, the large game focus shifts from deer to wild pig during the Mid Holocene, when the deer becomes increasingly rare and subsequently extinct. Climatic proxies on Palawan for the Holocene suggest the expansion of closed rainforest, and in this sense, we can attribute these records to the growing archaeological record of tropical rainforest foraging histories.

The Holocene record of Minori and Musang Caves in northeastern Luzon show long records of inland riverine occupation by foragers. The on-site subsistence base consisted of terrestrial and freshwater resources gathered in and around the Pinacanauan river. On Luzon, there is a more limited array of human prey species compared to Palawan, and in the vertebrate fauna analysed, the hunting focus detected is expectedly on deer and wild pigs. Late Holocene additions include the domestic pig and the introduced macaque, but the prey base still largely consists of the two native species. As noted in the previous chapter, deer exceeds pig relative abundances in the non-ceramic levels of the two cave sites, whereas pig remains become equally or more abundant in Neolithic and later periods. These faunal records contrast with ethnographic accounts of Agta foragers that inhabit northeastern Luzon, wherein wild pig is reportedly the preferred and most hunted wild game. The present-day focus on wild pig may partially have to do with diminishing deer populations.

All the cave sites analysed are situated near major rivers or tributaries. Ethnographically, it is known that such waterways are important not just for its resources; their significance extends to being principle foci of social identity for foragers (Griffin 1985, Minter 2010, Rai 1982). In this sense, these landscape features are important for investigating not just resource acquisition but also ancient social networks. As explored in the previous chapter, the symbolic marking of karsts and caves in Palawan is another example of how particular features in the landscape were potentially socially significant to past foraging communities. This follows the work of Paz (2012), who has documented the use of caves in northern Palawan (some of which are today labelled as 'Pasimbahan' or place of worship) as burial grounds and sites of votive offerings across the Holocene. To this we can add the potential significance of Pilanduk Cave and Magmisi Peak to local foragers during its period of occupation. In Pilanduk, the zooarchaeological data suggests that highly-valued food resources were likely shared within the foraging group(s) and the attendant skills involved in the processing of such resources (e.g. hunting, butchery, tool manufacture, etc.) may have also been performed and shared.

As has also been shown in the thesis, archaeofaunal records provide data to investigate how human societies are affected by and adapt to regional environmental and biodiversity changes. On Palawan, the conspicuous example pertains to diminishing populations of a highly valued animal resource (deer). This may have posed ecological challenges to local populations, along with a suite of environmental changes that include vegetation shifts and rapid sea level rise occurring during the Pleistocene-Holocene transition. As we also go further back in time on Palawan, we are presented with an ecological landscape that has no present-day analogue on the Philippine archipelago, and wherein much of the large mammal guild of the island has become extinct. The presence of the tiger on Palawan would also likely have been of importance to local inhabitants; human ecological interactions within a landscape that possessed a large top carnivore would have been variably different from that where it was absent. Where tigers naturally occur, they typically are held in awe or fear, and form part of local lore and animistic beliefs (e.g. Beggiora 2012; Wessing 1993, 1995). Vestiges of local tiger lore in the Philippines may be glimpsed in modern Austronesian languages and cognate sets. In Malay, the word for tiger is *harimau* and the Proto-Malayo-Western-Polynesian reconstruction for wild feline is **qari-maquŋ* (Blust and Trussel 2016). In Philippine languages, there appears to be no native word for the tiger; instead the Spanish loan word *tigre* is used. However, the term *halimaw* is used to refer to a ferocious beast or mythical monster. This term may have been a loan word from Malay, but it may also allude to the previous presence of this iconic creature on Palawan.

Lastly, the faunal records show evidence for ecological modification of forests involving animal translocations. The regional literature on 'cultured forests' have focused on management of plant resources (e.g Barker et al. 2017; Summerhayes et al. 2017). Less attention has been appointed to the manipulation of environments using invasive wild taxa, and the possible impacts introduced animals have had on island faunas. After their Late Holocene introduction into the oceanic Philippines, macaques and civets have been fully naturalised across the archipelago. Local inhabitants recognise them as native species, and until fairly recently, biologists did so as well. Translocation of exotic animals are forms of ecological interventions that potentially reflect a changing logic of engagement of people to their environment.

As such, the diachronic records presented here demonstrate not only long-term and localised ecological engagements of foragers to their changing environments, but also show how such societies can instigate pervasive impacts on local habitats. These records hopefully lend some further nuance to otherwise stereotypical and highly politicized depictions of indigenous communities as 'noble green primitives' or wasteful agents of overkill. The subject of aboriginal conservation is highly contested and complex, and at present goes beyond the scope of this short discussion. What must be noted, nonetheless, is that the understanding, goals and lived experiences of conservation and environmentalism vary across cultures, including that as defined by Western environmentalism (Berkes et al. 2000; Perez 2018; Redford and Stearman 1993; Roberts et al. 1995). Archaeological records show that human societies have greatly impacted local biotas and transformed landscapes across time, including those in tropical rainforests. However, it must be noted that there is no singular indigenous identity that can be imposed on any region, since human populations change and adapt through time. From what we know of contemporary indigenous communities, there is much variation in the transmission and distribution of traditional ecological knowledge within and across groups (e.g. Camacho et al. 2012; Fernández-Llamazares et al. 2015; Ruddle 1993). As such, monothetic ascriptions of 'conservationist' or 'anti-environmentalist' can be gross simplifications. At present, defaunation and biodiversity loss directly impact the lives of modern hunter-gatherers and various indigenous communities (Fernández-Llamazares et al. 2017; Minter 2010; Nasi et al. 2011; Virtanen 2017). Whereas ancient human populations have instigated defaunation and extinction processes, the pace of biodiversity loss has markedly increased during the Anthropocene (Dirzo et al. 2014; Ellis 2011). In the face of rapid and expansive global environmental change brought about by industrialisation and urbanisation, indigenous forms of ecological stewardship remain an invaluable resource for social-ecological resilience and repositories of adaptive management (Gómez-Baggethun et al. 2013; Fernández-Llamazares et al. 2015; Reyes-García and Pyhälä 2017). In this sense, archaeological records of foraging lifeways add to the understanding of long-term dynamics among people, plants, animals, and landscapes (e.g. Barker et al. 2017; Hayashida 2005; Heckenberger and Neves 2009). These archaeological contributions are important for chronicling indigenous practices of ecological stewardship, which are borne of multi-generational (or even millennial-scale) ecological engagements in local landscapes. In turn, these IEK systems are necessary to conserve the remaining and persisting components of global biodiversity.

9.4 Concluding Statements and Future Work

The results presented in this thesis have both drawn from new field explorations and from studying old museum collections. Both sets of investigations have yielded novel and surprising fossil discoveries. Looking at two neighbouring islands in the Philippine archipelago, one might expect that they would yield similar patterns that tell a general story for this part of Southeast

Asia. Yet, the tale of these two islands chronicle distinctive narratives based on each island's unique ecology and shifting environments across the Late Pleistocene and Holocene. On the one hand, these dissimilar patterns exemplify the differences between Sundaic faunas and the oceanic faunas of Southeast Asia. On the other hand, they also document the variation in human adaptations and impacts in these highly biodiverse and shifting tropical environments.

The work portrayed here has pieced together new and old faunal studies to build biostratigraphic sequences and long-term subsistence records. Unexpectedly, gaps do remain, and further chronological resolution is necessary to specify the timing of colonisation, extinction and other biogeographic processes. The recent announcement of *Homo luzonensis* from Callao Cave has opened new frontiers in Philippine archaeology. More broadly, the ground-breaking endeavours documenting Pleistocene humans in the tropical oceanic islands of SEA have thrust the region into the evolutionary limelight. Whether one is wary or in favour of species-splitting, the evidence from ISEA certainly underscores the morphological and behavioural variability of human populations across the Late Quaternary. The evidence also points to tropical rainforest and other tropical island environments to be part and parcel of human diversification and adaptation. The findings also raise new questions, such as that of the timing of modern human occupation in the oceanic Philippines and Wallacean islands.

The records presented here scratch at the surface of Holocene extinction processes in ISEA. Extinction chronologies must be further refined by direct dating on targeted taxa. Given the highly biodiverse and endemic nature of Philippine faunas, the Luzon record also hints at the likelihood that more unknown and possibly extinct lowland taxa await discovery across the archipelago. The extinct giant cloud rats reported here require proper systematic description, and this will be done during publication. Associated post-cranial remains of giant murids also require further study, and these can shed further light on the morphology and ecology of these enigmatic creatures. The significance of these findings highlights how biogeography and conservation biology can greatly benefit from synergistic efforts combining neobiology and palaeobiology.

Lastly, the thesis has taken some initial steps towards linking archaeological knowledge and indigenous ecological knowledge systems within local settings. This initial attempt has utilised familiar methods in the zooarchaeology toolkit to explore this relatively under-reported theme in Southeast Asian archaeology. This dataset can be further enriched by further taphonomic analyses, particularly on the well-preserved Pilanduk Cave assemblage. Further work on mortality profiles of hunted species would also provide data on seasonality and scheduling of hunting activities. The work can also be much improved by incorporating additional ethnographic and ethnoarchaeological data. More importantly, this endeavour requires the incorporation of indigenous interpretations through more inclusive and participatory collaborations with local community members. This contrasts with the current mainstream practice of top-down implementation of archaeological projects and extraction of archaeological data. Language translation is also essential, and these acts of translation can potentially enrich interpretation both ways. With respect to indigenous discourses, Southeast Asian and Philippine archaeology can hopefully break new ground, not just in heritage studies and public archaeology, but also in theory, praxis and methodology.

References

Achmadi, A. S., Esselstyn, J. A., Rowe, K. C., Maryanto, I. & Abdullah, M. T. (2013). Phylogeny, diversity, and biogeography of Southeast Asian spiny rats (*Maxomys*). *Journal of Mammalogy*. 94 (6), 1412–1423.

Agrawal, A. (1995). Indigenous and Scientific knowledge: Some critical comments. *Indigenous Knowledge and Development Monitor*. 3 (3), 3–6.

Allen, M. (1985). The rain forest of northeast Luzon and Agta foragers. In: Griffin, P. B. & Estioko-Griffin, A. A. (eds.) *The Agta of northeastern Luzon: Recent studies.* Cebu, San Carlos Publications, pp. 45–68.

Alves, R. R. N. (2012). Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiology and Conservation*. 1 (0), 1-69.

Amano, N. (2011). *The faunal remains of Nagsabaran in Cagayan, northern Philippines: Subsistence strategies in the Late Holocene*. Master's thesis. University of the Philippines, Diliman.

Amano, N. (2017). *Late Pleistocene to Mid-Holocene paleoenvironments and human subsistence strategies in East Java: Evidence from Song Terus and Braholo Cave*. PhD thesis. Muséum National d'Histoire Naturelle.

Amano, N., Moigne, A.-M., Ingicco, T., Sémah, F., Awe, R. D. & Simanjuntak, T. (2015). Subsistence strategies and environment in Late Pleistocene–Early Holocene Eastern Java: Evidence from Braholo Cave. *Quaternary International*. 416, 46–63.

Amano, N., Piper, P. J., Hung, H. & Bellwood, P. (2013). Introduced Domestic Animals in the Neolithic and Metal Age of the Philippines: Evidence from Nagsabaran, Northern Luzon. *Journal of Island & Coastal Archaeology*. 8 (3), 317–335.

Anderson, E. N. (2011). Ethnobiology: Overview of a growing field. In: Anderson, E. N., Pearsall, D., Hunn, E. & Turner, N. (eds.) *Ethnobiology*. Hoboken, New Jersey, USA, John Wiley and Sons, Ltd., pp. 1–14.

Andrews, P. (1990). *Owls, Caves and Fossils*. Chicago, University of Chicago Press.

Anshari, G., Kershaw, A. P., Kaars, S. V. D. & Jacobsen, G. (2004). Environmental change and peatland forest dynamics in the Lake Sentarum area, West Kalimantan, Indonesia. *Journal of Quaternary Science*. 19 (7), 637–655.

Aplin, K. P. & Helgen, K. M. (2010). Quaternary murid rodents of Timor. Part 1: New material of *Coryphomys buehleri* Schaub, 1937, and description of a second species of the genus. *Bulletin of the American Museum of Natural History.* 341, 1-80.

Arrhenius, O. (1921). Species and area. *Journal of Ecology*. 9 (1), 95–99.

Atalay, S. (2006). Indigenous archaeology as decolonizing practice. *The American Indian Quarterly*. 30 (3), 280–310.

Aubert, M., Brumm, A., Ramli, M., Sutikna, T., Saptomo, E. W., Hakim, B., Morwood, M. J., Van den Bergh, G. D., Kinsley, L. & Dosseto, A. (2014). Pleistocene cave art from Sulawesi, Indonesia. *Nature*. 514 (7521), 223–227.

Bailey, R. C., Head, G., Jenike, M., Owen, B., Rechtman, R. & Zechenter, E. (1989). Hunting and gathering in tropical rain forest: Is it possible? *American Anthropologist*. 91 (1), 59–82.

Baillie, I. C., Evangelista, P. M., & Inciong N. B. (2000). Differentiation of upland soils on the Palawan ophiolitic complex, Philippines. *CATENA*. 39 (4), 283–299.

Baker, K., Carden, R. & Madgwick, R. (eds.). (2015). *Deer and People*. Oxford, UK, Windgather Press.

Balete, D. S., Alviola, P. A., Duya, M. R. M., Duya, M. V., Heaney, L. R. & Rickart, E. A. (2011). The mammals of the Mingan Mountains, Luzon: Evidence for a new center of mammalian endemism. *Fieldiana Life and Earth Sciences*. 2, 75–87.

Balete, D. S., Rickart, E. A., Heaney, L. R. & Jansa, S. A. (2015). A new species of *Batomys* (Muridae, Rodentia) from southern Luzon Island, Philippines. *Proceedings of the Biological Society of Washington*. 128 (1), 22–39.

Balmford, A. (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution*. 11 (5), 193–196.

Bankoff, G. (2007). One island too many: Reappraising the extent of deforestation in the Philippines prior to 1946. *Journal of Historical Geography*. 33 (2), 314–334.

Barker, G., Barton, H., Bird, M., Daly, P., Datan, I., Dykes, A., Farr, L., Gilbertson, D., Harrisson, B., Hunt, C., Higham, T., Kealhofer, L., Krigbaum, J., Lewis, H., McLaren, S., Paz, V. J., Pike, A., Piper, P. J., Pyatt, B., Rabett, R., Reynolds, T., Rose, J., Rushworth, G., Stephens, M., Stringer, C., Thompson, J. & Turney, C. (2007). The "human revolution" in lowland tropical Southeast Asia: The antiquity and behavior of anatomically modern humans at Niah Cave (Sarawak, Borneo). *Journal of Human Evolution*. 52 (3), 243–261.

Barker, G. & Farr, L. (eds.). (2016). *Archaeological Investigations in the Niah Caves, Sarawak, 1954-2004,* Volume 2. Cambridge, UK, McDonald Institute for Archaeological Research.

Barker, G., Hunt, C., Barton, H., Gosden, C., Jones, S., Lloyd-Smith, L., Farr, L., Nyirí, B. & O'Donnell, S. (2017). The "cultured rainforests" of Borneo. *Quaternary International*. 448, 44–61.

Barker, G., Hunt, C. O. & Carlos, J. B. (2011). Transitions to farming in Island Southeast Asia: Archaeological, biomolecular and palaeoecological perspectives. In: Barker, G. & Janowski, M. (eds.) *Why cultivate? Anthropological and archaeological approaches to foraging-farming transitions in Southeast Asia*. Cambridge, UK, McDonald Institute for Archaeological Research, pp. 59-72.

Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Leal, C. G., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J. & Graham, N. (2018). The future of hyperdiverse ecosystems. *Nature.* 559 (7715), 517-526.

Barnosky, A. D., Carrasco, M. A. & Graham, R. W. (2011). Collateral mammal diversity loss associated with late Quaternary megafaunal extinctions and implications for the future. *Geological Society, London, Special Publications*. 358 (1), 179–189.

Bar-Oz, G. & Munro, N. D. (2004). Beyond cautionary tales: A multivariate taphonomic approach for resolving equifinality in zooarchaeological studies. *Journal of Taphonomy*. 2 (4), 201–220.

Barton, H. (2005). The case for rainforest foragers: The starch record at Niah Cave, Sarawak. *Asian Perspectives*. 44 (1), 56–72.

Barton, H. & Denham, T. (2018). Vegecultures and the social–biological transformations of plants and people. *Quaternary International*. 489, 17–25.

Barton, H., Paz, V. J. & Carlos, A. J. (2016). Plant food remains from the Niah caves: Macroscopic and microscopic approaches. In: Barker, G. & Farr, L. (eds.) *Archaeological investigations in the Niah Caves, Sarawak: The archaeology of the Niah Caves, Sarawak,* Volume 2. Cambridge, McDonald Institute for Archaeological Research, pp. 455–468.

Barton, H., Piper, P. J., Rabett, R. & Reeds, I. (2009). Composite hunting technologies from the Terminal Pleistocene and Early Holocene, Niah Cave, Borneo. *Journal of Archaeological Science*. 36 (8), 1708–1714.

Beggiora, S. (2013). Tigers, tiger spirits and were-tigers in tribal Orissa. *Religions of South Asia*. 7 (1-3), 93–107.

Bellwood, P. (ed.). (1988). *Archaeological Research in South-eastern Sabah,* Volume 2. Sabah, Sabah Museum and State Archives.

Bellwood, P. (2004). *First Farmers: The Origins of Agricultural Societies*. Malden, Massachusetts, John Wiley & Sons.

Bellwood, P. & Dizon, E. (2013). The chronology of Batanes prehistory. In: Bellwood, P. & Dizon, E. (eds.) *4000 years of migration and cultural exchange,* Terra Australis Volume 40. Canberra, Australian National University Press, pp. 67–76.

Berkes, F., Colding, J. & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications*. 10 (5), 1251–1262.

Beyer, H. O. (1947). Outline review of Philippine archaeology by islands and provinces. *Philippine Journal of Science*. 77, 205–390.

Bian, Y., Jian, Z., Weng, C., Kuhnt, W., Bolliet, T. & Holbourn, A. (2011). A palynological and palaeoclimatological record from the southern Philippines since the Last Glacial Maximum. *Chinese Science Bulletin*. 56 (22), 2359–2365.

Binford, L. R. (1978). *Nunamiut Ethnoarchaeology*. New York, Academic Press.

Binford, L. R. (2001). *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*. Berkeley, University of California Press.

Bird, M. I., Boobyer, E. M., Bryant, C., Lewis, H. A., Paz, V. J. & Stephens, W. E. (2007). A long record of environmental change from bat guano deposits in Makangit Cave, Palawan, Philippines. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*. 98 (1), 59–69.

Bird, M. I., Taylor, D., & Hunt, C. (2005). Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: A savanna corridor in Sundaland? *Quaternary Science Reviews*. 24 (20), 2228–2242.

Blancher, A., Aarnink, A., Tanaka, K., Ota, M., Inoko, H., Yamanaka, H., Nakagawa, H., Apoil, P.-A. & Shiina, T. (2012). Study of cynomolgus monkey (*Macaca fascicularis*) Mhc DRB gene polymorphism in four populations. *Immunogenetics*. 64 (8), 605–614.

Blancher, A., Bonhomme, M., Crouau-Roy, B., Terao, K., Kitano, T. & Saitou, N. (2008). Mitochondrial DNA sequence phylogeny of 4 populations of the widely distributed cynomolgus macaque (*Macaca fascicularis fascicularis*). *Journal of Heredity*. 99 (3), 254–264.

Blasco, R., Rosell, J., Gopher, A. & Barkai, R. (2014). Subsistence economy and social life: A zooarchaeological view from the 300 kya central hearth at Qesem Cave, Israel. *Journal of Anthropological Archaeology*. 35, 248–268.

Blouch, R., McCarthy, A., Moore, D., & Wemmer, C. M. (1998). *Deer: Status survey and conservation action plan*. IUCN.

Blumenschine, R. J. (1986). Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *Journal of Human Evolution*. 15 (8), 639–659.

Blust, R. & Trussel, S. (2016). *Austronesian Comparative Dictionary*. Available from: http://www.trussel2.com/ACD/ [Accessed: December 10, 2018].

Bobrowsky, P. T. (1982). Olsen and Olsen's identity crisis in faunal studies. *American Antiquity*. 47 (1), 180–183.

Boivin, N., Fuller, D. Q., Dennell, R., Allaby, R. & Petraglia, M. D. (2013). Human dispersal across diverse environments of Asia during the Upper Pleistocene. *Quaternary International*. 300, 32–47.

Bosch, M. D., Nigst, P. R., Fladerer, F. A. & Antl-Weiser, W. (2012). Humans, bones and fire: Zooarchaeological, taphonomic, and spatial analyses of a Gravettian mammoth bone accumulation at Grub-Kranawetberg (Austria). *Quaternary International*. 252, 109–121.

Brain, C. K. (1969). The contribution of Namib Desert Hottentots to an understanding of australopithecine bone accumulations. *Scientific Papers of the Namib Desert Research Station*. 1969 (39), 13–22.

Brightman, M., Grotti, V. E. & Ulturgasheva, O. (eds.) (2012). *Animism in Rainforest and Tundra: Personhood, Animals, Plants and Things in Contemporary Amazonia and Siberia*. New York, Berghahn Books.

Bromage, T. G. & Boyde, A. (1984). Microscopic criteria for the determination of directionality of cutmarks on bone. *American Journal of Physical Anthropology*. 65 (4), 359–366.

Brosius, J. P. (1991). Foraging in tropical rain forests: The case of the Penan of Sarawak, East Malaysia (Borneo). *Human Ecology*. 19 (2), 123–150.

Brown, K. S., Marean, C. W., Herries, A. I. R., Jacobs, Z., Tribolo, C., Braun, D., Roberts, D. L., Meyer, M. C. & Bernatchez, J. (2009). Fire as an engineering tool of early modern humans. *Science*. 325 (5942), 859–862.

Brown, P., Sutikna, T., Morwood, M. J., Soejono, R. P., Jatmiko, Saptomo, E. W. & Awe, R. D. (2004). A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*. 431 (7012), 1055–1061.

Brown, R. M. & Diesmos, A. C. (2001). Application of lineage-based species concepts to oceanic island frog populations: The effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. *Silliman Journal*. 42 (1), 133–162.

Brown, R. M. & Diesmos, A. C. (2009). Philippines, biology. In: Gillespie, R. & Clague, D. (eds.) *Encyclopedia of islands.* Berkeley, University of California Press, pp. 723-732.

Brown, R. M. & Guttman, S. I. (2002). Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: Reconsideration of Huxley's modification of Wallace's Line at the Oriental–Australian faunal zone interface. *Biological Journal of the Linnean Society*. 76 (3), 393–461.

Brown, R. M., Siler, C. D., Diesmos, A. C. & Alcala, A. C. (2009). Philippine frogs of the genus *Leptobrachium* (Anura; Megophryidae): Phylogeny-based species delimitation, taxonomic review, and descriptions of three new species. *Herpetological Monographs*. 23 (1), 1–44.

Brown, R. M., Siler, C. D., Oliveros, C. H., Esselstyn, J. A., Diesmos, A. C., Hosner, P. A., Linkem, C. W., Barley, A. J., Oaks, J. R., Sanguila, M. B., Welton, L. J., Blackburn, D. C., Moyle, R. G., Peterson, A. T. & Alcala, A. C. (2013a). Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics*. 44, 411–435.

Brown, R. M., Siler, C. D., Oliveros, C. H, Welton, L. J, Rock, A., Swab, J., Van Weerd, M., Van Beijnen, J., Jose, E., Rodriguez, D., Jose, E. & Diesmos, A.C. (2013b). The amphibians and reptiles of Luzon Island, Philippines, VIII: The herpetofauna of Cagayan and Isabela Provinces, northern Sierra Madre Mountain Range. *ZooKeys*. 266, 1–120.

Brown, W. C. & Alcala, A. C. (1970). The zoogeography of the herpetofauna of the Philippine Islands, a fringing archipelago. *Proceedings of the California Academy of Sciences*. 38 (6), 105-130.

Brumm, A., Jensen, G. M., van den Bergh, G. D., Morwood, M. J., Kurniawan, I., Aziz, F. & Storey, M. (2010). Hominins on Flores, Indonesia, by one million years ago. *Nature*. 464 (7289), 748–752.

Brumm, A., Langley, M. C., Moore, M. W., Hakim, B., Ramli, M., Sumantri, I., Burhan, B., Saiful, A. M., Siagian, L., Suryatman, Sardi, R., Jusdi, A., Abdullah, Mubarak, A. P., Hasliana, Hasrianti, Oktaviana, A. A., Adhityatama, S., van den Bergh, G. D., Aubert, M., Zhao, J.-X., Huntley, J., Li, B., Roberts, R. G., Saptomo, E. W., Perston, Y. & Grün, R. (2017). Early human symbolic behavior in the Late Pleistocene of Wallacea. *Proceedings of the National Academy of Sciences*. 114 (16), 4105–4110.

Bulbeck, D. (2013). Craniodental affinities of Southeast Asia's "Negritos" and the concordance with their genetic affinities. *Human Biology*. 85 (1/3), 95–134.

Bulbeck, D., Hiscock, P. & Sumantri, I. (2004). Leang Sakapao 1, a second dated Pleistocene site from South Sulawesi, Indonesia. In: Keates, S.G. & Pasveer, J.M. (eds.) *Modern Quaternary research in Southeast Asia: Quaternary research in Indonesia,* Volume 18. Leiden, A.A. Balkema Publishers, pp. 106-166.

Bulbeck, D., Pasqua, M. & Di Lello, A. (2000). Culture history of the Toalean of South Sulawesi, Indonesia. *Asian Perspectives*. 39 (1/2), 71–108.

Bulbeck, F. D. (2003). Hunter-gatherer occupation of the Malay Peninsula from the Ice Age to the Iron Age. In: Mercader, J. (ed.) *Under the canopy: The archaeology of tropical rain forests.* New Jersey, Rutgers University Press, pp. 119–160.

Cain, C. R. (2005). Using burned animal bone to look at Middle Stone Age occupation and behavior. *Journal of Archaeological Science*. 32 (6), 873–884.

Camacho, L. D., Combalicer, M. S., Yeo-Chang, Y., Combalicer, E. A., Carandang, A. P., Camacho, S. C., de Luna, C. C. & Rebugio, L. L. (2012). Traditional forest conservation knowledge/technologies in the Cordillera, Northern Philippines. *Forest Policy and Economics*. 22, 3–8.

Cannon, C. H., Morley, R. J. & Bush, A. B. G. (2009). The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences*. 106 (27), 11188–11193.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science.* 309 (5738), 1239–1241.

Catibog-Sinha, C. & Heaney, L. R. (2006). *Philippine Biodiversity: Principles and Practice*. Quezon City, Haribon Foundation.

Céline, B., Phillip, C. & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*. 12 (2), 20150623.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*. 9 (2), 129–136.

Choa, O. (2018). *A geochemical history of Tabon Cave (Palawan, Philippines): Environment, climate, and early modern humans in the Philippine archipelago.* PhD thesis. Muséum national d'histoire naturelle.

Costamagno, S., Thery-Parisot, I., Brugal, J. P. & Gubiert, R. (2005). Taphonomic consequences of the use of bones as fuel. Experimental data and archaeological applications. In: O'Connor, T. (ed.) *Biosphere to lithosphere: New studies in vertebrate taphonomy*: *Proceedings of the 9th Conference of the International Council or Archaeozoology, Durham, August 2002.* Oxford, Oxbow Books, pp. 51-62.

Cox, R. (1987). The Philippine spotted deer and the Visayan warty pig. *Oryx*, *21*(1), 37–42.

Croft, D. A., Heaney, L. R., Flynn, J. J. & Bautista, A. P. (2006). Fossil remains of a new, diminutive *Bubalus* (Artiodactyla: Bovidae: Bovini) from Cebu Island, Philippines. *Journal of Mammalogy*. 87 (5), 1037–1051.

Cucchi, T., Fujita, M. & Dobney, K. (2008). New insights into pig taxonomy, domestication and human dispersal in Island South East Asia: Molar shape analysis of *Sus* remains from Niah Caves, Sarawak. *International Journal of Osteoarchaeology*. 19 (4), 508–530.

Damm, C. (2005). Archaeology, ethno-history and oral traditions: Approaches to the indigenous past. *Norwegian Archaeological Review*. 38 (2), 73–87.

Dam, R. A., Van der Kaars, S. & Kershaw, A. P. (2001). Quaternary environmental change in the Indonesian region. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 171 (3), 91–95.

De Deckker, P., Tapper, N. J. & van der Kaars, S. (2003). The status of the Indo-Pacific Warm Pool and adjacent land at the Last Glacial Maximum. *Global and Planetary Change*. 35 (1), 25–35.

Delaney-Rivera, C., Plummer, T. W., Hodgson, J. A., Forrest, F., Hertel, F. & Oliver, J. S. (2009). Pits and pitfalls: Taxonomic variability and patterning in tooth mark dimensions. *Journal of Archaeological Science.* 36 (11), 2597–2608.

De Leon, A. (2017). The ceramics from Pilanduk Cave, Palawan. Manila, National Museum of the Philippines.

Delfin, F. (2015). The population history of the Philippines: A genetic overview. *Philippine Studies: Historical & Ethnographic Viewpoints.* 63 (4), 449-476.

Delfin, F., Salvador, J. M., Calacal, G. C., Perdigon, H. B., Tabbada, K. A., Villamor, L. P., Halos. S. C., Gunnarsdóttir, E., Myles, S., Hughes, D. A., Xu, S., Jin, L., Lao, O., Kayser, M., Hurles, M. E., Stoneking, M. & De Ungria, M. C. A. (2011). The Y-chromosome landscape of the Philippines: Extensive heterogeneity and varying genetic affinities of Negrito and non-Negrito groups. *European Journal of Human Genetics*. 19 (2), 224–230.

Deloria, V. (1997). *Red Earth, White Lies: Native Americans and The Myth of Scientific Fact*. Golden, Colorado, Fulcrum Publishing.

Demeter, F., Shackelford, L., Westaway, K., Barnes, L., Duringer, P., Ponche, J.-L., Dumoncel, J., Sénégas, F., Sayavongkhamdy, T., Zhao, J.-X., Sichanthongtip, P., Patole-Edoumba, E., Dunn, T., Zachwieja, A., Coppens, Y., Willerslev, E. & Bacon, A.-M. (2017). Early modern humans from Tam Pà Ling, Laos: Fossil review and perspectives. *Current Anthropology*. 58 (S17), S527-S538.

Denham, T. P., Haberle, S. G., Lentfer, C., Fullagar, R., Field, J., Therin, M., Porch, N. & Winsborough, B. (2003). Origins of agriculture at Kuk swamp in the highlands of New Guinea. *Science*. 301 (5630), 189–193.

den Tex, R. -J., Thorington, R., Maldonado, J. E. & Leonard, J. A. (2010). Speciation dynamics in the SE Asian tropics: Putting a time perspective on the phylogeny and biogeography of Sundaland tree squirrels, *Sundasciurus*. *Molecular Phylogenetics and Evolution*. 55 (2), 711–720.

Détroit, F., Dizon, E., Falguères, C., Hameau, S., Ronquillo, W. & Sémah, F. (2004). Upper Pleistocene *Homo sapiens* from the Tabon cave (Palawan, The Philippines): Description and dating of new discoveries. *Comptes Rendus Palevol.* 3 (8), 705–712.

Détroit, F., Mijares, A. S. B., Corny, J., Daver, G., Zanolli, C., Dizon, E., Robles, E., Grün, R. & Piper, P. J. (2019). A new species of *Homo* from the Late Pleistocene of the Philippines. *Nature*. 568 (7751), 181.

De Vera-Alba, E. (1990). Minori Cave vertebrate skeletal remains: A preliminary study. Manila, National Museum of the Philippines.

De Vos, J. & Bautista, A. (2001). An update on the vertebrate fossils from the Philippines. *National Museum Papers*. 11 (1), 58–62.

De Vos, J., & Bautista, A. (2003). Preliminary notes on the vertebrate fossils from the Philippines. *Proceedings of the Society of Philippine Archaeologists*. 1, 42–62.

Diamond, J. M. & Gilpin, M. E. (1983). Biogeographic umbilici and the origin of the Philippine avifauna. *Oikos*. 41 (3), 307–321.

Dickerson, R. E., McGregor, R. C., Schultze, W. & Taylor, E. (1928). *Distribution of life in the Philippines*. Manila, Bureau of Printing.

Dietl, G. P. & Flessa, K. W. (eds.). (2009). *Conservation Paleobiology: Using the Past to Manage for the Future*. Bethesda, Paleontological Society.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*. 345 (6195), 401–406.

Dizon, E. Z., Détroit, F., Sémah, F., Falguères, C., Hameau, S., Ronquillo, W. & Cabanis, E. (2002). Notes on the morphology and age of the Tabon Cave fossil *Homo sapiens*. *Current Anthropology*. 43 (4), 660–666.

Dizon, E. Z. & Pawlik, A. F. (2010). The Lower Palaeolithic record in the Philippines. *Quaternary International*. 223-224, 444–450.

Dobney, K. M., Cucchi, T. & Larson, G. (2008). The pigs of Island Southeast Asia and the Pacific: New evidence for taxonomic status and human-mediated dispersal. *Asian Perspectives*. 47 (1), 59–74.

Dobney, K. M. & Reilly, K. (1988). A method for recording archaeological animal bones: the use of diagnostic zones. *Circaea*. 5 (2), 79–96.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G. & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*. 113 (40), 11261–11265.

Domínguez-Rodrigo, M., de Juana, S., Galán, A. B. & Rodríguez, M. (2009). A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science.* 36 (12), 2643–2654.

Domínguez-Rodrigo, M. & Piqueras, A. (2003). The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science*. 30 (11), 1385–1391.

Dommain, R., Couwenberg, J., Glaser, P. H., Joosten, H. & Suryadiputra, I. N. N. (2014). Carbon storage and release in Indonesian peatlands since the last deglaciation. *Quaternary Science Reviews.* 97, 1–32.

Donlan, C. J., Berger, J., Bock, C. E., Bock, J. H., Burney, D. A., Estes, J. A., Foreman, D., Martin, P. S., Roemer, G. W., Smith, F. A., Soulé, M. E. & Greene, H. W. (2006). Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *The American Naturalist*. 168 (5), 660–681.

Driscoll, C. A., Yamaguchi, N., Bar-Gal, G. K., Roca, A. L., Luo, S., Macdonald, D. W. & O'Brien, S. J. (2009). Mitochondrial phylogeography illuminates the origin of the extinct Caspian tiger and its relationship to the Amur tiger. *PLoS ONE*. 4 (1), e4125. Available from: https://doi.org/10.1371/journal.pone.0004125.

Dunbar, R. I. M. (2014). How conversations around campfires came to be. *Proceedings of the National Academy of Sciences*. 111 (39), 14013–14014.

Dyble, M. J. (2016). *The behavioural ecology and evolutionary implications of hunter-gatherer social organisation.* PhD thesis. University College London.

Dyble, M. J., Thompson, J., Smith, D., Salali, G. D., Chaudhary, N., Page, A. E., Vinicius, L., Mace, R. & Migliano, A. B. (2016). Networks of food sharing reveal the functional significance of multilevel sociality in two hunter-gatherer groups. *Current Biology*. 26 (15), 2017–2021.

Eder, J. F. (1987). *On the Road to Tribal Extinction: Depopulation, Deculturation, and Adaptive Well-being Among the Batak of the Philippines*. Berkeley, University of California Press.

Eder, J. F. (1990). Deforestation and detribalization in the Philippines: The Palawan case. *Population and Environment*. 12 (2), 99–115.

Ellen, R. (2004). From ethno-science to science, or 'What the indigenous knowledge debate tells us about how scientists define their project'. *Journal of Cognition and Culture*. 4 (3), 409–450.

Ellen, R. & Harris, H. (2005). Introduction. In: Ellen, R., Parkes, P. & Bicker, A. (eds.) *Indigenous enviromental knowledge and its transformations: Critical anthropological perspectives.* Amsterdam, Harwood Academic Publishers, pp. 1–29.

Ellis, E. C. (2011). Anthropogenic transformation of the terrestrial biosphere. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369 (1938), 1010–1035.

Erlandson, J. M. (2001). The archaeology of aquatic adaptations: Paradigms for a new millennium. *Journal of Archaeological Research*. 9 (4), 287–350.

Esselstyn, J. A. & Brown, R. M. (2009). The role of repeated sea-level fluctuations in the generation of shrew (Soricidae: *Crocidura*) diversity in the Philippine Archipelago. *Molecular Phylogenetics and Evolution*. 53 (1), 171–181.

Esselstyn, J. A., Maher, S. P. & Brown, R. M. (2011). Species interactions during diversification and community assembly in an island radiation of shrews. *PLoS ONE.* 6 (7), e21885.

Esselstyn, J. A., Oliveros, C. H., Moyle, R. G., Peterson, A. T., McGuire, J. A. & Brown, R. M. (2010). Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line. *Journal of Biogeography*. 37 (11), 2054–2066.

Esselstyn, J. A., Widmann, P. & Heaney, L. R. (2004). The mammals of Palawan island, Philippines. *Proceedings of the Biological Society of Washington*. 117 (3), 271–302.

Estioko, A. A. & Griffin, P. B. (1975). The Ebuked Agta of northeastern Luzon. *Philippine Quarterly of Culture and Society*. 3 (4), 237–244.

Estioko-Griffin, A. A. (1985). Women as hunters: The case of an eastern Cagayan Agta group. In: Griffin, P. B. & Estioko-Griffin, A. A. (eds.) *The Agta of northeastern Luzon: Recent studies*. Cebu City, University of San Carlos Publications, pp. 18-32.

Estioko-Griffin, A. A. & Griffin, P. B. (1981a). The beginning of cultivation among Agta hunter-gatherers in northeast Luzon. In: Olofson, H. (ed.) *Adaptive strategies and change in*

Philippine swidden-based societies. Laguna, Philippines, Forest Research Institute, pp. 55-72.

Estioko-Griffin, A. A. & Griffin, P. B. (1981b). Woman the hunter: The Agta. In: Dahlberg, F. (ed.) *Woman the gatherer*. New Haven, Connecticut, Yale University Press, pp. 121–151.

Evans, B. J., Brown, R. M., McGuire, J. A., Supriatna, J., Andayani, N., Diesmos, A., Iskandar, D., Melnick, D. J. & Cannatella, D. C. (2003). Phylogenetics of fanged frogs: Testing biogeographical hypotheses at the interface of the Asian and Australian faunal zones. *Systematic Biology*. 52 (6), 794–819.

Fabre, P.-H., Hautier, L. & Douzery, E. J. P. (2015). A synopsis of rodent molecular phylogenetics, systematics and biogeography. In: Cox, P. G. & Hautier, L. (eds.) *Evolution of the rodents: Advances in phylogeny, functional morphology and development.* Cambridge, Cambridge University Press, pp. 19–69.

Fernández-Jalvo, Y. & Andrews, P. (2016). *Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification,* Vertebrate Paleobiology and Paleoanthropology Series. Dordrecht, Springer Science + Business Media.

Fernández-Llamazares, Á., Díaz-Reviriego, I., Luz, A. C., Cabeza, M., Pyhälä, A. & Reyes-García, V. (2015). Rapid ecosystem change challenges the adaptive capacity of local environmental knowledge. *Global Environmental Change*. 31, 272–284.

Fernández-Llamazares, Á., Díaz-Reviriego, I. & Reyes-García, V. (2017). Defaunation through the eyes of the Tsimane'. In: Reyes-García, V. & Pyhälä, A. (eds.) *Hunter-gatherers in a changing world.* Cham, Springer International Publishing, pp. 77–90.

Fernández, N., Navarro, L. M. & Pereira, H. M. (2017). Rewilding: A call for boosting ecological complexity in conservation. *Conservation Letters*. 10 (3), 276–278.

Flannery, T. F. (1995). *Mammals of the South-West Pacific & Moluccan Islands*. New York, Cornell University Press.

Flenley, J. R. (1998). Tropical forests under the climates of the last 30,000 years. *Climatic Change*. 39 (2), 177–197.

Fooden, J. (1991). Systematic review of Philippine macaques (Primates, Cercopithecidae: *Macaca fascicularis* subspp.). *Fieldiana Zoology*. 64, 1–44.

Fooden, J. (2006). Comparative review of *Fascicularis*-group species of macaques (Primates: *Macaca*). *Fieldiana Zoology*. 2006 (107), 1–43.

Fox, R. B. (1970). *The Tabon Caves*. Manila, National Museum.

Fox, R. B. (1971). Ancient man and Pleistocene fauna in Cagayan Valley, northern Luzon, Philippines: A progress report. Manila, National Museum of the Philippines.

Freudenthal, M. & Martín-Suárez, E. (2013). Estimating body mass of fossil rodents. *Scripta Geologica.* (145), 1-131.

Gagan, M. K., Ayliffe, L. K., Hopley, D., Cali, J. A., Mortimer, G. E., Chappell, J., McCulloch, M. T. & Head, M. J. (1998). Temperature and surface-ocean water balance of the mid-Holocene tropical Western Pacific. *Science*. 279 (5353), 1014–1018.

Gagan, M. K., Hendy, E. J., Haberle, S. G. & Hantoro, W. S. (2004). Post-glacial evolution of the Indo-Pacific Warm Pool and El Niño-Southern oscillation. *Quaternary International*. 118-119, 127–143.

Gathorne-Hardy, F. J., Syaukani, Davies, R. G., Eggleton, P., & Jones D. T. (2002). Quaternary rainforest refugia in south-east Asia: Using termites (Isoptera) as indicators. *Biological Journal of the Linnean Society*. 75 (4), 453–466.

Gentry, A. H. (1992). Tropical forest biodiversity: Distributional patterns and their conservational significance. *Oikos.* 63 (1), 19–28.

Gifford-Gonzalez, D. (2018). *An Introduction to Zooarchaeology*. Cham, Springer.

Glover, I. (1976). Ulu Leang Cave, Maros : A preliminary sequence of post-Pleistocene cultural development in South Sulawesi. *Archipel*. 11 (1), 113–154.

Glover, I. (1986). *Archaeology in Eastern Timor, 1966–67*, Tierra Australis Volume 11. Canberra, Australian National University Press.

Gómez-Baggethun, E., Corbera, E. & Reyes-García, V. (2013). Traditional ecological knowledge and global environmental change: Research findings and policy implications. *Ecology and Society: A Journal of Integrative Science for Resilience and Sustainability*. 18 (4), 1-12.

Goodman, M. J., Griffin, P. B., Estioko-Griffin, A. A. & Grove, J. S. (1985). The compatibility of hunting and mothering among the Agta hunter-gatherers of the Philippines. *Sex Roles.* 12 (11–12), 1199–1209.

Goodrich, J., Lynam, A, Miquelle, D., Wibisono, H., Kawanishi, K. & Karanth, U. (2015). *Panthera tigris. The IUCN Red List of Threatened Species*. International Union for Conservation of Nature. Available from: https://www.iucnredlist.org/details/15955/0 [Accessed 28 February 2018].

Gower, D., Johnson, K., Richardson, J., Rosen, B., Rüber, L. & Williams, S. (2012). *Biotic Evolution and Environmental Change in Southeast Asia*. Cambridge, Cambridge University Press.

Grayson, D. K. (1984). *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Orlando, Academic Press.

Greenfield, H. J. (1999). The origins of metallurgy: Distinguishing stone from metal cut-marks on bones from archaeological sites. *Journal of Archaeological Science.* 26 (7), 797–808.

Greenfield, H. J. (2013). "The fall of the House of Flint": A zooarchaeological perspective on the decline of chipped stone tools for butchering animals in the Bronze and Iron Ages of the Southern Levant. *Lithic Technology*. 38 (3), 161–178.

Griffin, P. B. (1984). Forager resource and land use in the humid tropics: The Agta of northeastern Luzon, the Philippines. In: Schrire, C. (ed.) *Past and present in hunter gatherer studies*. Florida, Academic Press, pp. 95–121.

Griffin, P. B. (1985). Population movements and socio-economic change in the Sierra Madre. In: Griffin, P. B. & Estioko-Griffin, A. A. (eds.) *The Agta of northeastern Luzon: Recent studies*. Cebu City, University of San Carlos Publications, pp. 85-101.

Griffin, P. B. (1989). Hunting, farming, and sedentism in a rain forest foraging society. In: Kent, S. (ed.) *Farmers as hunters: The implications of sedentism*, pp. 60-70.

Griffin, P. B. (1997). Technology and variation in arrow design among the Agta of northeastern Luzon. In: Knecht, H. (ed.) *Projectile technology*. New York, Springer Science+Business Media, pp. 267–286.

Griffin, P. B. (2013). Apache farmers, Agta hunters and Bunong elephant keepers: A career in ethnoarchaeology. *Ethnoarchaeology*. 5 (1), 56–72.

Griffin, P. B. & Griffin, M. B. (2000). Agta hunting and sustainability of resource use in north-eastern Luzon, Philippines. In: Robinson, J. G. & Bennett, E. L. (eds.) *Hunting for sustainability in tropical forests*. New York City, Columbia University Press, pp. 325-335.

Griffin, P. B. & Solheim, W. (1988). Ethnoarchaeological research in Asia. *Asian Perspectives*. 28 (2), 145–162.

Guthe, C. E. (1927). The University of Michigan Philippine expedition. *American Anthropologist*. 29 (1), 69–76.

Hall, R. (1998). The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall, R. & Holloway, J. D. (eds.) *Biogeography and geological evolution of SE Asia*. Leiden, Backhuys Publshers, pp. 99–131.

Hall, R. (2002). Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: Computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*. 20 (4), 353–431.

Hall, R. (2013). The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology*. 72 (s2), 1-17.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). PAST: Paleontological Statistics software package for education and data analysis (Version 3.19) [Software]. Available from: https://folk.uio.no/ohammer/past/.

Hanebuth, T. J. J., Stattegger, K. & Bojanowski, A. (2009). Termination of the Last Glacial Maximum sea-level lowstand: The Sunda-shelf data revisited. *Global and Planetary Change*. 66 (1–2), 76–84.

Hanebuth, T. J. J., Stattegger, K. & Grootes, P. M. (2000). Rapid flooding of the Sunda shelf: A Late-Glacial sea-level record. *Science*. 288 (5468), 1033–1035.

Harkin, M. E. & Lewis, D. R. (eds.). (2007). *Native Americans and the Environment: Perspectives on the Ecological Indian*. Lincoln, University of Nebraska Press.

Harland, J. F., Barrett, J. H., Carrott, J., Dobney, K. & Jaques, D. (2003). The York System: An integrated zooarchaeological database for research and teaching. *Internet Archaeology*. 13.

Harper, D. (1999). *Numerical Palaeobiology: Computer-Based Modelling and Analysis of Fossils and Their Distributions*. New York, John Wiley & Sons, Ltd.

Harrison, T. (1998). Vertebrate faunal remains from the Madai Caves (MAD 1/28), Sabah, East Malaysia. *Bulletin of the Indo-Pacific Prehistory Association*. 17, 85–92.

Hawkes K., O´Connell J. F. & Blurton Jones, N. G. (1991). Hunting income patterns among the Hadza: Big game, common goods, foraging goals and the evolution of the human diet. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*. 334 (1270), 243–251.

Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. (2001). Hadza meat sharing. *Evolution and Human Behavior*. 22 (2), 113–142.

Hawkins, S., Samper-Carro, S. C., Louys, J., Aplin, K., O'Connor, S. & Mahirta. (2018). Human palaeoecological interactions and owl roosting at Tron Bon Lei, Alor Island, Eastern Indonesia. *The Journal of Island and Coastal Archaeology*. 13 (3), 371–387.

Hayashida, F. M. (2005). Archaeology, ecological history, and conservation. *Annual Review of Anthropology*. 34 (1), 43–65.

Haynes, G. (1983). A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology*. 9 (2), 164–172.

Hayward, M. W., Jędrzejewski, W. & Jêdrzejewska, B. (2012). Prey preferences of the tiger *Panthera tigris*. *Journal of Zoology*. 286 (3), 221–231.

Headland, T. N. (1983). An ethnobotanical anomaly: The dearth of binomial specifics in a folk taxonomy of a Negrito hunter-gatherer society in the Philippines. *Journal of Ethnobiology.* 3 (2), 109-120.

Headland, T. N. (1987). The wild yam question: How well could independent hunter-gatherers live in a tropical rain forest ecosystem? *Human Ecology*. 15 (4), 463–491.

Headland, T. N. (1988). Ecosystemic change in a Philippine tropical rainforest and its effect on a Negrito foraging society. *Journal of Tropical Ecology.* 29 (2), 121-135.

Headland, T. N. (1991). How Negrito foragers live in a Philippine rainforest. *International Symposium on Food and Nutrition in the Tropical Rainforest: Biocultural Interactions and Applications to Development.* Paris, 10-13 September. UNESCO.

Headland, T. N. & Bailey, R. C. (1991). Have hunter-gatherers ever lived in tropical rain forest independently of agriculture? *Human Ecology*. 19 (2), 115–122.

Headland, T. N., Headland, J. D. and Uehara, R. T. (2011). *Agta demographic database: Chronicle of a hunter-gatherer community in transition, Version 2.0*. SIL Language and Culture Documentation and Description 2.

Headland, T. N., Reid, L. A., Bicchieri, M. G., Bishop, C. A., Blust, R., Flanders, N. E., Gardner, P. M. Hutterer, K. L., Marciniak, A., Schroeder, R. F. & Seitz, S. (1989). Hunter-gatherers and their neighbors from prehistory to the present. *Current Anthropology*. 30 (1), 43–66.

Heaney, L. R. (1985). Zoogeographic evidence for Middle and Late Pleistocene land bridges to the Philippine islands. *Modern Quaternary Research in Southeast Asia*. 9, 127–144.

Heaney, L. R. (1986). Biogeography of mammals in SE Asia: Estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*. 28 (1-2), 127–165.

Heaney, L. R. (1991). A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change*. 19 (1-2), 53–61.

Heaney, L. R. (2001). Small mammal diversity along elevational gradients in the Philippines: An assessment of patterns and hypotheses. *Global Ecology and Biogeography*. 10 (1), 15–39.

Heaney, L. R., Balete, D., Rickart, E. A., Veluz, M. J. & Jansa, S. (2009). A new genus and species of small "tree-mouse" (Rodentia, Muridae) related to the Philippine giant cloud rats. *Bulletin of the American Museum of Natural History*. 331, 205–229.

Heaney, L. R., Balete, D. & Rickart, E. (2016a). *The Mammals of Luzon Island*. Baltimore, Maryland, Johns Hopkins University Press.

Heaney, L. R., Balete, D. S., Duya, M. R. M., Duya, M. V., Jansa, S. A., Steppan, S. J. & Rickart, E. A. (2016b). Doubling diversity: A cautionary tale of previously unsuspected mammalian diversity on a tropical oceanic island. *Frontiers of Biogeography*. 8 (2), e29667.

Heaney, L. R., Balete, D. S., Dolar, M. L., Alcala, A. C., Dans, A. T. L., Gonzales, P. C., Ingle, N. R., Lepiten, M. V., Oliver, W. L. R., Ong, P. S., Rickart, E. A., Tabaranza, B. R. & Utzurrum, R. C. B. (1998). A synopsis of the mammalian fauna of the Philippine islands. *Fieldiana Zoology.* (88), 1-61.

Heaney, L. R., Balete, D. S., Rickart, E. A., Alviola, P. A., Duya, M. R. M., Duya, M. V., Veluz, M. J., Van de Vrede, L. & Steppan, S. J. (2011). Seven new species and a new subgenus of forest mice (Rodentia: Muridae: *Apomys*) from Luzon Island. *Fieldiana Life and Earth Sciences*. 2, 1–60.

Heaney, L. R., Balete, D. S., Rickart, E. A., Veluz, M. J. & Jansa, S. A. (2014). Three new species of *Musseromys* (Muridae, Rodentia), the endemic Philippine tree mouse from Luzon Island. *American Museum Novitates*. (3802), 1-27.

Heaney, L. R., Balete, D. S., Utzurrum, R. C. B., Rickart, E. A. & Gonzales, P. C. (1999). Mammalian diversity on Mount Isarog : A threatened center of endemism on southern Luzon Island, Philippines. *Fieldiana Zoology*. 95, 1–62.

Heaney, L. R., Dolar, M. L., Balete, D. S., Esselstyn, J. A., Rickart, E. A., Sedlock, J. L., Alcala, A. C., Alviola, P. A., Duya, M. R. M., Duya, M. V., Ingle, N. R., Lepiten, M. V., Oliver, W. L. R., Ong, P. S., Paguntalan, L. M., Tabaranza, B. R., Utzurrum, R. C. B. & Veluz, M. J. (2010). *Synopsis of Philippine mammals*. Available from: http://www.fieldmuseum.org/philippine_mammals/ [Accessed: 25 July 2018].

Heaney, L. R., Piper, P. J. & Mijares, A. S. B. (2011). The first fossil record of endemic murid rodents from the Philippines: A Late Pleistocene cave fauna from northern Luzon. *Proceedings of the Biological Society of Washington*. 124 (3), 234–247.

Heckeberg, N. S., Erpenbeck, D., Wörheide, G. & Rössner, G. E. (2016). Systematic relationships of five newly sequenced cervid species. *PeerJ*. 4, e2307.

Heckenberger, M. & Neves, E. G. (2009). Amazonian archaeology. *Annual Review of Anthropology*. 38 (1), 251–266.

Heinsohn, T. (2003). Animal translocation: Long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). *Australian Zoologist*. 32, 351–376.

Heinsohn, T. (2010). Marsupials as introduced species: Long-term anthropogenic expansion of the marsupial frontier and its implications for zoogeographic interpretation. In: Haberle, S. G., Stevenson, J. & Prebble, M. (eds.) *Altered ecologies: Fire, climate and human influence on terrestrial landscapes,* Terra Australis Volume 32. Canberra, Australian National University, pp. 133-176.

Helmus, M. R., Mahler, D. L. & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*. 513 (7519), 543–546.

Hemmer, H., Kahlke, R.-D. & Vekua, A. K. (2011). The cheetah *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems. *Quaternary Science Reviews.* 30 (19-20), 2703-2714.

Herrera, M. B. (2010). *An archaeogenetic study of the genus* Sus *in the Philippines and its propositions for understanding human translocation in Island Southeast Asia*. Master's thesis. University of the Philippines, Diliman.

Hofreiter, M. & Barnes, I. (2010). Diversity lost: Are all Holarctic large mammal species just relict populations? *BMC Biology*. 8 (46), 1-3.

Holland, S. (2003). *Analytic Rarefaction* (Version 1.3). [Software] UGA Stratigraphy Lab. Available from https://strata.uga.edu/software/anRareReadme.html

Holmes, N. D., Spatz, D. R., Oppel, S., Tershy, B., Croll, D. A., Keitt, B., Genovesi, P., Burfield, I. J., Will, D. J., Bond, A. L., Wegmann, A., Aguirre-Muñoz, A., Raine, A. F., Knapp, C. R., Hung, C.-H., Wingate, D., Hagen, E., Méndez-Sánchez, F., Rocamora, G., Yuan, H.-W., Fric, J., Millett, J., Russell, J., Liske-Clarke, J., Vidal, E., Jourdan, H., Campbell, K., Springer, K., Swinnerton, K., Gibbons-Derechong, L., Langrand, O., Brooke, M. D. L., McMinn, M., Bunbury, N., Oliveira, N., Sposimo, P., Geraldes, P., McClelland, P., Hodum, P., Ryan, P. G., Borroto-Páez, R., Pierce, R., Griffiths, R., Fisher, R. N., Wanless, R., Pasachnik, S. A., Cranwell, S., Micol, T. & Butchart, S. H. M. (2019). Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLoS ONE*. 14 (3), e0212128.

Hopkins, S. S. B. (2008). Reassessing the mass of exceptionally large rodents using toothrow length and area as proxies for body mass. *Journal of Mammalogy*. 89 (1), 232–243.

Horton, B. P., Gibbard, P. L., Mine, G. M., Morley, R. J., Purintavaragul, C. & Stargardt, J. M. (2005). Holocene sea levels and palaeoenvironments, Malay-Thai peninsula, southeast Asia. *The Holocene*. 15 (8), 1199–1213.

Houston, D. B. & Schreiner, E. G. (1995). Alien species in national parks: Drawing lines in space and time. *Conservation Biology*. 9 (1), 204–209.

Hung, H.-C. (2009). *Migration and cultural interaction in Southern Coastal China, Taiwan and the northern Philippines, 3000 BC TO AD 100 : The early history of the Austronesian-speaking populations*. PhD thesis. Australian Natioanl University.

Hung, H.-C. (2005). Neolithic interaction between Taiwan and northern Luzon: The pottery and jade evidence from the Cagayan Valley. *Journal of Austronesian Studies*. 1, 109–134.

Hung, H.-C., Carson, M. T., Bellwood, P., Piper, P. J., Dizon, E., Bolunia, M. J., L., Oxenham, M. & Chi, Z. (2011). The first settlement of remote Oceania: The Philippines to the Marianas. *Antiquity*. 85 (329), 909-926.

Hunt, C., Kealhofer, L., Premathilake, R., Rushworth, G., Gilbertson, D., Jones, S., & Thompson, G. (2016). Palynology, phytoliths, diatoms and wood in the West Mouth: Stratigraphic and taphonomic studies of Late Quaternary vegetation history. In: Barker, G. & Farr, L. (eds.) *Archaeological investigations in the Niah Caves, Sarawak, 1954-2004,* Volume 2. Cambridge, McDonald Institute for Archaeological Research, pp. 149–176.

Hunt, C. O., Gilbertson, D. D. & Rushworth, G. (2012). A 50,000-year record of Late Pleistocene tropical vegetation and human impact in lowland Borneo. *Quaternary Science Reviews*. 37, 61–80.

Hunt, C. O. & Premathilake, R. (2012). Early Holocene vegetation, human activity and climate from Sarawak, Malaysian Borneo. *Quaternary International*. 249, 105–119.

Hunt, C. O. & Rabett, R. J. (2014). Holocene landscape intervention and plant food production strategies in island and mainland Southeast Asia. *Journal of Archaeological Science*. 51, 22–33.

Hutterer, K. L. (1974). The Evolution of Philippine Lowland Societies. *Mankind*, *9*(4), 287–299.

Hutterer, K. L. (1983). The natural and cultural history of Southeast Asian agriculture. *Anthropos*, 78, 169–212.

Hutterer, K. L. & Macdonald, W. K. (eds.). (1982). *Houses Built on Scattered Poles: Prehistory and Ecology in Negros Oriental, Philippines*. Cebu, University of San Carlos Publications.

Hutterer, R., Balete, D. S., Giarla, T. C., Heaney, L. R. & Esselstyn, J. A. (2018). A new genus and species of shrew (Mammalia: Soricidae) from Palawan Island, Philippines. *Journal of Mammalogy*. 99 (3), 518–536.

Huxley, T. H. (1868). On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London*. 294–319.

Ingicco, T., Van den Bergh, G. D., Jago-on, C., Bahain, J.-J., Chacón, M. G., Amano, N., Forestier, H., King, C., Manalo, K., Nomade, S., Pereira, A., Reyes, M. C., Sémah, A.-M., Shao, Q., Voinchet, P., Falguères, C., Albers, P. C. H., Lising, M., Lyras, G., Yurnaldi, D., Rochette, P., Bautista, A. & De Vos, J. (2018). Earliest known hominin activity in the Philippines by 709 thousand years ago. *Nature*. 557 (7704), 233–237.

Ingicco, T., Piper, P. J., Amano, N., Paz, V. J. & Pawlik, A. F. (2017). Biometric differentiation of wild Philippine pigs from introduced *Sus scrofa* in modern and archaeological assemblages. *International Journal of Osteoarchaeology*. 27 (5), 768–784.

Ingicco, T., Van den Bergh, G., de Vos, J., Castro, A., Amano, N. & Bautista, A. (2016). A new species of *Celebochoerus* (Suidae, Mammalia) from the Philippines and the paleobiogeography of the genus *Celebochoerus* Hooijer, 1948. *Geobios*. 49 (4), 285–291.

Ingold, T. (2000). *The Perception of the Environment* (1st edition). London, Routledge.

Janowski, M. & Langub, J. (2011). Footprints and marks in the forest: The Penan and the Kelabit of Borneo. In: Barker, G. & Janowski, M. (eds.) *Why cultivate? Anthropological and archaeological approaches to foraging-farming transitions in Southeast Asia.* Cambridge, McDonald Institute for Archaeological Research, pp. 121-132.

Jansa, S. A., Barker, F. K. & Heaney, L. R. (2006). The pattern and timing of diversification of Philippine endemic rodents: Evidence from mitochondrial and nuclear gene sequences. *Systematic Biology*. 55 (1), 73–88.

Jinam, T, A., Phipps, M. E., Aghakhanian, F., Majumder, P.P., Datar, F., Stoneking, M., Sawai, H., Nishida, N., Tokunaga, K., Kawamura, S., Omoto, K. & Saitou, N. (2017). Discerning the origins of the Negritos, first Sundaland people: Deep divergence and archaic admixture. *Genome Biology and Evolution.* 9 (8), 2013-2022.

Jocano, F. L. (1975). *Philippine Prehistory: An Anthropological Overview of the Beginnings of Filipino Society and Culture.* Quezon City, Philippine Center For Advanced Studies, University of the Philippines.

Johnson, E. (1985). Current developments in bone technology. In: Schiffer, M. B. (ed.) *Advances in archaeological method and theory*. New York, Academic Press, pp. 157-235.

Jones, S., Hunt, C., Barton, H., Lentfer, C. J. & Reimer, P. J. (2013). Forest disturbance, arboriculture and the adoption of rice in the Kelabit Highlands of Sarawak, Malaysian Borneo. *The Holocene*. 23 (11), 1528–1546.

Junker, L. L. (1999). *Raiding, Trading, and Feasting: The Political Economy of Philippine Chiefdoms*. Honolulu, University of Hawaii Press.

Junker, L. L. (2002a). Economic specialization and inter-ethnic trade between foragers and farmers in the prehispanic Philippines. In: Morrison, K. D. & Junker, L. L. (eds.) *Forager-traders in South and Southeast Asia: Long-term histories.* Cambridge, Cambridge University Press, pp. 203–241.

Junker, L. L. (2002b). Southeast Asia: Introduction. In: Morrison, K. D. & Junker, L. L. (eds.) *Forager-traders in South and Southeast Asia: Long-term histories.* Cambridge, Cambridge University Press, pp. 131–166.

Justiniano, R., Schenk, J. J., Balete, D. S., Rickart, E. A., Esselstyn, J. A., Heaney, L. R. & Steppan, S. J. (2015). Testing diversification models of endemic Philippine forest mice (*Apomys*) with nuclear phylogenies across elevational gradients reveals repeated colonization of isolated mountain ranges. *Journal of Biogeography.* 42 (1), 51-64.

Kelly, R. L. (1983). Hunter-gatherer mobility strategies. *Journal of Anthropological Research*. 39 (3), 277-306.

Kelly, R. L. (2007). *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways* (Reprint edition). Clinton Corners, New York, Eliot Werner Publications.

Kelly, R. L. (2013). *The Lifeways of Hunter-Gatherers: The Foraging Spectrum* (2nd revised edition). Cambridge, Cambridge University Press.

Kitchener, A. C. & Yamaguchi, N. (2010). What is a tiger? Biogeography, morphology, and taxonomy. In: Tilson, R. & Nyhus, P. J. (eds.) *Tigers of the world: The science, politics, and conservation of* Panthera tigris, Noyes Series in Animal Behavior, Ecology, Conservation, and Management. Boston, William Andrew Publishing, pp. 53–84.

Kitchener, D. J., Boeadi, Charlton, L. & Maharadatunkamsi. (1990). Wild mammals of Lombok Island. *Records of the Western Australian Museum Supplement*. 33, 1–129.

Koch, P. L. & Barnosky, A. D. (2006). Late Quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*. 37 (1), 215–250.

Kouvari, M. & Van der Geer, A. A. E. (2018). Biogeography of extinction: The demise of insular mammals from the Late Pleistocene till today. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 505, 295–304.

Kress, J. H. (1977). Contemporary and prehistoric subsistence patterns on Palawan. In: Wood, W. (ed.) *Cultural-ecological Perspectives on Southeast Asia: A symposium*, Ohio University Center for International Studies Southeast Asia Series, No. 41. Athens, Ohio, Ohio University Press, pp. 29-47.

Kress, J. H. (1980). The ceramics from Pilanduk Cave and Sa'gung Rockshelter, Quezon municipality, Palawan Island, Philippines. *Asian Perspectives*. 21 (1), 58–85.

Kress, J. H. (2000). The malacoarchaeology of Palawan island. *Journal of East Asian Archaeology*, 2 (1), 285–328.

Lambeck, K., Esat, T. M. & Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature*. 419, 199–206.

Lambertini, M., Leape, J., Marton-Lefèvre, J., Mittermeier, R. A., Rose, M., Robinson, J. G., Stuart, S. N., Waldman, B. & Genovesi, P. (2011). Invasives: A major conservation threat. *Science*. 333 (6041), 404–405.

Lam, Y. M., Chen, X. & Pearson, O. M. (1999). Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *American Antiquity*. 64 (2), 343–362.

Lam, Y. M. & Pearson, O. M. (2004). The fallibility of bone density values and their use in archaeological analyses. *Journal of Taphonomy*. 2 (1-4), 99–116.

Lam, Y. M. & Pearson, O. M. (2005). Bone density studies and the interpretation of the faunal record. *Evolutionary Anthropology: Issues, News, and Reviews*. 14 (3), 99–108.

Lane, P. (2006). Comments on Charlotte Damm (2005): Archaeology, ethnohistory and oral traditions. *Norwegian Archaeological Review*. 39 (1), 70–79.

Lane, P. (2011). Possibilities for a postcolonial archaeology in sub-Saharan Africa: Indigenous and usable pasts. *World Archaeology*. 43 (1), 7–25.

Lara, M., Paz, V. J., Lewis, H. & Solheim, W. (2015). Bone modifications in an Early Holocene cremation burial from Palawan, Philippines. *International Journal of Osteoarchaeology*, 25 (5), 637–652.

Larson, G., Cucchi, T., Fujita, M., Matisoo-Smith, E., Robins, J., Anderson, A., Rolett, B., Spriggs, M., Dolman, G., Kim, T.-H., Nguyen, T. D. T., Randi, E., Doherty, M., Awe, R. D., Bollt, R., Djubiantono, T., Griffin, B., Intoh, M., Keane, E., Kirch, P., Li, K.-T., Morwood, M., Pedriña, L. M., Piper, P. J., Rabett, R. J., Shooter, P., Van den Bergh, G., West, E., Wickler, S., Yuan, J., Cooper, A. & Dobney, K. (2007). Phylogeny and ancient DNA of *Sus* provides insights into Neolithic expansion in Island Southeast Asia and Oceania. *Proceedings of the National Academy of Sciences*. 104 (12), 4834–4839.

Lazzari, V., Guy, F., Salais, P.-E., Euriat, A., Charles, C., Viriot, L., Tafforeau, P. & Michaux, J. (2015). *Convergent evolution of molar topography in Muroidea (Rodentia, Mammalia): Connections between chewing movements and crown morphology*. In: Cox. P. G. & Hautier, L. (eds.) *Evolution of the rodents: Advances in phylogeny, functional morphology and development.* Cambridge, Cambridge University Press, pp. 448-477.

Lecompte, E., Aplin, K., Denys, C., Catzeflis, F., Chades, M. & Chevret, P. (2008). Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC Evolutionary Biology*. 8 (1), 199.

Lee, R. B. & DeVore, I. (eds.). (1968). *Man the Hunter: The First Intensive Survey of a Single, Crucial Stage of Human Development – Man's Once Universal Hunting Way of Life*. Chicago, Aldine Publishing Company.

Legge, A. J. (1978). Archaeozoology—or zooarchaeology? In: Brothwell, D. R., Thomas, K. D. & Clutton-Brock, J. (eds.) *Research problems in zooarchaeology*. London, Routledge, pp. 129-132.

Leslie, D. M. (2011). *Rusa unicolor* (Artiodactyla: Cervidae). *Mammalian Species*, *43*(1), 1–30.

Lewis, H., Johnson, K. & Ronquillo, W. (2007). Preliminary results of speleothem dating from Tabon Cave, Palawan, Philippines: Moisture increase at the Last Glacial Maximum. *Hukay*. 12, 35–50.

Lewis, H., Paz, V. J., Lara, M., Barton, H., Piper, P. J., Ochoa, J., Vitales, T., Carlos, A. J., Higham, T., Neri, L., Hernandez, V., Stevenson, J., Robles, E. C., Ragragio, A., Padilla, R., Solheim, W. & Ronquillo, W. (2008). Terminal Pleistocene to mid-Holocene occupation and an early cremation burial at Ille Cave, Palawan, Philippines. *Antiquity*. 82 (316), 318–335.

Liebherr, J. K. & Porch, N. (2015). Reassembling a lost lowland carabid beetle assemblage (Coleoptera) from Kauai, Hawaiian Islands. *Invertebrate Systematics*. 29 (2), 191–213.

Liedigk, R., Kolleck, J., Böker, K. O., Meijaard, E., Md-Zain, B. M., Abdul-Latiff, M. A. B., Ampeng, A., Lakim, M., Abdul-Patah, P., Tosi, A. J., Brameier, M., Zinner, D. & Roos, C. (2015). Mitogenomic phylogeny of the common long-tailed macaque (*Macaca fascicularis fascicularis*). *BMC Genomics*. 16 (1), 222.

Li, T. M. (2005). Locating indigenous environmental knowledge in Indonesia. In: Bicker, A., Ellen, R. & Parkes, P. (eds.) *Indigenous enviromental knowledge and its transformations: Critical anthropological perspectives*. London, Routledge, pp. 121-150.

Locatelli, E., Awe, R. D., Jatmiko, & Van den Hoek Ostende, L. W. (2015). Middle-sized murids from Liang Bua (Flores, Indonesia): Insular endemics, human introductions and palaeoenvironment. *Palaeobiodiversity and Palaeoenvironments*. 95 (3), 497–512.

Locatelli, E., Awe, R. D., Van den Bergh, G. D., & Van den Hoek Ostende, L. W. (2012). Pleistocene survivors and Holocene extinctions: The giant rats from Liang Bua (Flores, Indonesia). *Quaternary International*. 281, 47–57.

Lomolino, M. V. (2000). Ecology's most general, yet protean 1 pattern: The species-area relationship. *Journal of Biogeography*. 27 (1), 17–26.

Lomolino, M. V., Riddle, B. R. & Whittaker, R. J. (2016). *Biogeography* (Fifth edition). Oxford, Oxford University Press.

Louys, J., Corlett, R. T., Price, G. J., Hawkins, S. & Piper, P. J. (2014). Rewilding the tropics, and other conservation translocations strategies in the tropical Asia-Pacific region. *Ecology and Evolution*. 4 (22), 4380–4398.

Louys, J., Curnoe, D. & Tong, H. (2007). Characteristics of Pleistocene megafauna extinctions in Southeast Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 243 (1), 152–173.

Louys, J., O'Connor, S. & Aplin, K. (2015). Holocene extinction of Timor's endemic giant murid community, and implication for modern murid conservation on islands. *Journal of Vertebrate Paleontology Program and Abstracts*. 2015, 167–168.

Louys, J., O'Connor, S., Mahirta, Higgins, P., Hawkins, S. & Maloney, T. (2018). New genus and species of giant rat from Alor Island, Indonesia. *Journal of Asia-Pacific Biodiversity*. 11 (4), 503–510.

Lucchini, V., Meijaard, E., Diong, C. H., Groves, C. P. & Randi, E. (2005). New phylogenetic perspectives among species of South-east Asian wild pig (*Sus* sp.) based on mtDNA sequences and morphometric data. *Journal of Zoology*. 266 (1), 25–35.

Luo, S.-J., Johnson, W. E., Smith, J. L. D. & O'Brien, S. J. (2010). What is a tiger? Genetics and phylogeography. In: Tilson, R. & Nyhus, P. J. (eds.) *Tigers of the world: The science, politics, and conservation of* Panthera tigris, Noyes Series in Animal Behavior, Ecology, Conservation, and Management. Boston, William Andrew Publishing, pp. 35–51.

Luo, S.-J., Kim, J.-H., Johnson, W. E., Van der Walt, J., Martenson, J., Yuhki, N., Miquelle, D. G., Uphyrkina, O., Goodrich, J. M., Quigley, H. B., Tilson, R., Brady, G., Martelli, P., Subramaniam, V., McDougal, C., Hean, S., Huang, S.-Q., Pan, W., Karanth, U. K., Sunquist, M., Smith, J. L. D. & O'Brien, S. J. (2004). Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *PLoS Biology*. 2 (12), e442.

Lycett, S. J. & Norton, C. J. (2010). A demographic model for Palaeolithic technological evolution: The case of East Asia and the Movius Line. *Quaternary International*. 211 (1), 55–65.

Lyman, R. L. (1984). Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology*. 3 (4), 259–299.

Lyman, R. L. (1987). Archaeofaunas and butchery studies: A taphonomic perspective. *Advances in Archaeological Method and Theory*. 10, 249–337.

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge, Cambridge University Press.

Lyman, R. L. (1996). Applied zooarchaeology: The relevance of faunal analysis to wildlife management. *World Archaeology*. 28 (1), 110–125.

Lyman, R. L. (2006). Paleozoology in the service of conservation biology. *Evolutionary Anthropology: Issues, News, and Reviews*. 15 (1), 11–19.

Lyman, R. L. (2008). *Quantitative Paleozoology*. Cambridge, Cambridge University Press.

Lyman, R. L. (2012). A warrant for applied palaeozoology. *Biological Reviews*. 87 (3), 513–525.

Lyman, R. L. (2015). Paleozoology is valuable to conservation biology. In: Isendahl, C. & Stump, D. (eds.) *The Oxford handbook of historical ecology and applied archaeology*. Oxford, Oxford University Press. Available from: https://www.oxfordhandbooks.com/view/10.1093/oxfordhb/9780199672691.001.0001/oxfordhb-9780199672691. [Accessed 7 May 2018].

MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*. 100 (916), 603–609.

MacArthur, R. H. & Wilson, E. O. (1967). *The Theory of Island Biogeography*. New Jersey, Princeton University Press.

MacKinnon, J. R., Ong, P. & Gonzales, J. (2015). *Rusa marianna. The IUCN Red List of Threatened Species*. International Union for Conservation of Nature. Available from: https://www.iucnredlist.org/details/15955/0 [Accessed 1 September 2018]

Maeda, Y., Siringan, F., Omura, A., Berdin, R., Hosono, Y., Atsumi, S. & Nakamura, T. (2004). Higher-than-present Holocene mean sea levels in Ilocos, Palawan and Samar, Philippines. *Quaternary International*. 115, 15–26.

Magurran, A. E. (1988). *Ecological diversity and its measurement*. New York, Princeton University Press.

Magurran, A. E. (2004). *Measuring Biological Diversity*. Malden, Massachusetts, John Wiley & Sons.

Manipon, D. (2017). A preliminary report of the lithic artifacts from Trench 3, Pilanduk cave, Palawan. Quezon City, UP Archaeological Studies Program.

Marciniak, A. (2005). *Placing Animals in the Neolithic: Social Zooarchaeology of Prehistoric Farming Communities*. London, University College London.

Marean, C., Abe, Y., Nilssen, P. J. & Stone, E. C. (2001). Estimating the minimum number of skeletal elements (MNE) in zooarchaeology: A review and a new image-analysis GIS approach. *American Antiquity*. 66 (2), 333–348.

Marlowe, F. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Berkeley, University of California Press.

Martin, P. S. & Steadman, D. W. (1999). Prehistoric extinctions on islands and continents. In MacPhee, R. D. E. (ed.) *Extinctions in near time: Causes, contexts, and consequences*, Advances in Vertebrate Paleobiology. Boston, Masachusetts, Springer US, pp. 17–55.

Mathisen, M. E. & Vondra, C. F. (1983). The fluvial and pyroclastic deposits of the Cagayan Basin, Northern Luzon, Philippines—an example of non-marine volcaniclastic sedimentation in an interarc basin. *Sedimentology*. 30 (3), 369–392.

Mayne Correia, P. (1997). Fire modification of bone: A review of the literature. In: Haglund, W.D. & Sorg, M. (eds.) *Forensic taphonomy: The postmortem fate of human remains*. Boca Raton, USA, CRC Press, pp. 435–450.

Mazák, J. H., Christiansen, P. & Kitchener, A. C. (2011). Oldest known pantherine skull and evolution of the tiger. *PLoS ONE*. 6 (10), e25483.

McGuinness, K. A. (1984). Species–area curves. *Biological Reviews*. 59 (3), 423–440.

Meadow, R. H. (1978). Bonecode: A system of numerical coding for faunal data from Middle Eastern sites. *Approaches to Faunal Analysis in the Middle East*. 169–186.

Medin, L. W. M., Medin, D. L.& Atran, S. (1999). *Folkbiology*. Massachusetts, MIT Press.

Meijaard, E. (2003). Mammals of south-east Asian islands and their Late Pleistocene environments. *Journal of Biogeography*. 30 (8), 1245–1257.

Meijaard, E. & Groves, C. P. (2004). Morphometrical relationships between South-east Asian deer (Cervidae, tribe Cervini): Evolutionary and biogeographic implications. *Journal of Zoology*. 263 (2), 179–196.

Meijer, H. J. M., Louys, J. & O'Connor, S. (2019). First record of avian extinctions from the Late Pleistocene and Holocene of Timor Leste. *Quaternary Science Reviews*. 203, 170–184.

Meijer, H. J. M., Van den Hoek Ostende, L. W., Van den Bergh, G. D. & De Vos, J. (2010). The fellowship of the hobbit: The fauna surrounding Homo floresiensis. *Journal of Biogeography*. 37 (6), 995–1006.

Mellars, P. (2006). Going east: New genetic and archaeological perspectives on the modern human colonization of Eurasia. *Science*. 313 (5788), 796–800.

Mercader, J. (ed.). (2002). *Under the Canopy: The Archaeology of Tropical Rainforests*. New Jersey, Rutgers University Press.

Metcalfe, D. & Jones, K. T. (1988). A reconsideration of animal body-part utility indices. *American Antiquity*. 53 (3), 486–504.

Mijares, A. S. B. (2002). *The Minori Cave Expedient Lithic Technology*. Quezon City, University of the Philippines Press.

Mijares, A. S. B. (2007). *Unearthing Prehistory: The Archaeology of Northeastern Luzon, Philippine Islands*. Oxford, BAR Publishing.

Mijares, A. S. B. (2008). The Late Pleistocene to Early Holocene foragers of northern Luzon. *Bulletin of the Indo-Pacific Prehistory Association*. 28, 99–107.

Mijares, A. S. B. (2001). An expedient lithic technology in northern Luzon (Philippines). *Lithic Technology*. 26 (2), 138–152.

Mijares, A. S. B. (2005). The Archaeology of Peñablanca Cave Sites, Northern Luzon, Philippines. *Journal of Austronesian Studies*. 1 (2), 65–93.

Mijares, A. S. B. & Lewis, H. A. (2009). Cave sites in northeastern Luzon, Philippines: A preliminary soil micromorphological study. *Asian Perspectives*. 48 (1), 98–118.

Mijares, A. S. B., Détroit, F., Piper, P. J., Grün, R., Bellwood, P., Aubert, M., Champion, G., Cuevas, N., De Leon, A. & Dizon, E. (2010). New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. *Journal of Human Evolution*. 59 (1), 123–132.

Miller, G. S. (1912). *Catalogue of the Mammals of Western Europe (Europe Exclusive of Russia) in the Collection of the British Museum*. London, British Museum.

Minter, T. (2010). *The Agta of the northern Sierra Madre: Livelihood strategies and resilience among Philippine hunter-gatherers*. PhD thesis. Leiden University.

Mittermeier, R. A., Mittermeier, C. G. & Robles-Gil, P. (1997). *Megadiversity: Earth's Biologically Wealthiest Nations*. Mexico City, CEMEX.

Moigne, A.-M., Awe, R. D., Sémah, F. & Sémah, A.-M. (2004). The cervids from the Ngebung site (Kabuh series, Sangiran Dome, central Java) and their biostratigraphical significance. *Modern Quaternary Research in Southeast Asia*. 18, 31–44.

Molengraaff, G. A. F. (1921). Modern deep-sea research in the east Indian Archipelago. *The Geographical Journal*. 57 (2), 95–118.

Moore, M. W. & Brumm, A. (2007). Stone artifacts and hominins in island Southeast Asia: New insights from Flores, eastern Indonesia. *Journal of Human Evolution*. 52 (1), 85–102.

Morin, E. (2007). Fat composition and Nunamiut decision-making: A new look at the marrow and bone grease indices. *Journal of Archaeological Science*. 34 (1), 69–82.

Morin, E. & Soulier, M.-C. (2017). New criteria for the archaeological identification of bone grease processing. *American Antiquity*. 82 (1), 96–122.

Morley, R. J. (1981). Development and vegetation dynamics of a lowland ombrogenous peat swamp in Kalimantan Tengah, Indonesia. *Journal of Biogeography*. 8 (5), 383–404.

Morley, R. J. (2018). Assembly and division of the South and South-East Asian flora in relation to tectonics and climate change. *Journal of Tropical Ecology*. 34 (4), 209–234.

Morley, R. J., Morley, H. P., Wonders, A. A. H., Sukarno & Van der Kaars, S. (2004). Biostratigraphy of modern (Holocene and Late Pleistocene) sediment cores from the Makassar Straits. *IPA-AAPG Deepwater and Frontier Symposium, 2004.* 361–371.

Morrison, K. D. (2002). Historicizing adaptation, adapting to history: Forager-traders in South and Southeast Asia. In: Morrison, K. D. & Junker, L. L. (eds.) *Forager-traders in South and Southeast Asia: Long-term histories.* Cambridge, Cambridge University Press, pp. 1-17.

Morwood, M. J. (2014). Faunal biogeography in Island Southeast Asia. In: Dennell, R. & Porr, M. (eds.) *Southern Asia, Australia, and the search for human origins.* Cambridge, Cambridge University Press, pp. 108–117.

Movius, H. L. (1948). The Lower Palaeolithic cultures of southern and eastern Asia. *Transactions of the American Philosophical Society*. 38 (4), 329–420.

Mudar, K. (1985). Bearded pigs and beardless men: Predator-prey relationships between pigs and Agta in northeastern Luzon, Philippines. In Griffin, P. B. & Estioko-Griffin, A. A. (eds.) *The Agta of Northeastern Luzon: Recent studies.* Cebu, San Carlos Publications, pp. 69–84.

Mudar, K. (1997). Patterns of animal utilization in the Holocene of the Philippines: A comparison of faunal samples from four archaeological sites. *Asian Perspectives*. 36 (1), 67–105.

Musser, G. G. (1981). The giant rat of Flores and its relatives east of Borneo and Bali. *Bulletin of the American Museum of Natural History.* 169, article 2, 67-176.

Musser, G. G. & Carleton, M. (2005). Superfamily Muroidea. In: Wilson, D. & Reeder, D. (eds.) *Mammal species of the world* (3rd edition). Maryland, Johns Hopkins University Press, pp. 894-1531.

Musser, G. G. & Gordon, L. K. (1981). A new species of *Crateromys* (Muridae) from the Philippines. *Journal of Mammalogy*. 62 (3), 513–525.

Musser, G. G., & Heaney, L. R. (1992). Philippine rodents: Definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). *Bulletin of the American Museum of Natural History.* (211), 1-138.

Musser, G. G., Heaney, L. R., & Tabaranza, B. R. (1998). Philippine rodents : Redefinitions of known species of *Batomys* (Muridae, Murinae) and description of a new species from Dinagat Island. *American Museum Novitates.* (3237), 1-51.

Myers, N. (1988). Threatened biotas: "Hot spots" in tropical forests. *Environmentalist.* 8 (3), 187–208.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature.* 403 (6772), 853–858.

Nasi, R., Taber, A. & Van Vliet, N. (2011). *Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins.* Available from: https://www.ingentaconnect.com/content/cfa/ifr/2011/00000013/00000003/art00008 [Accessed 17th April 2019].

Navarro, A. M. (2000). *Ang Bagong Kasaysayan sa Wikang Filipino: Kalikasan, Kaparaanan, Pagsasakasaysayan*. Quezon City, Bagong Kasaysayan.

Nicholas, G. P. (1997). *At a Crossroads: Archaeology and First Peoples in Canada*. Vancouver, Simon Fraser University.

Novellino, D. (1998). The ominous switch: From indigenous forest management to conservation - the case of the Batak on Palawan Island, the Philippines. In: Colchester, M. & Erni, C. (eds.) *Indigenous peoples and protected areas in South and Southeast Asia*. Copenhagen, International Work Group for Indigenous Affairs, pp. 250-297.

Novellino, D. (2001). Pälawan Attitudes towards illness. *Philippine Studies*. 49 (1), 78-93.

Novellino, D. (2002). The relevance of myths and worldviews in Palawan classification, perceptions and management of honey bees. In: Stepp, J. R., Wyndham, F. S. & Zarger, R. K. (eds.) *Ethnobiology and biocultural diversity: Proceedings of the 7th International Congress of Ethnobiology*. Athens, International Society of Ethnobiology, pp. 189-206.

Novellino, D. (2007). Cycles of politics and cycels of nature. In: Ellen, R. (ed.) *Modern crises and traditional strategies: Local ecological knowledge in Island Southeast Asia*. New York, Berghahn Books, pp. 189–219.

Ochoa, J. P. (2009). *Terrestrial vertebrates of Ille Cave, northern Palawan, Philippines: Subsistence and palaeoeoclogy in the Terminal Pleistocene to the Holocene*. Master's thesis. University of the Philippines, Quezon City.

Ochoa, J. P., Paz, V. J., Lewis, H., Carlos, J., Robles, E., Amano, N., Ferreras, M. R., Lara, M., Vallejo, B., Velarde, G., Villaluz, S. A., Ronquillo, W. & Solheim, W. (2014). The archaeology and palaeobiological record of Pasimbahan-Magsanib site, northern Palawan, Philippines. *Philippine Science Letters*. 7 (1), 22–36.

Ochoa, J. P. & Piper, P. J. (2017). Holocene large mammal extinctions in Palawan Island, Philippines. In: Monks, G. (ed.) *Climate change and human responses: A zooarchaeological perspective*. Dordrecht, Springer, pp. 69-86.

O'Connor, S. (2015). Crossing the Wallace Line: The maritime skills of the earliest colonists in the Wallacean archipelago. In: Kaifu, Y., Izuho, M., Gobel, T., Sato, H. & Ono, A. (eds.) *Emergence and diversity of modern human behavior in Paleolithic Asia*. Texas, Texas A&M University, pp. 214-224.

O'Connor, S. (2015). Rethinking the Neolithic in Island Southeast Asia, with particular reference to the archaeology of Timor-Leste and Sulawesi. *Archipel.* (90), 15–47.

O'Connor, S. & Bulbeck, D. (2014). *Homo sapiens* societies in Indonesia and South-eastern Asia. In: Cummings, V., Jordan, P. & Zvelebil, M. (eds.) *The Oxford handbook of the archaeology and anthropology of hunter-gatherers.* Oxford, Oxford University Press, pp. 1–12.

O'Connor, S., Louys, J., Kealy, S. & Samper Carro, S. C. (2017). Hominin dispersal and settlement east of Huxley's Line: The role of sea level changes, island size, and subsistence behavior. *Current Anthropology*. 58 (S17), S567–S582.

O'Connor, S., Ono, R. & Clarkson, C. (2011). Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science*. 334 (6059), 1117–1121.

O'Connor, S., Robertson, G. & Aplin, K. P. (2014). Are osseous artefacts a window to perishable material culture? Implications of an unusually complex bone tool from the Late Pleistocene of East Timor. *Journal of Human Evolution*. 67, 108–119.

O'Connor, S., Spriggs, M. & Veth, P. (2002). Excavation at Lene Hara Cave establishes occupation in East Timor at least 30,000–35,000 years ago. *Antiquity*. 76 (291), 45–49.

O'Connor, S. & Veth, P. (2000). The world's first mariners: Savanna dwellers in an island continent. *Modern Quaternary Research in Southeast Asia*. 16, 99–137.

O'Connor, T. (2008). *The Archaeology of Animal Bones*. Texas, Texas A&M University Press.

O'Donnell, S. A. (2016). *Human-rainforest interactions in Island Southeast Asia: Holocene vegetation history in Sarawak (Malaysian Borneo) and Palawan (western Philippines).* PhD thesis. University of Cambridge.

Oliver, W. L. R. (ed.) (1993). *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan*. IUCN.

Oliveros, C. H. & Moyle, R. G. (2010). Origin and diversification of Philippine bulbuls. *Molecular Phylogenetics and Evolution*. 54 (3), 822–832.

Olsen, S. L. & Shipman, P. (1988). Surface modification on bone: Trampling versus butchery. *Journal of Archaeological Science*. 15 (5), 535–553.

Ono, R., Soegondho, S. & Yoneda, M. (2009). Changing marine exploitation during Late Pleistocene in northern Wallacea: Shell remains from Leang Sarru Rockshelter in Talaud Islands. *Asian Perspectives*. 48 (2), 318–341.

Orogo, F. (1982). Progress report: Minori Cave Chamber A archaeological excavation. Manila, National Museum of the Philippines.

Orton, D. C. (2012). Taphonomy and interpretation: An analytical framework for social zooarchaeology. *International Journal of Osteoarchaeology*. 22 (3), 320–337.

Outram, A. K. (2001). A new approach to identifying bone marrow and grease exploitation: Why the "indeterminate" fragments should not be ignored. *Journal of Archaeological Science*, 28 (4), 401–410.

Outram, A. K. (2002). Bone fracture and within-bone nutrients: An experimentally based method for investigating levels of marrow extraction. In: Miracle, P. & Milner, N. (eds.) *Consuming passions and patterns of consumption*. Cambridge, McDonald Institute for Archaeological Research, pp. 51-63.

Oxenham, M., Willis, A., Hung, H.-C., Page, R. & Matsumura, H. (2015). Dealing with death in the Late Neolithic to Metal Period Nagsabaran, the Philippines. In: Oxenham, M. & Buckley, H. (eds.) *The Routledge handbook of bioarchaeology in Southeast Asia and the Pacific Islands*. Oxon, Routledge, pp. 311-338.

Page, A. E., Viguier, S., Dyble, M., Smith, D., Chaudhary, N., Salali, G. D., Thompson, J., Vinicius, L., Mace, R. & Migliano, A. B. (2016). Reproductive trade-offs in extant hunter-gatherers suggest adaptive mechanism for the Neolithic expansion. *Proceedings of the National Academy of Sciences*. 113 (17), 4694–4699.

Parkinson, J. A., Plummer, T. & Hartstone-Rose, A. (2015). Characterizing felid tooth marking and gross bone damage patterns using GIS image analysis: An experimental feeding study with large felids. *Journal of Human Evolution*. 80, 114–134.

Patou, M.-L., Wilting, A., Gaubert, P., Esselstyn, J. A., Cruaud, C., Jennings, A. P., Fickel, J. & Veron, G. (2010). Evolutionary history of the *Paradoxurus* palm civets–a new model for Asian biogeography. *Journal of Biogeography*. 37 (11), 2077–2097.

Pawlik, A. F. (2009). Is the functional approach helpful to overcome the typology dilemma of lithic archaeology in Southeast Asia? *Bulletin of the Indo-Pacific Prehistory Association*. 29 (0), 6–14.

Paz, V. J. (2005). Rock shelters, caves, and archaeobotany in Island Southeast Asia. *Asian Perspectives*. 44 (1), 107–118.

Paz, V. J. (2012). Accessing past cosmologies through material culture and the landscape in the Philippines. In: Rountree, K., Morris, C. & Peatfield, A. A. D. (eds.) *Archaeology of spiritualities,* One World Archaeology. New York, Springer, pp. 131-161.

Paz, V. J. (2017). An outlined history of Philippine archaeology and its periodization. In: Habu, J., Lape, P. V. & Olsen, J. W. (eds.) *Handbook of East and Southeast Asian archaeology.* New York, Springer, pp. 151–156.

Paz, V. J. (2003). Terms to ponder for a Southeast Asian archaeologist. *Proceedings of the Society of Philippine Archaeologists*. 1, 1–8.

Paz, V. J. (2014). Global themes in the archaeology of Palawan. In: Eder, J. F. & Evangelista, O. L. (eds.) *Palawan and its global connections*. Quezon City, Ateneo de Manila Press, pp. 36–67.

Paz, V. J., Ronquillo, W. P., Lewis, H., Piper, P. J., Carlos, J. B., Robles, E., Hernandez, V., Vitales, T., Ochoa, J., Reyes, T. & Xhauflair, H. (2008). Palawan Island Palaeohistoric Research Project: Report on the 2008 Dewil Valley field season. Quezon City, UP Archaeological Studies Program.

Perez, P. (2018). *Green Entanglements: Nature Conservation and Indigenous Peoples' Rights in Indonesia and the Philippines*. Quezon City, University of the Philippines Press.

Peterson, J. (1990). *Ecology of Social Boundaries: Agta Foragers of the Philippines*. Urbana, University of Illinois Press.

Peterson, W. (1974). Summary report of two archaeological sites from north-eastern Luzon. *Archaeology & Physical Anthropology in Oceania*. 9 (1), 26–35.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*. 344 (6187), 1246752.

Pimm, S. L. & Raven, P. (2000). Extinction by numbers. *Nature*. 403 (6772), 843-845.

Piper, P. J., Cranbrook, E. O. & Rabett, R. J. (2007). Confirmation of the presence of the tiger *Panthera tigris* in Late Pleistocene and Holocene Borneo. *Malayan Nature Journal*. 59 (3), 259–267.

Piper, P. J. (2017). Changing patterns in hunting across Island Southeast Asia before the Neolithic. In: Bellwood, P. (ed.) *First islanders: Prehistory and human migration in Island Southeast Asia*. New Jersey, John Wiley & Sons, pp. 165-167.

Piper, P. J., Hung, H., Campos, F. Z. & Bellwood, P. (2009). A 4000 year-old introduction of domestic pigs into the Philippine Archipelago: Implications for understanding routes of human migration through Island Southeast Asia and Wallacea. *Antiquity*. 83 (321), 687-695.

Piper, P. J., & Mijares, A. S. B. (2007). A preliminary report on a Late Pleistocene animal bone assemblage from Callao Cave, Peñablanca, northern Luzon, Philippines. Quezon City, UP Archaeological Studies Program.

Piper, P. J., Ochoa, J., Lewis, H., Paz, V. J. & Ronquillo, W. P. (2008). The first evidence for the past presence of the tiger *Panthera tigris* (L.) on the island of Palawan, Philippines: Extinction in an island population. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 264 (1-2), 123–127.

Piper, P. J., Ochoa, J., Robles, E. C., Lewis, H. & Paz, V. J. (2011). Palaeozoology of Palawan Island, Philippines. *Quaternary International*. 233 (2), 142–158.

Piper, P. J. & Rabett, R. (2016). Vertebrate fauna from the Niah Caves. In: Barker, G. & Farr, L. (eds.) *Archaeological investigations in the Niah Caves, Sarawak, 1954-2004*, Volume 2. Cambridge, McDonald Institute for Archaeological Research, pp. 401–438.

Piper, P. J. & Rabett, R. J. (2009). Hunting in a tropical rainforest: Evidence from the Terminal Pleistocene at Lobang Hangus, Niah Caves, Sarawak. *International Journal of Osteoarchaeology*. 19 (4), 551–565.

Pope, G. G. (1989). Bamboo and human evolution. *Natural History*. 10, 49–57.

Pregill, G. K. & Steadman, D. W. (2009). The prehistory and biogeography of terrestrial vertebrates on Guam, Mariana Islands. *Diversity and Distributions*. 15 (6), 983–996.

Pritchard, J. S. (1989). Ilin Island cloud rat extinct? *Oryx*. 23, 126.

R Core Team. (2018). R: A language and environment for statistical computing (Version 3.4.4) [Software]. R Foundation for Statistical Computing. Available from: https://cran.r-project.org/bin/windows/base/old/3.4.4/.

Rabett, R. J., Barker, G., Hunt, C. O., Naruse, T., Piper, P. J., Raddatz, E., Reynolds, T., Nguyễn, V. S., Stimpson, C., Szabó, K., Nguyễn, C. T., & Wilson, J. (2009). The Tràng An Project: Late-to-Post-Pleistocene settlement of the lower Song Hong Valley, North Vietnam. *Journal of the Royal Asiatic Society*. 19 (1), 83–109.

Rabett, R. J. (2005). The early exploitation of Southeast Asian mangroves: Bone technology from caves and open sites. *Asian Perspectives*. 44 (1), 154–179.

Rabett, R. J. (2012). *Human Adaptation in the Asian Palaeolithic*. Cambridge, Cambridge University Press.

Rabett, R. J. (2016). Bone and tusk tools from the West Mouth and Lobang Hangus. In: Barker, G. & Farr, L. (eds.) *Archaeological investigations in the Niah Caves, Sarawak, 1954-2004,* Volume 2. Cambridge, McDonald Institute for Archaeological Research, pp. 301–324.

Rabett, R. J. (2017). The early human occupation of East and Southeast Asia. In: Habu, J., Lape, P. V. & Olsen, J. W. (eds.) *Handbook of East and Southeast Asian archaeology.* New York, Springer, pp. 159–193.

Rabett, R. J. & Piper, P. J. (2012). Eating your tools: Early butchery and craft modification of primate bones in tropical southeast Asia. In: Seetah, K. & Gravina, B. (eds.) *Bones for tools–tools for bones: The interplay between objects and objectives.* Cambridge, McDonald Institute for Archaeological Research, pp. 131–142.

Rabett, R. J., Piper, P. J., & Barker, G. (2006). Bones from "Hell": Preliminary results of new work on the Harrisson faunal assemblage from the deepest part of Niah Cave, Sarawak. In: Bacus, E. A., Glover, I, & Pigott, V. (eds.) *Uncovering Southeast Asia's past: Selected papers from the 10th International Conference of the European Association of Southeast Asian archaeologists*. London, British Museum, pp. 46–29.

Raes, N., Cannon, C. H., Hijmans, R. J., Piessens, T., Saw, L. G., Van Welzen, P. C. & Slik, J. W. F. (2014). Historical distribution of Sundaland's dipterocarp rainforests at Quaternary glacial maxima. *Proceedings of the National Academy of Sciences.*. 111 (47), 16790–16795.

Rai, N. K. (1982). *From Forest to Field: A Study of Philippine Negrito Foragers in Transition.* Hawaii, University of Hawaii.

Rai, N. K. (1990). *Living in a Lean-To: Philippine Negrito Foragers in Transition*. Ann Arbor, Museum of Anthropology, University of Michigan.

Ramsey, C. B. (2017). Methods for summarizing radiocarbon datasets. *Radiocarbon*. 59 (6), 1809–1833.

Redford, K. H., & Stearman, A. M. (1993). Forest-dwelling native Amazonians and the conservation of biodiversity: Interests in common or in collision? *Conservation Biology*. 7 (2), 248–255.

Rehm, S. K. (2006). *The miocene carbonates in time and space on- and offshore SW Palawan, Philippines.* PhD thesis. Christian-Albrechts Universität.

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., Buck, C. E., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T. J., Hoffman, D. L., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Staff, R. A., Turney, C. S. M. & van der Plicht, J. (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*. 55 (4), 1869–1887.

Reis, K. R. & Garong, A. M. (2001). Late Quaternary terrestrial vertebrates from Palawan Island, Philippines. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 171 (3), 409–421.

Reitz, E. J. & Wing, E. S. (1999). *Zooarchaeology*. Cambridge, Cambridge University Press.

Revel, N. (1996). Kudaman: An Oral Epic in the Palawan Highlands. *Oral Tradition.* 11(1), 108-132.

Reyes-García, V., & Pyhälä, A. (eds.). (2017). *Hunter-gatherers in a Changing World*. Switzerland, Springer International Publishing.

Reyes, M. C., Ingicco, T., Piper, P. J., Amano, N. & Pawlik, A. F. (2017). First fossil evidence of the extinct Philippine cloud rat *Crateromys paulus* (Muridae: Murinae: Phloeomyini) from Ilin Island, Mindoro, and insights into its Holocene abundance. *Proceedings of the Biological Society of Washington*. 130 (1), 84–97.

Richards, P. (1996). *The Tropical Rain Forest: An Ecological Study* (2nd edition). Cambridge, Cambridge University Press.

Rickart, E. A., Balete, D. S., Alviola, P. A., Veluz, M. J. & Heaney, L. R. (2016). The mammals of Mt. Amuyao: A richly endemic fauna in the Central Cordillera of northern Luzon Island, Philippines. *Mammalia*. 80 (6), 579–592.

Rickart, E. A., Balete, D. S. & Heaney, L. R. (2007). Habitat disturbance and the ecology of small mammals in the Philippines. *Journal of Environmental Science and Management*. 10 (1), 34–41.

Rickart, E. A., Balete, D. S., Rowe, R. J. & Heaney, L. R. (2011). Mammals of the northern Philippines: Tolerance for habitat disturbance and resistance to invasive species in an endemic insular fauna. *Diversity and Distributions*. 17 (3), 530–541.

Rickart, E. A., Balete, D. S., Timm, R. M., Alviola, P. A., Esselstyn, J. A. & Heaney, L. R. (2019). Two new species of shrew-rats (*Rhynchomys*: Muridae: Rodentia) from Luzon Island, Philippines. *Journal of Mammalogy.* 100 (4), 1112-1129.

Roberts, M., Norman, W., Minhinnick, N., Wihongi, D. & Kirkwood, C. (1995). Kaitiakitanga: Maori perspectives on conservation. *Pacific Conservation Biology*. 2 (1), 7–20.

Roberts, P. (2017). Forests of plenty: Ethnographic and archaeological rainforests as hotspots of human activity. *Quaternary International*. 448, 1–4.

Roberts, P. & Amano, N. (2019). Plastic pioneers: Hominin biogeography east of the Movius Line during the Pleistocene. *Archaeological Research in Asia*. 117, 181-192.

Roberts, P., Perera, N., Wedage, O., Deraniyagala, S., Perera, J., Eregama, S., Gledhill, A., Petraglia, M. D. & Lee-Thorp, J. A. (2015). Direct evidence for human reliance on rainforest resources in Late Pleistocene Sri Lanka. *Science*. 347 (6227), 1246–1249.

Roberts, P., & Petraglia, M. (2015). Pleistocene rainforests: Barriers or attractive environments for early human foragers? *World Archaeology*. 47 (5), 718–739.

Robles, E., Piper, P. J., Ochoa, J., Lewis, H., Paz, V. J. & Ronquillo, W. (2015). Late Quaternary sea-level changes and the palaeohistory of Palawan Island, Philippines. *The Journal of Island and Coastal Archaeology*. 10 (1), 76–96.

Roeder, D. (2012). Convergent margins and orogenic belts. In: Roberts, D. G. & Bally. A. W. (eds.) *Regional geology and tectonics: Principles of geologic analysis.* Amsterdam, Elsevier, pp. 112–177.

Ronquillo, W. P. (1981). *Minori Cave Archaeology*. Manuscript. Manila, National Museum of the Philippines.

Ronquillo, W. P. & Santiago, R. (1977). *Archaeological caves and open sites exploration at Peñablanca, Cagayan Province*. Manuscript. National Museum of the Philippines.

Rosenthal, Y., Oppo, D. W. & Linsley, B. K. (2003). The amplitude and phasing of climate change during the last deglaciation in the Sulu Sea, western equatorial Pacific. *Geophysical Research Letters*. 30 (8), 1428.

Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge, Cambridge University Press.

Rowe, K. C., Achmadi, A. S., & Esselstyn, J. A. (2016). A new genus and species of omnivorous rodent (Muridae: Murinae) from Sulawesi, nested within a clade of endemic carnivores. *Journal of Mammalogy*. 97 (3), 978–991.

Rowsey, D. M., Heaney, L. R. & Jansa, S. A. (2018). Diversification rates of the "Old Endemic" murine rodents of Luzon Island, Philippines are inconsistent with incumbency effects and ecological opportunity. *Evolution*. 72 (7), 1420–1435.

Ruddle, K. (1993). The transmission of traditional ecological knowledge. In: Inglis, J. (ed.) *Traditional ecological knowledge: Concepts and cases*. Ottawa, International Program on Traditional Ecological Knowledge and International Development Research Centre, pp. 17-32.

Russell, N. (2011). *Social Zooarchaeology: Humans and Animals in Prehistory*. Cambridge, Cambridge University Press.

Sala, N. & Arsuaga, J. L. (2018). Regarding beasts and humans: A review of taphonomic works with living carnivores. *Quaternary International.* 466, 131–140.

Salazar, Z. A. (1998). *The Malayan Connection: Ang Pilipinas sa Dunia Melayu*. Quezon City, Palimbagan ng Lahi.

Salazar, Z. A. (2004). *Kasaysayan ng Kapilipinuhan: Bagong Balangkas*. Quezon City, Bagong Kasaysayan.

Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. (2014). Global Late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society of London B: Biological Sciences*. 281 (1787), 20133254.

Sathiamurthy, E. & Voris, H. K. (2006). Maps of Holocene sea level transgression and submerged lakes on the Sunda shelf. *The Natural History Journal of Chulalongkorn University*. 2, 1–43.

Schmidt, C. W. & Uhlig, R. (2012). Light microscopy of microfractures in burned bone. In: Bell, L. S. (ed.) *Forensic microscopy for skeletal tissues: Methods and protocols.* Totowa, New Jersey, Humana Press, pp. 227–234.

Scholes, C., Siddle, K., Ducourneau, A., Crivellaro, F., Järve, M., Rootsi, S., Bellatti, M., Tabbada, K., Mormina, M., Riedla, M., Kivisild, T., Lahr, M. M. & Migliano, A. B. (2011). Genetic diversity and evidence for population admixture in Batak Negritos from Palawan. *American Journal of Physical Anthropology*. 146 (1), 62–72.

Scoones, I., & Thompson, J. (1994). *Beyond Farmer First: Rural People's Knowledge, Agricultural Research and Extension Practice*. Warwickshire, Practical Action Publishing.

Scott, W. H. (1984). *Prehispanic Source Materials for the Study of Philippine History*. Quezon City, New Day Publishers.

Scott, W. H. (1989). *Filipinos in China Before 1500*. Manila, China Studies Program, De La Salle University.

Sémah, F., Sémah, A.-M., Falguères, C., Détroit, F., Gallet, X., Hameau, S., Moigne, A.-M., & Simanjuntak, T. (2004). The significance of the Punung karstic area (Eastern Java) for the chronology of the Javanese Palaeolithic, with special reference to the Song Terus cave. In: Keates, S.G. & Pasveer, J. M. (eds.) *Modern Quaternary research in Southeast Asia: Quaternary research in Indonesia,* Volume 18. Leiden, A.A. Balkema Publishers, pp. 45-62.

Shimelmitz, R., Kuhn, S. L., Jelinek, A. J., Ronen, A., Clark, A. E. & Weinstein-Evron, M. (2014). "Fire at will": The emergence of habitual fire use 350,000 years ago. *Journal of Human Evolution*. 77, 196–203.

Shipman, P. & Rose, J. (1983). Early hominid hunting, butchering, and carcass-processing behaviors: Approaches to the fossil record. *Journal of Anthropological Archaeology*. 2 (1), 57–98.

Siler, C. D., Alcala, A. C., Diesmos, A. C., Brown, R. M. & Harvey, M. (2009). A new species of limestone-forest frog, genus *Platymantis* (Amphibia: Anura: Ceratobatrachidae) from eastern Samar Island, Philippines. *Herpetologica*. 65 (1), 92–104.

Siler, C. D., Oaks, J. R., Esselstyn, J. A., Diesmos, A. C. & Brown, R. M. (2010). Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution*. 55 (2), 699–710.

Sillitoe, P. (1998). The development of indigenous knowledge: A new applied anthropology. *Current Anthropology*. 39 (2), 223–252.

Simanjuntak, T. (2004). New insights on the prehistoric chronology of Gunung Sewu, Java, Indonesia. In: Keates, S.G. & Pasveer, J. M. (eds.) *Modern Quaternary research in Southeast Asia: Quaternary research in Indonesia,* Volume 18. Leiden, A.A. Balkema Publishers, pp. 9-30.

Simanjuntak, T. & Asikin, I. (2004). Early Holocene human settlement in eastern Java. *Bulletin of the Indo-Pacific Prehistory Association*. 24, 13-19.

Slik, Ferry J. W., Arroyo-Rodriguez, V., Aiba, S., Alvarez-Loayza, P., Alves, L., Ashton, P., Balvanera, P., Bastian, M. L., Bellingham, P. J., van den Berg, E., Bernacci, L., Bispo, P. D. C., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., Breur-Ndoundou Hockemba, M., Bunyavejchewin, S., Calderado Leal Matos, D., Castillo-Santiago, M., Catharino, E. L. M., Chai, S.-L., Chen, Y., Colwell, R. K., Chazdon, R. L., Clark, C., Clark, D. B., Clark, D. A., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., DeWalt, S. J., Doucet, J.-L., Duque, A., Durigan, G., Eichhorn, K. A. O., Eisenlohr, P. V., Eler, E., Ewango, C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., Filho, A. T. D. O., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J.-F., Amarnath, G., Griffith, D. M., Grogan, J., Gunatillehe, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. A., Holy, C. A., de Jong, B. H. J., Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F., Lawes, M. J., Leao do Amaral, I., Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E. H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Metzger, J. P., Millet, J., Mohandass, D., Montero, J. C., Morisson Valeriano, M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Onrizal, Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M. T. F., Pitman, N. C. A., Poorter, L., Poulsen, A. D., Poulsen, J., Powers, J., Prasad, R. C., Puyravaud, J.-P., Razafimahaimodison, J.-C., Reitsma, J., Roberto dos Santos, J., Roberto Spironello, W., Romero-Saltos, H., Rovero, F., Rozak, A. H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B. A., Santos, F., Sarker, S. K., Satdichanh, M., Schmitt, C. B., Schöngart, J., Schulze, M., Suganuma, M. S., Sheil, D., da Silva Pinheiro, E., Sist, P., Stevart, T., Sukumar, R., Sun, I.-F., Sunderland, T., Suresh, H. S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D. W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J. L. C. H., Van Do, T., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S. A., Webb, C. O., Whitfeld, T., Wich, S. A., Williams, J., Wittmann, F., Wöll, H., Yang, X., Yao, C. Y. A., Yap, S. L., Yoneda, T., Zahawi, R. A., Zakaria, R., Zang, R., de Assis, R. L., Luize, B. G. & Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences.* 112 (24), 7472-7477.

Smith, C. & Wobst, H. M. (2005). The next step: An archaeology for social justice. In Smith, C. & Wobst, H. M. (eds.) *Indigenous archaeologies: Decolonising theory and practice*. Oxon, Routledge, pp. 392-394.

Smith, D. G., Ng, J., George, D., Trask, J. S., Houghton, P., Singh, B., Villano, J. & Kanthaswamy, S. (2014). A genetic comparison of two alleged subspecies of Philippine cynomolgus macaques. *American Journal of Physical Anthropology*. 155 (1), 136–148.

Smith, D., Schlaepfer, P., Major, K., Dyble, M., Page, A. E., Thompson, J., Chaudhary, N., Salali, G. D., Mace, R., Astete, L., Ngales, M., Vinicius, L. & Migliano, A. B. (2017). Cooperation and the evolution of hunter-gatherer storytelling. *Nature Communications*. 8 (1853), 1-9.

Smith, L. T. (2013). *Decolonizing Methodologies: Research and Indigenous Peoples*. London, Zed Books Ltd.

Snow, B. E., Shutler, R., Nelson, D. E., Vogel, J. S. & Southon, J. R. (1986). Evidence of early rice cultivation in the Philippines. *Philippine Quarterly of Culture and Society*. 14 (1), 3–11.

Solheim, W. (1972). The "new look" of Southeast Asian prehistory. *The Journal of the Siam Society*. 60, 1–20.

Soulier, M.-C. & Costamagno, S. (2017). Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. *Journal of Archaeological Science: Reports.* 11, 782–802.

Steadman, D. W. (2006). *Extinction and Biogeography of Tropical Pacific Birds*. Chicago, University of Chicago Press.

Stegner, M. A. & Holmes, M. (2013). Using palaeontological data to assess mammalian community structure: Potential aid in conservation planning. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 372, 138–146.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, New Jersey, Princeton University Press.

Stevenson, J., Siringan, F., Finn, J., Madulid, D. & Heijnis, H. (2010). Paoay Lake, northern Luzon, the Philippines: A record of Holocene environmental change. *Global Change Biology*. 16 (6), 1672–1688.

Stiner, M. C., Gopher, A. & Barkai, R. (2011). Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *Journal of Human Evolution*. 60 (2), 213–233.

Stiner, M. C., Kuhn, S. L., Weiner, S. & Bar-Yosef, O. (1995). Differential burning, recrystallization, and fragmentation of archaeological bone. *Journal of Archaeological Science*. 22 (2), 223–237.

Stuijts, I., Newsome, J. C. & Flenley, J. R. (1988). Evidence for Late quaternary vegetational change in the Sumatran and Javan highlands. *Review of Palaeobotany and Palynology*. 55 (1), 207–216.

Stump, D. (2015). Digging for indigenous knowledge. In: Isendahl, C. & Stump, D. (eds.) *The Oxford handbook of historical ecology and applied archaeology*. Oxford, Oxford University Press, pp.

Sugár, L. & Nagy, I. (1992). Fatty acid composition in the bone marrow fats of Cervidae. In R. D. Brown (ed.) *The biology of deer.* New York, Springer, p. 460.

Sulkin, C. D. L. (2005). Inhuman beings: Morality and perspectivism among Muinane people (Colombian Amazon). *Ethnos*. 70 (1), 7–30.

Summerhayes, G. R., Field, J. H., Shaw, B. & Gaffney, D. (2017). The archaeology of forest exploitation and change in the tropics during the Pleistocene: The case of northern Sahul (Pleistocene New Guinea). *Quaternary International*. 448, 14–30.

Summerhayes, G. R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A. & Fullagar, R. (2010). Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science.* 330 (6000), 78–81.

Sun, D., Gagan, M. K., Cheng, H., Scott-Gagan, H., Dykoski, C. A., Edwards, R. L. & Su, R. (2005). Seasonal and interannual variability of the mid-Holocene East Asian monsoon in coral δ18O records from the South China Sea. *Earth and Planetary Science Letters*. 237 (1), 69–84.

Sunquist, M. (2010). What is a tiger? Ecology and behavior. In: Tilson, R. & Nyhus, P. J. (eds.) *Tigers of the world: The science, politics, and conservation of* Panthera tigris, Noyes Series in Animal Behavior, Ecology, Conservation, and Management. Boston, William Andrew Publishing, pp. 19-33.

Sun, X., Li, X., Luo, Y. & Chen, X. (2000). The vegetation and climate at the last glaciation on the emerged continental shelf of the South China Sea. *Palaeogeography, Palaeoclimatology. Palaeoecology*. 160 (3), 301–316.

Suzuki, S., Peña, R. E., Tam, T. A., Yumul, G. P., Dimalanta, C. B., Usui, M. & Ishida, K. (2017). Development of the Philippine mobile belt in northern Luzon from Eocene to Pliocene. *Journal of Asian Earth Sciences*. 142, 32–44.

Suzuki, S., Takemura, S., Yumul, G. P., David, S. D. & Asiedu, D. K. (2000). Composition and provenance of the Upper Cretaceous to Eocene sandstones in Central Palawan, Philippines: Constraints on the tectonic development of Palawan. *Island Arc*. 9 (4), 611–626.

Szabó, K. & Amesbury, J. R. (2011). Molluscs in a world of islands: The use of shellfish as a food resource in the tropical island Asia-Pacific region. *Quaternary International*. 239 (1–2), 8–18.

Szabó , K., Bellwood, P. & Brumm, A. (2007). Shell artefact production at 32,000–28,000 BP in Island Southeast Asia: Thinking across media? *Current Anthropology*. 48 (5), 701–723.

Szabó, K., Dizon, E., Batoon, L., Cameron, J., Lacsina, L., Ochoa, J., Peñalosa, A., Piper, P. J., Vitales, T. J. (2007). The Archaeology of Linaminan Central Palawan: A Preliminary Report on Excavations (Images). *Hukay*. 11(1), 1-45.

Szabó, K., Swete-Kelly, M. C. & Peñalosa, A. (2004). Preliminary results from excavations in the eastern mouth of Ille cave, northern Palawan. In: Paz, V. J. (ed.) *Southeast Asian archaeology: Wilhelm G. Solheim II festschrift.* Quezon City University of the Philippines Press, pp. 209–224.

Tershy, B. R., Shen, K.-W., Newton, K. M., Holmes, N. D. & Croll, D. A. (2015). The importance of islands for the protection of biological and linguistic diversity. *BioScience*. 65 (6), 592–597.

Thangaraj, K., Singh, L., Reddy, A. G., Rao, V. R., Sehgal, S. C., Underhill, P. A., Pierson, M., Frame, I. G. & Hagelberg, E. (2003). Genetic affinities of the Andaman Islanders, a vanishing human population. *Current Biology*. 13 (2), 86–93.

Thiel, B. (1990). Excavations at Musang Cave, Northeast Luzon, Philippines. *Asian Perspectives*. 28 (1), 61–81.

Thomas, O. (1895). Preliminary diagnoses of new mammals from Northern Luzon, collected by Mr. John Whitehead. *The Annals and Magazine of Natural History London*. 15, 160–164.

Thompson, T. J. U. (2004). Recent advances in the study of burned bone and their implications for forensic anthropology. *Forensic Science International*. 146, S203–S205.

Thompson, T. J. U. (2005). Heat-induced dimensional changes in bone and their consequences for forensic anthropology. *Journal of Forensic Science*. 50 (5), JFS2004297–JFS2004298.

Tjia, H. D. (1980). The Sunda shelf, Southeast Asia. *Z. Geomorph.* 24, 405–427.

Tjia, H. D. (1996). Sea-level changes in the tectonically stable Malay-Thai Peninsula. *Quaternary International*. 31, 95–101.

Tosi, A. J., Morales, J. C., Melnick, D. J. & Huelsenbeck, J. (2003). Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution*. 57 (6), 1419–1435.

Towns, D. R. & Daugherty, C. H. (1994). Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. *New Zealand Journal of Zoology*. 21 (4), 325–339.

Turvey, S. T. (ed.). (2009). *Holocene Extinctions*. Oxford, Oxford University Press.

Turvey, S. T., Crees, J. J., Hansford, J., Jeffree, T. E., Crumpton, N., Kurniawan, I., Setiyabudi, E., Guillerme, T., Paranggarimu, Dosseto, A. & Van den Bergh, G. D. (2017). Quaternary vertebrate faunas from Sumba, Indonesia: Implications for Wallacean biogeography and evolution. *Proceedings of the. Royal Society B*. 284 (1861), 20171278.

Turvey, S. T. & Fritz, S. A. (2011). The ghosts of mammals past: Biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*. 366 (1577), 2564–2576.

Vallejo, B. (2011). The Philippines in Wallacea. In: Telnov, D. (ed.) *Biodiversity, biogeography and nature conservation in Wallacea and New Guinea,* Volume 1. Riga, The Entomological Society of Latvia, pp. 27–42.

Vallejo, B. (2014). Biogeography of Luzon Island, Philippines. In Telnov, D. (ed.) *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea*, Volume 2. Riga, The Entomological Society of Latvia, pp. 47-59

Van den Bergh, G. D., De Vos, J. & Sondaar, P. Y. (2001). The Late Quaternary palaeogeography of mammal evolution in the Indonesian archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 171 (3), 385–408.

Van den Bergh, G. D., Li, B., Brumm, A., Grün, R., Yurnaldi, D., Moore, M. W., Kurniawan, I., Setiawan, R., Aziz, F., Roberts, R. G., Suyono, Storey, M., Setiabudi, E. & Morwood, M. J. (2016). Earliest hominin occupation of Sulawesi, Indonesia. *Nature*. 529 (7585), 208–211.

Van den Bergh, G. D., Meijer, H. J. M., Awe, R. D., Morwood, M. J., Szabó, K., Van den Hoek Ostende, L. W., Saptomo, E. W., Piper, P. J. & Dobney, K. M. (2009). The Liang Bua faunal remains: A 95 k.yr. sequence from Flores, East Indonesia. *Journal of Human Evolution*. 57 (5), 527–537.

Van der Geer, A. A. E., Lomolino, M. V. & Lyras, G. A. (2017). "Island life" before man: Biogeography of palaeo-insular mammals. *Journal of Biogeography*. 44 (5), 995–1006.

Van der Geer, A., Lyras, G., De Vos, J. & Dermitzakis, M. (2010). *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands*. Oxford, Wiley-Blackwell.

Van der Kaars, S., Bassinot, F., De Deckker, P. & Guichard, F. (2010). Changes in monsoon and ocean circulation and the vegetation cover of southwest Sumatra through the last 83,000 years: The record from marine core BAR94-42. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 296 (1), 52–78.

Van der Kaars, S. & Dam, R. (1997). Vegetation and climate change in West-Java, Indonesia during the last 135,000 years. *Quaternary International*. 37, 67–71.

Van der Kaars, S., Williams, M. A. J., Bassinot, F., Guichard, F., Moreno, E., Dewilde, F. & Cook, E. J. (2012). The influence of the ~73 ka Toba super-eruption on the ecosystems of northern Sumatra as recorded in marine core BAR94-25. *Quaternary International*. 258, 45–53.

Van der Kaars, S., Wang, X., Kershaw, P., Guichard, F. & Setiabudi, D. A. (2000). A Late Quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 155 (1), 135–153.

Van der Kaars, W. A. (1991). Palynology of eastern Indonesian marine piston-cores: A Late Quaternary vegetational and climatic record for Australasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 85 (3), 239–302.

Van der Kaars, W. A. & Dam, M. A. C. (1995). A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 117 (1), 55–72.

Venkataraman, V. V., Kraft, T. S., Dominy, N. J. & Endicott, K. M. (2017). Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proceedings of the National Academy of Sciences*. 114 (12), 3097-3102.

Veron, G., Patou, M.-L., Tóth, M., Goonatilake, M. & Jennings, A. P. (2015). How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal of Zoological Systematics and Evolutionary Research*. 53 (2), 161–174.

Veron, G., Willsch, M., Dacosta, V., Patou, M.-L., Seymour, A., Bonillo, C., Couloux, A., Wong, S. T., Jennings, A. P., Fickel, J. & Wilting, A. (2014). The distribution of the Malay civet *Viverra tangalunga* (Carnivora: Viverridae) across Southeast Asia: Natural or human-mediated dispersal? *Zoological Journal of the Linnean Society*. 170 (4), 917–932.

Villa, P. & Mahieu, E. (1991). Breakage patterns of human long bones. *Journal of Human Evolution*. 21 (1), 27–48.

Virtanen, P. K. (2017). The death of the chief of peccaries: The Apurinã and the scarcity of forest resources in Brazilian Amazonia. In: Reyes-García, V. & Pyhälä, A. (eds.) *Hunter-gatherers in a changing world.* Cham, Springer International Publishing, pp. 97-105.

Von den Driesch, A. (1976). *A Guide to the Measurement of Animal Bones from Archaeological Sites: As Developed by the Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin of the University of Munich*. Boston, Massachusetts, Peabody Museum of Archaeology and Ethnology, Harvard University.

Von Koenigswald, G. H. R. (1958). Preliminary report on a newly-discovered stone-age culture from northern Luzon. *Asian Perspectives*. 2 (2), 69–70.

Voris, H. K. (2000). Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *Journal of Biogeography*. 27 (5), 1153–1167.

Wallace, A. R. (1860). On the zoological geography of the Malay Archipelago. *Journal of the Proceedings of the Linnean Society of London*. 4 (16), 172–184.

Wallace, A. R. (1869). *The Malay Archipelago: The Land of the Orang-utan, and the Bird of Paradise.* London, Macmillan.

Wallace, A. R. (1876). *The Geographical Distribution of Animals*. New York, Harper & Brothers.

Wallace, A. R. (1881). *Island Life*. London, Macmillan.

Ward, J. V. & Bulalacao, L. J. (1999). Pollen analysis of Laguna de Bay, Luzon. *National Museum Papers*. 9, 1–26.

Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. B., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. & Wolfe, A. P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*. 351 (6269), aad2622.

Webster, P. J. (1994). The role of hydrological processes in ocean-atmosphere interactions. *Reviews of Geophysics*. 32 (4), 427–476.

Wedage, O., Amano, N., Langley, M. C., Douka, K., Blinkhorn, J., Crowther, A., Deraniyagala, S., Kourampas, N., Simpson, I., Perera, N. Picin, A., Boivin, N., Petraglia, M. & Roberts, P. (2019). Specialized rainforest hunting by *Homo sapiens* ~45,000 years ago. *Nature Communications*. 10 (1), 739.

Welton, L. J., Siler, C. D., Bennett, D., Diesmos, A., Duya, M. R., Dugay, R., Rico, E. L. B., Van Weerd, M. & Brown, R. M. (2010). A spectacular new Philippine monitor lizard reveals a hidden biogeographic boundary and a novel flagship species for conservation. *Biology Letters*. 6 (5), 654–658.

Wessing, R. (1993). A change in the forest: Myth and history in West Java. *Journal of Southeast Asian Studies*. 24 (1), 1–17.

Wessing, R. (1995). The last tiger in East Java: Symbolic continuity in ecological change. *Asian Folklore Studies*. 54 (2), 191–218.

Westaway, K. E., Louys, J., Awe, R. D., Morwood, M. J., Price, G. J., Zhao, J. -X., Aubert, M., Joannes-Boyau, R., Smith, T. M., Skinner, M. M., Compton, T., Bailey, R. M., van den Bergh, G. D., de Vos, J., Pike, A. W. G., Stringer, C., Saptomo, E. W., Rizal, Y., Zaim, J., Santoso, W. D., Trihascaryo, A., Kinsley, L. & Sulistyanto, B. (2017). An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature*. 548 (7667), 322–325.

Whitehead, K. 1993. *The Whitehead Encyclopedia of Deer*. Stillwater, MN: Swan Hill Press.

Whitmore, T. C. (1992). *An Introduction to Tropical Rainforests*. Oxford, Clarendon Press.

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M. & Willis, K. J. (2005). Conservation biogeography: Assessment and prospect. *Diversity and Distributions*. 11 (1), 3–23.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* [Code]. Available from: https://ggplot2.tidyverse.org

Widlok, T. & Tadesse, W. G. (2005). *Property and Equality: Ritualisation, Sharing, Egalitarianism*. New York, Berghahn Books.

Widmann, P. & Lastica, E. (2015). *Axis calamianensis*. *The IUCN Red List of Threatened Species*. International Union for Conservation of Nature. Available from: https://www.iucnredlist.org/details/15955/0 [Accessed]

Wiessner, P. W. (2014). Embers of society: Firelight talk among the Ju/'hoansi Bushmen. *Proceedings of the National Academy of Sciences*. 111 (39), 14027–14035.

Wikramanayake, E. D., Dinerstein, E. & Loucks, C. J. (2002). *Terrestrial Ecoregions of the Indo-Pacific: A Conservation Assessment*. Washington, Island Press.

Williams, J. W. & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*. 5 (9), 475–482.

Winterhalder, B. (2001). The behavioural ecology of hunter-gatherers. In: Panter-Brick, C., Layton, R. H. & Rowley-Conwy, P. (eds.) *Hunter-gatherers: An interdisciplinary perspective*. Cambridge, Cambridge University Press, pp. 12–38.

Winterhalder, B. & Smith, E. A. (2000). Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology: Issues, News, and Reviews*. 9 (2), 51–72.

Wolverton, S. & Lyman, R. (eds.). (2012). *Conservation Biology and Applied Zooarchaeology* (2nd edition). Tucson, University of Arizona Press.

Wood, J. R., Alcover, J. A., Blackburn, T. M., Bover, P., Duncan, R. P., Hume, J. P., Louys, J., Meijer, H. J. M., Rando, J. C. & Wilmshurst, J. M. (2017). Island extinctions: Processes, patterns, and potential for ecosystem restoration. *Environmental Conservation*. 44 (4), 348–358.

Worthy, T. & Holdaway, R. (2002). *The Lost World of the Moa: Prehistoric Life of New Zealand*. Bloomington, Indiana University Press.

Wrangham, R. & Carmody, R. (2010). Human adaptation to the control of fire. *Evolutionary Anthropology: Issues, News, and Reviews*. 19 (5), 187–199.

Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D. & Conklin-Brittain, N. (1999). The raw and the stolen: Cooking and the ecology of human origins. *Current Anthropology*. 40 (5), 567–594.

Wroe, S., Field, J., Fullagar, R. & Jermin, L. S. (2004). Megafaunal extinction in the Late Quaternary and the global overkill hypothesis. *Alcheringa: An Australasian Journal of Palaeontology*. 28 (1), 291–331.

Wurster, C. M., Bird, M. I., Bull, I. D., Creed, F., Bryant, C., Dungait, J. A. J. & Paz, V. J. (2010). Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. *Proceedings of the National Academy of Sciences*. 107 (35), 15508–15511.

Wurster, C. M., Rifai, H., Zhou, B., Haig, J. & Bird, M. I. (2019). Savanna in equatorial Borneo during the Late Pleistocene. *Scientific Reports.* 9 (1), 1-7.

Xhauflair, H., Pawlik, A. F., Gaillard, C., Forestier, H., Vitales, T. J., Callado, J. R., Tandang, D., Amano, N., Manipon, D. & Dizon, E. (2016). Characterisation of the use-wear resulting from bamboo working and its importance to address the hypothesis of the existence of a bamboo industry in prehistoric Southeast Asia. *Quaternary International*. 416, 95–125.

Xue, H.-R., Yamaguchi, N., Driscoll, C. A., Han, Y., Bar-Gal, G. K., Zhuang, Y., Mazak, J. H., Macdonald, D. W., O'Brien, S. J. & Luo, S.-J. (2015). Genetic ancestry of the extinct Javan and Bali tigers. *Journal of Heredity*. 106 (3), 247–257.

Yang, F.-C. & Grote, P. J. (2018). Riverine vegetation and environments of a Late Pleistocene river terrace, Khorat Plateau, Southeast Asia. *Palynology*. 42 (2), 158–167.

Yokoyama, Y., Suzuki, A., Siringan, F., Maeda, Y., Abe-Ouchi, A., Ohgaito, R., Kawahat, H. & Matsuzaki, H. (2011). Mid-Holocene palaeoceanography of the northern South China Sea using coupled fossil-modern coral and atmosphere-ocean GCM model. *Geophysical Research Letters*. 38 (8), L00F03.

Yumul, G. P., Cruz, N. A., Servando, N. T. & Dimalanta, C. B. (2011). Extreme weather events and related disasters in the Philippines, 2004–08: A sign of what climate change will mean? *Disasters*. 35 (2), 362–382.

Yumul, G. P., Dimalanta, C. B., Marquez, E. J. & Queaño, K. L. (2009). Onland signatures of the Palawan microcontinental block and Philippine mobile belt collision and crustal growth process: A review. *Journal of Asian Earth Sciences*. 34 (5), 610–623.

Yumul, G. P., Dimalanta, C. B., Tamayo, R. A. & Maury, R. C. (2003). Collision, subduction and accretion events in the Philippines: A synthesis. *Island Arc*. 12 (2), 77–91.

Zalasiewicz, J., Williams, M., Haywood, A., & Ellis, M. (2011). The Anthropocene: A new epoch of geological time? *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*. 369 (1938), 835–841.

Zeder, M. A. (2012). The Broad Spectrum Revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations. *Journal of Anthropological Archaeology*. 31 (3), 241–264.

Appendices

Appendix A Description of Tooth Measurements for *Carpomys* and *Musseromys*

Maxillary

1. M1-2 crown length occlusal: crown length taken on the occlusal surface along the midline, from the anterior edge of the M1 t2 to the posterior edge of the M2 posterior cingulum
2. M1-3 crown length occlusal: crown taken on the occlusal surface along the midline, from the anterior edge of the M1 t2 to the posterior edge of the M3 posterior cingulum
3. M1-3 crown length cervical: crown length taken along the midline on the cervical margin of the tooth enamel (above the cementum-enamel junction), from the anterior rim of the M1 to the posterior edge of the M3 posterior cingulum
4. M1 length: greatest length taken on the occlusal surface from the anterior edge of t2 to the posterior edge of the posterior cingulum
5. M1 width: taken on the occlusal surface from the lingual edge of t4 to labial edge of t9
6. M2 length: greatest length taken on the occlusal surface from the anterior edge of t1 to the posterior edge of the posterior cingulum
7. M2 width: taken on the occlusal surface on the anterior loph (from t4 to t6)
8. M3 length: greatest length taken on the occlusal surface from the anterior edge of t1 to the posterior edge of the posterior cingulum
9. M3 width: taken on the occlusal surface on the anterior loph (from t4 to t6)

Mandibular

1. m1-2 crown length occlusal: crown length taken on the occlusal surface along the midline, from the anterior edge of the m1 anteroconid to the posterior edge of the m2 posterior cingulum
2. m1-3 crown length occlusal: crown taken on the occlusal surface along the midline, from the anterior edge of the m1 anteroconid to the posterior edge of the m3 posterior cingulum
3. m1-3 crown length cervical: crown length taken along the midline on the cervical margin of the tooth enamel (above the cementum-enamel junction), from the anterior rim of the m1 anteroconid to the posterior edge of m3 posterior cingulum
4. m1 length: greatest length taken on the occlusal surface along the midline from the anterior edge of the m1 anteroconid to the posterior edge of the posterior cingulum
5. m1 width: taken on the occlusal surface of the posterior loph (from the hypoconid to the ectoconid)
6. m2 length: greatest length taken on the occlusal surface from the anterior edge of the anterolabial cusp to the posterior edge of the posterior cingulum
7. m2 width: taken on the occlusal surface on the anterior loph (from the protoconid to the metaconid)
8. m3 length: greatest length taken on the occlusal surface along the midline from the anterior edge of the first loph (protoconid to the metaconid) to the posterior edge of the posterior cingulum

Appendix B NISP Counts for Diversity Measures

NISP counts for Palawan Island Assemblages

Taxon	Pilanduk	Ille Terminal Pleistocene	Ille Holocene	Pasimbahan	Tarung-tarung
Axis calamianensis	85		5	14	
Rusa sp.	251	288	57		
Sus ahoenobarbus	91	14	560	476	10
Cuon/Canis		2	6		
Canis lupus familiaris			1		
Panthera tigris	9	2			
Prionailurus bengalensis			5		
Arctictis binturong			2		
Paradoxurus/Viverra			24	26	
Aonyx cinereus			2		1
Herpestes brachyurus		1	2	2	
Mydaus marchei			14	6	
Macaca fascicularis	6	13	173	174	111
Crocidura batakorum			1		
Crocidura palawensis					3
Manis culionensis			14	3	
Sundamys muelleri			11		
Rattus tiomanicus			1		2
Maxomys panglima					3
Chiropodomys calamianensis					2
Hystrix pumila	2	1	26	14	3
Hylopetes nigripes			5		1
Sundasciurus sp.	2	5	7	5	2
Cynopterus brachyotis			26		1
Pteropus sp.			1	2	
Hipposideros diadema	4		91	1	9
Hipposideros ater			1		
Rhinolophus creaghi			13		2
Myotis macrotarsus			1		
Emballonura alecto					2
Megaderma spasma					23
Eonyteris spelea			1		2
Cyclemys dentata	5		27	3	
Cuora amboinensis			2	5	
Varanus salvator	2	7	192	104	3
Bufo sp.					1
Microhylidae sp.					2
Rana sp.					1
Bronchocela sp.					1
Scincinidae sp.					15
Naja naja					1
Elapidae					1
Collocalia esculenta					4
Timaliidae sp.					1
Zoothera dauma					2
Sylviidae sp.					5
Hypothymis azurea					1
Motacilla sp.					1
Dicaeum sp.					1
Zosterops extinct					1
Total	457	333	1271	835	218

Appendix B continued: NISP Counts for Diversity Measures

NISP counts for Luzon Island Assemblages

Taxon	Callao	Minori	Musang	Nagsabaran	Pintu
Rusa marianna	139	356	169	298	157
Sus philippensis	7	162	64	634	123
Bovid sp.	2				
Bos/Bubalus			8	32	4
Paradoxurus philippinensis		2			
Macaca fascicularis		51	5		7
Phloeomys pallidus		2			
Crateromys undescr. sp.		2			
Carpomys undescr. sp.		6	1		
Bullimus/Rattus sp.		2	1		
Batomys sp.	2				
Apomys microdon	1				
Varanus			8	1	
Dogania subplana				2	
Pelochelys cantorii				1	
Python reticulata					5
Ardeidae sp.				1	
Total	151	583	256	969	296

NISP = number of identified specimens

Sources:

Comparative data for Palawan are derived from Ille, Pasimbahan and Tarung-tarung Cave sites (Ochoa 2009; Ochoa et al. 2014; Reis and Garong 2001, respectively).

For Luzon, comparative data come from Callao Cave, Pintu Rockshelter and Nagsabaran site (Piper and Mijares 2007, Mudar 1997, Amano et al. 2013, respectively).

Appendix C Pilanduk Cave Taphonomy

Counts are expressed as TNF (total number of fragments)

Percentages are expressed as TNF (taphonomic imprint)/ TNF per layer, unless otherwise indicated

Weathering and abrasion

Context	TNF	TNF with weathering	% Weathered	TNF with abrasion	% abrasion
surface	261	0	0	0	0
111	2174	263	12.1	190	8.7
112	2322	80	3.4	54	2.3
117	2561	12	0.5	3	0.1
118	506	6	1.2	0	0
Total	7824	361	4.6	247	3.2

Carbonate concretion

Context	TNF	TNF with concretion	% concretion
surface	261	120	46.0
111	2174	1	0.0
112	2322	2	0.1
117	2561	3	0.1
118	506	0	0
Total	7824	126	1.6

Mineral staining

Context	TNF	TNF with Mineral staining	% Mineral staining
surface	261	2	0.8
111	2174	241	11.1
112	2322	111	4.8
117	2561	24	0.9
118	506	2	0.4
Total	7824	380	4.9

Appendix C continued: Pilanduk Cave Taphonomy

Gnawing

Context	TNF	TNF with gnawing	% gnawing
surface	261	0	0
111	2174	5	0.23
112	2322	4	0.17
117	2561	3	0.12
118	506	1	0.20
Total	7824	13	0.17

Burning

Context	TNF	charred	calcined	total burnt	% burnt	>40mm	% > 40mm	burnt 90-100%	% burnt 90-100%
surface	261	32	3	35	13.4	9	3.4	28	80.0
111	2174	964	32	996	45.8	900	41.4	800	80.3
112	2322	879	48	927	39.9	970	41.8	797	86.0
117	2561	1117	66	1183	46.2	931	36.4	1059	89.5
118	506	126	15	141	27.9	119	23.5	125	88.7
	7824	3118	164	3282	41.9	2929	37.4	2809	85.6

total burnt = charred and calcined fragments

>40 mm = fragments >40 mm in size

burnt 90-100% = fragments with bone surface showing near-complete to complete charring and/or calcination

% burnt 90-100% = percentage of burnt fragments (total burnt) showing near-complete to complete charring and/or calcination

Proportions of burning for spongy and compact bone

Layer	burnt				unburnt			
	spongy		compact		spongy		compact	
	TNF	%	TNF	%	TNF	%	TNF	%
111	207	38.0	338	62.0	187	32.6	386	67.4
112	220	43.5	286	56.5	196	25.4	577	74.6
117	352	37.8	579	62.2	388	36.2	683	63.8
118	42	38.5	67	61.5	92	35.2	169	64.8

Appendix C continued: Pilanduk Cave Taphonomy

Cutmarks

Context	TNF	TNF with cutmarks	% cutmarks
surface	261	1	0.4
111	2174	15	0.7
112	2322	14	0.6
117	2561	38	1.5
118	506	0	0
Total	7824	68	0.9

Helical fractures

Context	TNF long bone	TNF helical	% helical
surface	91	42	46.2
111	688	464	67.4
112	795	473	59.5
117	1183	201	17.0
118	221	18	8.1
Total	2978	1198	1.7

TNF long bone = total number of long bone fragments
TNF helical = total number of long bone fragments showing helical fractures

Fracture outline

Counts pertain to number of long bone fragments displaying each fracture type (specimens can display more than one type). Definitions of bone fracture outlines follow Outram 2002.

Context	Helical	Longitudinal	Transverse	Diagonal	Columnar
111	61	79	52	8	5
112	57	75	52	13	2
117	62	148	118	25	2
118	16	28	25	6	2
Total	196	330	247	52	11

Freshness Fracture Index Scores

Following methodology by Outram (2001, 2002)

FFI scores are taken for long bone fragments only

Context	FFI Scores						
	0	1	2	3	4	5	6
surface	9	13	15	11	3	2	1
111	1	30	21	446	98	15	2
112	6	26	12	473	84	41	3
117	0	10	34	176	619	58	9
118			1	14	122	7	1
Total	16	79	83	1120	926	123	16

Fragment size classes

Context	0-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100+
surface	1	12	29	42	57	34	39	8	10	15
111	1244	394	298	177	22	14	8	7	0	4
112	1425	385	252	169	53	6	12	6	2	10
117	1392	500	308	241	74	21	9	7	3	3
118	287	60	36	34	6	4	3	1	1	1

Size classes in mm.

Notes on tiger bone taphonomy

All nine tiger bones were casted by the National Museum Archaeology Division. The casting process has left traces on the bones that should be distinguished from butchery and and other taphonomic marks. These traces include: red marks/lines, white powder (used in casting) and peeling of the cortical bone. Peeling of the bone surface has affected the morphology of certain butchery marks, particularly on Pil-5393 (subterminal phalanx), wherein possible scrape marks appear shallower because some of the bone surface has been removed and damaged by casting. These were observed by the author because the specimens were inspected under a microscope before and after casting.

Appendix D Bone Mineral Density Data

scan site	*Rangifer*	*Odocoileus*	Pilanduk cervid - combined	
	Lam et al. 1999	Lyman 1994	MAU	%MAU
SP1	1.01	0.36	5	41.7
SP2	1.04	0.49	2	16.7
SP3	0.73	0.23	0.5	4.2
SP4	1.01	0.34	0.5	4.2
HU1	0.26	0.24	4	33.3
HU2	0.44	0.25	1	8.3
HU3	1.12	0.53	1	8.3
HU4	1.08	0.63	4	33.3
HU5	0.48	0.39	5	41.7
RA1	0.53	0.42	12	100.0
RA2	1.08	0.62	3	25.0
RA3	1.09	0.68	2	16.7
RA4	0.97	0.38	0.5	4.2
RA5	0.49	0.43	4.5	37.5
MC1	0.92	0.56	10	83.3
MC2	1.08	0.69	7	58.3
MC3	1.1	0.72	3.5	29.2
MC4	1.01	0.58	2	16.7
MC5	0.48	0.49	6.5	54.2
MC6	0.68	0.51	5	41.7
FE1	0.39	0.41	7	58.3
FE2	0.52	0.36	1.5	12.5
FE3	0.74	0.33	4	33.3
FE4	1.15	0.57	4	33.3
FE5	0.61	0.37	2	16.7
FE6	0.32	0.28	4	33.3
FE7	0.3	\	0.5	4.2
TI1	0.35	0.3	4.5	37.5
TI2	1.01	0.32	6	50.0
TI3	1.13	0.74	6.5	54.2
TI4	1.12	0.51	3.5	29.2
TI5	0.73	0.5	5	41.7
MR1	0.9	0.55	5.5	45.8
MR2	1.1	0.65	4.5	37.5
MR3	1.08	0.74	12	100.0
MR4	1.08	0.57	1	8.3
MR5	0.41	0.46	4	33.3
MR6	0.59	0.5	4.5	37.5
CA1	0.52	0.41	3	25.0
CA2	0.94	0.64	3	25.0
CA3	0.66	0.57	4	33.3
CA4	0.73	0.33	2	16.7
AS1	0.68	0.47	10	83.3
AS2	0.7	0.62	8.5	70.8
P11	0.48	0.36	4.125	34.4
P12	0.92	0.42	5.875	49.0
P13	0.71	0.57	3.625	30.2
P21	0.61	0.28	3.125	26.0
P22	0.72	0.25	2.625	21.9
P31	0.48	0.25	4.125	34.4
DN1	0.65	0.55	2.5	20.8
DN2	1.05	0.57	3	25.0
DN4	1.06	0.57	8	66.7
DN5	1.05	0.57	2.5	20.8
DN6	0.84	0.31	2.5	20.8

Appendix D continued: Bone Mineral Density Data

scan site	*Rangifer* Lam et al. 1999	*Odocoileus* Lyman 1994	Pilanduk cervid-combined MAU	Pilanduk cervid-combined %MAU
DN7	1.01	0.36	3.5	29.2
AT1	0.47	0.13	4	33.3
AT2	0.42	0.15	4	33.3
AT3	0.49	0.26	4	33.3
AX1	0.62	0.16	5	41.7
CE1	0.45	0.19	2	16.7
TH1	0.38	0.24	1	8.3
TH2	0.53	0.27	1	8.3
LU1	0.49	0.29	2.3	19.4
LU3	0.51	0.29	0.167	1.4
SC1	0.37	0.19	3	25.0

Appendix D continued: Bone Mineral Density Data

	Rangifer	*Odocoileus*	Pilanduk cervid					
			context 111		context 112		context 117	
scan site	Lam et al. 1999	Lyman 1994	MAU	%MAU	MAU	%MAU	MAU	%MAU
SP1	1.01	0.36	0.5	14.3	2	40.0	2	66.7
SP2	1.04	0.49	0	0.0	0.5	10.0	0	0.0
SP3	0.73	0.23	0	0.0	0.5	10.0	0	0.0
SP4	1.01	0.34	0	0.0	0	0.0	0	0.0
HU1	0.26	0.24	2	57.1	1	20.0	1	33.3
HU2	0.44	0.25	0	0.0	0.5	10.0	0	0.0
HU3	1.12	0.53	0	0.0	0	0.0	0	0.0
HU4	1.08	0.63	0	0.0	0.5	10.0	0	0.0
HU5	0.48	0.39	0.5	14.3	1.5	30.0	1.5	50.0
RA1	0.53	0.42	3	85.7	5	100.0	2	66.7
RA2	1.08	0.62	0.5	14.3	1	20.0	0	0.0
RA3	1.09	0.68	0	0.0	0	0.0	0	0.0
RA4	0.97	0.38	0	0.0	0.5	10.0	0	0.0
RA5	0.49	0.43	1.5	42.9	1.5	30.0	1	33.3
UL1	0.49	0.3	0	0.0	2.5	50.0	0	0.0
UL2	0.84	0.45	0.5	14.3	4.5	90.0	0	0.0
UL3	0	0.44	1	28.6	0	0.0	0	0.0
UL4	0	0	0	0.0	0	0.0	0	0.0
MC1	0.92	0.56	2	57.1	3.5	70.0	2.5	83.3
MC2	1.08	0.69	0.5	14.3	0	0.0	0	0.0
MC3	1.1	0.72	0.5	14.3	0	0.0	0	0.0
MC4	1.01	0.58	0	0.0	0	0.0	0	0.0
MC5	0.48	0.49	0	0.0	0	0.0	0	0.0
MC6	0.68	0.51	0	0.0	0.5	10.0	0.5	16.7
AC1	0.39	0.27	0	0.0	0.5	10.0	1	33.3
IL1	0.52	0.2	0	0.0	0	0.0	0	0.0
IL2	0.74	0.49	0	0.0	1	20.0	0	0.0
PU1	1.15	0.46	0	0.0	0	0.0	0	0.0
IS1	0.61	0.41	0	0.0	0	0.0	0	0.0
FE1	0.39	0.41	1	28.6	3	60.0	2	66.7
FE2	0.52	0.36	0.5	14.3	0.5	10.0	0	0.0
FE3	0.74	0.33	0	0.0	1.5	30.0	0	0.0
FE4	1.15	0.57	0.5	14.3	0.5	10.0	0	0.0
FE5	0.61	0.37	0	0.0	0.5	10.0	0	0.0
FE6	0.32	0.28	0.5	14.3	1	20.0	1.5	50.0
FE7	0.3	0	0	0.0	0	0.0	0	0.0
TI1	0.35	0.3	1	28.6	1.5	30.0	0	0.0
TI2	1.01	0.32	0	0.0	4.5	90.0	3	100.0
TI3	1.13	0.74	2.5	71.4	1	20.0	0	0.0
TI4	1.12	0.51	1	28.6	0	0.0	0	0.0
TI5	0.73	0.5	1.5	42.9	3.5	70.0	0.5	16.7
MR1	0.9	0.55	1.5	42.9	1.5	30.0	1.5	50.0
MR2	1.1	0.65	2.5	71.4	1.5	30.0	0	0.0
MR3	1.08	0.74	0	0.0	1	20.0	0	0.0
MR4	1.08	0.57	0	0.0	0	0.0	0	0.0
MR5	0.41	0.46	1	28.6	0	0.0	0	0.0

Appendix D continued: Bone Mineral Density Data

	Rangifer	*Odocoileus*	Pilanduk cervid					
			context 111		context 112		context 117	
scan site	Lam et al. 1999	Lyman 1994	MAU	%MAU	MAU	%MAU	MAU	%MAU
MR6	0.59	0.5	0.5	14.3	0	0.0	0	0.0
CA1	0.52	0.41	0	0.0	1.5	30.0	1	33.3
CA2	0.94	0.64	0.5	14.3	1	20.0	0	0.0
CA3	0.66	0.57	0	0.0	1	20.0	0	0.0
CA4	0.73	0.33	0.5	14.3	0	0.0	0	0.0
AS1	0.68	0.47	3.5	100.0	5	100.0	0	0.0
AS2	0.7	0.62	0	0.0	0	0.0	0	0.0
P11	0.48	0.36	0.875	25.0	1.875	37.5	0	0.0
P12	0.92	0.42	0	0.0	0	0.0	0	0.0
P13	0.71	0.57	0.625	17.9	1.125	22.5	2.25	75.0
P21	0.61	0.28	1.125	32.1	0.875	17.5	1.25	41.7
P22	0.72	0.25	0.5	14.3	1.125	22.5	0	0.0
P31	0.48	0.25	1.125	32.1	2	40.0	1.125	37.5
DN1	0.65	0.55		0.0	1.5	30.0	0	0.0
DN2	1.05	0.57	0.5	14.3	0	0.0	0	0.0
DN3	1.07	0.55	0	0.0	0	0.0	0	0.0
DN4	1.06	0.57	2	57.1	3.5	70.0	3	100.0
DN5	1.05	0.57	0	0.0	0	0.0	0	0.0
DN6	0.84	0.31	1	28.6	0	0.0	0	0.0
DN7	1.01	0.36	0.5	14.3	0.5	10.0	0	0.0
DN8	0.99	0.61	0	0.0	0	0.0	0	0.0
AT1	0.47	0.13	0	0.0	2	40.0	1	33.3
AT2	0.42	0.15	0	0.0		0.0	0	0.0
AT3	0.49	0.26	0	0.0	2	40.0	0	0.0
AX1	0.62	0.16	2	57.1		0.0	1	33.3
AX2	0.42	0.1	0	0.0		0.0	0	0.0
AX3	0.42	0.16	0	0.0		0.0	0	0.0
CE1	0.45	0.19	0.57143	16.3	0.42857	8.6	0.14286	4.8
CE2	0.43	0.15	0	0.0		0.0	0	0.0
TH1	0.38	0.24	0	0.0	0.15385	3.1	0.61538	20.5
TH2	0.53	0.27	0	0.0		0.0	0	0.0
LU1	0.49	0.29	0.66667	19.0	0.66667	13.3	0.83333	27.8
LU2	0.45	0.3	0	0.0		0.0	0	0.0
LU3	0.51	0.29	0	0.0		0.0	0	0.0
SC1	0.37	0.19	0	0.0	1	20.0	0	0.0
SC2	0.4	0.16	0	0.0		0.0	0	0.0

Appendix D continued: Bone Mineral Density Data

scan site	*Rangifer* Lam et al. 1999	*Odocoileus* Lyman 1994	Minori Square 27 Cervids, aceramic levels	
			MAU	%MAU
RA1	0.53	0.42	1.00	66.7
RA3	1.09	0.68	0.50	33.3
MC1	0.92	0.56	1.00	66.7
MC3	1.1	0.72	1.00	66.7
MC6	0.68	0.51	0.50	33.3
FE4	1.15	0.57	1.00	66.7
FE5	0.61	0.37	1.00	66.7
TI1	0.35	0.3	0.50	33.3
TI2	1.01	0.32	0.50	33.3
MR1	0.9	0.55	0.50	33.3
MR3	1.08	0.74	1.50	100.0
CA1	0.52	0.41	0.50	33.3
CA2	0.94	0.64	0.50	33.3
AS1	0.68	0.47	0.50	33.3
P11	0.48	0.36	0.13	8.3
P12	0.92	0.42	0.13	8.3
P13	0.71	0.57	0.13	8.3
P21	0.61	0.28	0.13	8.3
P22	0.72	0.25	0.25	16.7
P31	0.48	0.25	0.13	8.3
DN1	0.65	0.55	0.50	33.3
DN3	1.07	0.55	1.00	66.7
DN7	1.01	0.36	0.50	33.3
CE1	0.45	0.19	0.14	9.5
CE2	0.43	0.15	0.57	38.1

Appendix E Food Utility Index (FUI) Data

Metcalfe and Jones 1988		Pilanduk Context 111	
element	caribou FUI	MAU	%MAU
scapula	44.7	0.5	14.3
P hum	44.7	2	57.1
D hum	36.8	0.5	14.3
P rad	25.8	3	85.7
D rad	20.2	1.5	42.9
P mc	9	2	57.1
P fem	100	1	28.6
D fem	100	0.5	14.3
P tib	62.8	1	28.6
D tib	44.1	1.5	42.9
P mt	19.5	2.5	71.4
D mt	15.4	1	28.6
calc	27.7	0.5	14.3
astr	27.7	3.5	100.0
phal 1	8.6	0.88	25.0
phal 2	8.6	1.125	32.1
phal 3	8.6	1.125	32.1
mand	31.1	2	57.1
axis	10.2	2	57.1
cervical	37.1	0.57	16.3
lumbar	33.2	0.67	19.0

Appendix E continued: Food Utility Index (FUI) Data

Metcalfe and Jones 1988		Pilanduk Context 112	
element	caribou FUI	MAU	%MAU
scapula	44.7	2.0	40.0
P hum	44.7	1.0	20.0
D hum	36.8	1.5	30.0
P rad	25.8	5.0	100.0
D rad	20.2	1.5	30.0
P mc	9	3.5	70.0
D mc	7.1	0.5	10.0
innominate	49.3	0.5	10.0
P fem	100	3.0	60.0
D fem	100	1.0	20.0
P tib	62.8	4.5	90.0
D tib	44.1	3.5	70.0
P mt	19.5	1.5	30.0
calc	27.7	1.5	30.0
astr	27.7	5.0	100.0
phal 1	8.6	1.9	37.5
phal 2	8.6	1.1	22.5
phal 3	8.6	2.0	40.0
mand	31.1	3.5	70.0
atlas	10.2	2.0	40.0
cervical	37.1	0.4	8.6
thoracic	47.3	0.2	3.1
lumbar	33.2	0.7	13.3
sternum	66.6	1.0	20.0

Appendix E continued: Food Utility Index (FUI) Data

Metcalfe and Jones 1988		Pilanduk Context 117	
element	caribou FUI	MAU	%MAU
scapula	44.7	2	66.7
P hum	44.7	1	33.3
D hum	36.8	1.5	50.0
P rad	25.8	2	66.7
D rad	20.2	1	33.3
P mc	9	2.5	83.3
D mc	7.1	0.5	16.7
innominate	49.3	1	33.3
P fem	100	2	66.7
D fem	100	1.5	50.0
P tib	62.8	3	100.0
D tib	44.1	0.5	16.7
P mt	19.5	1.5	50.0
calc	27.7	1	33.3
phal 1	8.6	2.25	75.0
phal 2	8.6	1.25	41.7
phal 3	8.6	1.125	37.5
mand	31.1	3	100.0
atlas	10.2	1	33.3
axis	10.2	1	33.3
cervical	37.1	0.14	4.8
thoracic	47.3	0.62	20.5
lumbar	33.2	0.83	27.8

Appendix E continued: Food Utility Index (FUI) Data

Marrow and grease indices for caribou (Binford 1978).

			Pilanduk NISP:MNE ratios for cervids per context			
element	marrow	grease	111	112	117	118
mandible	5.74	12.51	2	1.57	2.67	1
atlas	1	13.11	0	1	1	0
axis	1	12.93	1	1	1	0
cervical	1	17.46	1.25	1	1	0
thoracic	1	12.26	0	1	1	0
lumbar	1	14.82	1	1	1	0
sternum	1	26	0	1	0	0
scapula	6.4	7.69	1	2	1.25	1
P hum	29.69	75.46	1.25	3.5	6	0
D hum	28.33	27.84	5	2.3	4	1
P rad	43.64	37.56	1.67	1.8	3	1
D rad	66.11	32.7	3.33	6	6	0
P mc	61.68	16.71	2	1.43	2	3
D mc	67.08	42.47	0	1.25	1.43	0
pelvis	7.85	29.26	0	1.5	2.5	0
P fem	33.51	26.9	3	2.5	4.25	3
D fem	49.41	100	6	7.5	5.67	0
P tib	43.78	69.37	6	2.3	2.33	0
D tib	92.9	26.05	4	3	7	1.5
astr	1	32.47	1.43	1.2	0	0
calc	21.19	46.96	0	2.3	1	1
P mt	81.74	17.88	3	3	6.3	0
D mt	100	43.13	6	1.125	2.71	0
1st phal	30	33.27	1.43	1.73	1.39	1.5
2nd phal	22.15	24.77	1.86	1.78	1.8	1
3rd phal	1	13.59	1	1	1.22	1

Appendix F Minori Cave Taphonomy

Counts are expressed as TNF (total number of fragments).
Percentages are expressed as TNF (taphonomic imprint)/ TNF per layer, unless otherwise indicated.
Archaeological layers are categorised as ceramic or aceramic.

Weathering and abrasion

Square/ Layer	TNF	TNF weathering	% Weathered	TNF abrasion	% abrasion
Square 27					
Ceramic	369	103	27.9	8	2.2
Aceramic	1035	158	15.3	31	3.0
Total	1404	261	18.6	39	2.8
Square 37					
Ceramic	126	6	4.8	0	0
Aceramic	285	92	32.3	0	0
Total	411	98	23.8	0	0

Carbonate concretion

Square/ Layer	TNF	TNF with concretion	% concretion	TNF concretion ≥50%	% concretion ≥50%
Square 27					
Ceramic	369	77	20.9	61	79.2
Aceramic	1035	160	15.5	112	70
Total	1404	237	16.9	173	73.0
Square 37					
Ceramic	126	10	7.9	6	60
Aceramic	285	65	22.8	48	73.8
Total	411	75	18.2	54	72

TNF concretion ≥50% = fragments with bone surface covered 50% or more by carbonate concretions

% concretion ≥50% = TNF concretion ≥50%/ TNF with concretion * 100

Appendix F continued: Minori Cave Taphonomy

Mineral staining

Square/ Layer	TNF	TNF with mineral staining	% mineral staining
Square 27			
Ceramic	369	14	3.8
Aceramic	1035	34	3.3
Total	1404	48	3.4
Square 37			
Ceramic	126	0	0
Aceramic	285	11	3.9
Total	411	11	2.7

Gnawing

Square/ Layer	TNF	TNF with gnawing	% gnawing
Square 27			
Ceramic	369	8	2.2
Aceramic	1035	0	0
Total	1404	8	0.6
Square 37			
Ceramic	126	1	0.8
Aceramic	285	0	0
Total	411	1	0.2

Appendix F continued: Minori Cave Taphonomy

Burning

Square/ Layer	TNF	charred	calcined	total burnt	% burnt
Square 27					
Ceramic	434	42	7	49	11.3
Aceramic	970	55	26	81	8.4
Total	1404	97	33	130	9.3
Square 37					
Ceramic	126	1	0	1	0.8
Aceramic	285	4	3		0
Total	411	5	3	1	0.2

total burnt = charred and calcined fragments

Cutmarks

Square/ Layer	TNF	TNF with cutmarks	% cutmarks
Square 27			
Ceramic	369	10	2.7
Aceramic	1035	2	0.2
Total	1404	12	0.9
Square 37			
Ceramic	126	7	5.6
Aceramic	285	2	0.7
Total	411	9	2.2

Helical fractures

Square/ Layer	TNF	TNF long bone	TNF helical	% helical
Square 27				
Ceramic	434	203	56	27.6
Aceramic	970	774	64	8.3
Total	1404	977	120	12.3
Square 37				
Ceramic	126	39	19	48.7
Aceramic	285	107	30	28.0
Total	411	146	49	33.6

TNF long bone = total number of long bone fragments
TNF helical = total number of long bone fragments showing helical fractures

Appendix F continued: Minori Cave Taphonomy

Freshness Fracture Index Scores

Following methodology by Outram (2001, 2002)

FFI scores are taken for long bone fragments only

	FFI Scores						
Square 27	0	1	2	3	4	5	6
Ceramic	1	7	29	24	27	86	174
Aceramic	1	3	53	40	45	85	227
Total	2	10	82	64	72	171	401
Square 37							
Ceramic	1	3	11	12	8	3	38
Aceramic	0	2	21	23	15	34	95
Total	1	5	32	35	23	37	133

Fragment size classes

Square	0-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	100+
Sq 27	636	431	174	55	27	8	1	0	1
Sq 37	269	62	38	23	9	2	3	0	0

size classes in mm.

Appendix G Musang Cave Taphonomy

Counts are expressed as TNF (total number of fragments).
Percentages are expressed as TNF (taphonomic imprint)/ TNF per layer, unless otherwise indicated.

Weathering

Square G4

Level	TNF	TNF weathering	% Weathered
1	299	5	1.7
2	72	61	84.7
3	35	0	0
4	15	0	0
5	1	0	0
6	0	0	0
7	0	0	0
4a	116	35	30.2
5a	15	0	0
6a	21	0	0
7a	149	1	0.7
8	75	3	4
9	9	2	22.2
11	7	3	42.9
no level	39	10	25.6
Total	853	120	14.1

Square G5se1m

Level	TNF	TNF weathering	% Weathered
1	7	4	57.1
4a	29	0	0
5a	48	0	0
6a	14	0	0
7a	22	5	22.7
8	12	0	0
9	1	0	0
Total	133	9	6.8

Appendix G continued: Musang Cave Taphonomy

Carbonate concretion

Square G4

Level	TNF	TNF with concretion	% concretion	TNF concretion ≥50%	% concretion ≥50%
1	299	136	45.5	66	48.5
2	72	59	81.9	11	18.6
3	35	17	48.6	17	100
4	15	2	13.3	2	100
5	1	0	0	0	0
4a	116	0	0	0	0
5a	15	0	0	0	0
6a	21	10	47.6	0	0
7a	149	53	35.6	51	96.2
8	75	19	25.3	19	100
9	9	1	11.1	1	100
11	7	2	28.6	0	0
no level	39	24	61.5	23	95.8
Total	853	323	37.9	190	58.8

Square G5se1m

Level	TNF	TNF with concretion	% concretion	TNF concretion ≥50%	% concretion ≥50%
1	7	0	0	0	0
4a	29	21	72.4	20	95.2
5a	48	25	52.1	25	100
6a	14	10	71.4	8	80
7a	22	10	45.5	10	100
8	12	3	25	2	66.7
9	1	0	0	0	0
Total	133	69	51.9	65	94.2

TNF concretion ≥50% = fragments with bone surface covered 50% or more by carbonate concretions

% concretion ≥50% = TNF concretion ≥50%/ TNF with concretion * 100

Appendix G continued: Musang Cave Taphonomy

Mineral staining

Square G4

Level	TNF	TNF with mineral staining	% mineral staining
1	299	0	0
2	72	0	0
3	35	0	0
4	15	0	0
5	1	0	0
4a	116	1	0.9
5a	15	0	0
6a	21	0	0
7a	149	2	1.3
8	75	7	9.3
9	9	1	11.1
11	7	2	28.6
no level	39	9	23.1
Total	853	22	2.6

Square G5se1m

Level	TNF	TNF with mineral staining	% mineral staining
1	7	0	0
4a	29	0	0
5a	48	0	0
6a	14	0	0
7a	22	0	0
8	12	1	8.3
9	1	0	0
Total	133	1	0.8

Gnawing*

Levels	TNF	TNF with gnawing
2	72	1
4	15	1
7a	149	1
11	7	1

*Only four fragments in Square G4 had traces of gnawing in the whole Musang assemblage. All were from carnivore gnawing.

Appendix G continued: Musang Cave Taphonomy

Burning

Level	TNF	charred	calcined	total burnt	% burnt
G4					
1	299	6		6	2.0
3	35	4	7	11	31.4
7a	149	4		4	2.7
8	75	3		3	4.0
no level	39	1		1	2.6
Total	597	18	7	25	4.2
G5se1m					
5a	48	5		5	10.4

total burnt = charred and calcined fragments

Cutmarks*

Square G4

Level	TNF	TNF with cutmarks	% cutmarks
4a	116	7	6.03

*Only seven fragments in Level 4a in Square G4 were found with cutmarks. The low incidence/invisibility of cutmarks has partly to do with the high incidence of carbonate concretions that cover bone surfaces.

Appendix G continued: Musang Cave Taphonomy

Helical fractures

Square G4

Level	TNF	TNF long bone	TNF helical	% helical
1	299	182	37	20.3
2	72	70	3	4.3
3	35	28	1	3.6
4	15	2		0
5	1	0		0
4a	116	67	10	14.9
5a	15	0		0
6a	21	1		0
7a	149	108	45	41.7
8	75	60	30	50
9	9	4		0
11	7	0		0
no level	39	32	14	43.8
Total	853	554	140	25.3

Square G5se1m

Level	TNF	TNF long bone	TNF helical	% helical
1	7	5	1	20
4a	29	18	1	5.6
5a	48	14	7	50
6a	14	7	6	85.7
7a	22	7	2	28.6
8	12	8	1	12.5
9	1	0	0	0
Total	133	59	18	30.5

TNF long bone = total number of long bone fragments
TNF helical = total number of long bone fragments showing helical fractures

Appendix G continued: Musang Cave Taphonomy

Freshness Fracture Index Scores

Following methodology by Outram (2001, 2002)
FFI scores are taken for long bone fragments only

Square G4

	FFI Scores						
Level	0	1	2	3	4	5	6
1		1	1	35	18	72	2
2				3	14	44	1
3				5		16	
4					1		
5							
4a		1	1	17	2	8	30
5a							
6a							
7a		4	2	38	18	25	3
8		1	2	26	17	8	1
9					1		
11							
Total		7	6	124	71	173	37

Square G5se1m

	FFI Scores						
Level	0	1	2	3	4	5	6
1			1			4	
4a				1		10	2
5a			2	6	2		
6a		1		3	2		
7a				2	1	2	
8				1		2	
9							
Total		1	3	13	5	18	2

Fragment size classes

Layer	0-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100+
ceramic	145	114	107	62	18	5	1	1	0	0
aceramic	106	89	90	63	23	8	4	0	0	1

Size classes in mm.