



Australian
National
University

Modelling early modern human dispersal patterns through the Wallacean Archipelago

Shimona Kealy

Submitted December 2018

Thesis submitted for the degree of Doctor of Philosophy
of The Australian National University

©Copyright by Shimona Kealy 2018

All Rights Reserved

Declaration

Unless otherwise acknowledged in the text all work contained therein is the original research of the author

A handwritten signature in blue ink, appearing to read 'SKY', enclosed in a thin black rectangular border.

Shimona Kealy 2018

Acknowledgements

I would like to acknowledge the wonderful efforts of my supervisors; Dr Julien Louys and Professor Sue O'Connor, who have been truly amazing! Your support and advice throughout has been invaluable, I have learnt so much and am honoured to have had you as my supervisors. To my panel advisor; Dr Ken Aplin, thank you so much for continuing to take the time to share your incredible wealth of knowledge and experience with me no matter what. I have been incredibly lucky.

This research was funded by the Australian Research Council Laureate Project (FL120100156) awarded to Professor Sue O'Connor. During the course of my PhD I was also the recipient of funding via an Australian Archaeology Association Student Research Grant and the Australian National University's (ANU) Vice Chancellor's Student Travel Grant. Additional fieldwork and conference attendance funding was also provided by the School of Culture, History and Language at ANU.

Thanks must also be given to Marlon Ririmasse, Priyatno Hadi Sulistyarto (Pak Gupik), and Adhi Agus Octaviana from the Indonesian National Archaeological Research Centre for always being happy to answer my random Whatsapp questions about Indonesian archaeology and references. I would also like to acknowledge Ibu Dr Mahirta and the rest of the Universitas Gadjah Mada team, along with the staff of Balai Arkeologi Bali and Balai Arkeologi Maluku, for all their support and assistance with our Indonesian fieldwork over the last several years.

Thank you to Dr Steve Donnellan, Dr Micheal Herrera and Dr Kieren Mitchell for their willingness to work with me on the cuscus project and willingness to go above and beyond the original parameters of the project. I am grateful for all your sequencing efforts, along with the rest of the ancient DNA team at Adelaide University. I look forward to continuing our collaboration in the future.

To Dr Sandy Inglby at the Australian Museum and Dr Kenny Travouillon at the Western Australian Museum; thank you for granting me access to the mammal collections and for all your assistance with tracking specimens down and helping me with my analysis. Thank you to Dr Rachel Wood for your endless advice on radiocarbon dates and calibrations and for taking the time to teach me about Bayesian modelling. Thank you to Professor Michael Bird for your support and willing advice on modelling, and to you and your team for being so welcoming during my brief visit to James Cook Univeristy.

Dr Kirsten Crosby, Dr Anna Gillesby, Dr Robin Beck, and Professor Mike Archer, a big thank you for all your help, advice and access to data and specimens for my Phalangeridae study. Thank you to Dr Nick Matzke for your advice on the BioGeoBEARS package. Thank you to the curator of maps, Dr Martin Woods at the National Library of Australia, for your enthusiastic support of the project and assistance with tracking down those old charts, I look forward to continuing to work with you in the future.

I am eternally grateful to the entire Archaeology and Natural History department at ANU. All of you have been so lovely, welcoming and supportive, you have made this difficult journey a truly enjoyable one.

Last but not least, my darling Hendri, thank you for your endless support and confidence in me, and also for the many random bits of Indonesian translations I requested from you! I am excited to continue our research adventures into the future.

To all my friends and family – knowing I have had you all behind me has made it all a little easier, thank you, and thank you all for putting up with me while I've been living in my PhD bubble!!

Abstract

Archaeological records from Australia provide the earliest, indirect evidence for maritime crossings by early modern humans anywhere in the world. As the island archipelago of Wallacea has never been connected to the continental landmasses of Sunda in the west (mainland Southeast Asia) or Sahul in the east (Australia and New Guinea), water crossings through this region were essential for the human colonisation of Australia. The archaeological record for human movement in Wallacea is still a work in progress, however, and none of the evidence pre-dates the archaeological record from Sahul. In 1977 the American anthropologist Joseph B. Birdsell suggested two main initial routes from Sunda to Sahul, a northern route with a landing in New Guinea, and a southern route landing in northern Australia. Models of this significant colonisation event have since been suggested, however, there has been little consensus about which model describes the most parsimonious pathway for first landfall in Sahul. Likewise, later movements between islands is still in question. The dearth of sampled islands and sites in Wallacea has made testing movement models against archaeological evidence difficult, if not impossible.

This PhD attempted to examine inter-island movements using a three-pronged approach: 1) archaeological survey and excavation of Wallacean sites, combined with review and revision of the archaeological literature, to identify the timings of early human occupation in the region and enlarge the number of archaeological sample points; 2) reconstructing the palaeogeography of the Wallacean archipelago for the likely periods of initial human colonisation, and through this, model island connectivity and develop a model for human movement through the region; and 3) identify proxy records of human movement between islands to provide information on networks of connection between prehistoric island communities, and in doing so test the reliability of the model outcomes.

This study provides a much needed up date to Birdsell's model from over 40 years ago, with an innovative use of geographic information systems to digitise and expand upon the reconstructions of palaeo-Wallacea and the differing variables which would have impacted early modern human movements through the region. The resulting reconstructions and models identified a multitude of now-submerged islands throughout Wallacea which would have significantly increased the connectivity between islands in the prehistoric archipelago, produced the first reconstructions of palaeo-hydrology for the region, developed two measures of intervisibility between islands and in applying these calculations to the Wallacean archipelago, identified ca. 65 ka and ca. 45 ka as the periods of likely human arrival with the greatest intervisibility. This study is also the first to apply least-cost modelling techniques to sea travel, enabling the model to be expanded across the Wallacean archipelago for the first time. Models and palaeogeographic reconstructions constructed herein provide overwhelming support for an initial northern route through Wallacea, with a landing on the modern island of Misool, near the Papuan Bird's Head. Extensive archaeological research on islands of the southern route has so far failed to recover any dates which pre-date those for Sahul, and thus support this inference. Human translocations of cuscus (Phalangeridae) throughout Wallacea found good support for a humanly-assisted introduction from Papua to Timor ca. 3ka, supporting movement between these islands by at least the mid-Holocene.

Table of Contents

Title Page	i
Declaration	ii
Acknowledgements	iii
Abstract	iv
Table of Contents	v
List of Appendices	viii
List of Tables	x
List of Figures	xi
Chapter 1. Introduction	1
1.1. Overview	1
1.2. Research Project and Aims	2
1.3. Study Area: Wallacea	3
1.3.1. Geology and Biogeography	3
1.3.2. The Archaeological Record of Wallacea	4
1.4. The Maximum Bound: Out of Africa and into Asia	7
1.4.1. The Archaeological Record	7
1.4.2. The Genetic Record	8
1.4.3. Modelling Movement Out of Africa and through Asia	9
1.5. The Minimum Bound: Initial Occupation of Sahul	12
1.5.1. The Conundrum of Madjedbebe	12
1.5.2. Occupation of Australia Based on Regional Genetics	13
1.6. Modelling Movement into and Around Wallacea	14
1.6.1. Hypothetical Routes and Theoretical Models	14
1.6.2. Models in Practice	15
1.6.3. Proxies for Human Movement	17
1.7. Thesis Structure	18

Chapter 2. Methods	20
2.1. Palaeogeographic Reconstruction of Wallacea	20
2.1.1. The General Bathymetric Chart of the Oceans (GEBCO)	20
2.1.2. The Sea-Level Change Model	21
2.1.3. An Average Rate of Uplift for Wallacea	21
2.2. Visibility and Intervisibility in an Island Archipelago	21
2.3. Phylogeography and its Application to Questions in Archaeology	23
2.3.1. Morphological, Molecular, and Total Evidence Phylogenetics	24
2.3.2. Biogeography: Natural Dispersal vs. Human Translocation	24
Chapter 3. Islands Under the Sea: A Review of Early Modern Human Dispersal Routes and Migration Hypotheses Through Wallacea	26
3.1. Authorship Declaration	26
3.2. Kealy, S., Louys, J., & O'Connor, S. 2016. Islands under the sea: a review of early modern human dispersal routes and migration hypotheses through Wallacea. <i>Journal of Island and Coastal Archaeology</i> , 11(3), 364-384.	26
Chapter 4. A Geological and Spatial Approach to Prehistoric Archaeological Surveys on Small Islands: Case Studies from Maluku Barat Daya, Indonesia	27
4.1. Authorship Declaration	27
4.2. Kealy, S., Wattimena, L., O'Connor, S. 2018. A geological and spatial approach to prehistoric archaeological surveys on small islands: case studies from Maluku Barat Daya, Indonesia. <i>Kapata Arkeologi</i> , 4(1), 1-14.	27
Chapter 5. Reconstructing Palaeogeography and Inter-island Visibility in the Wallacean Archipelago During the Likely Period of Sahul Colonization, 65–45000 Years Ago	28
5.1. Authorship Declaration	28
5.2. Kealy, S., Louys, J., & O'Connor, S. 2017. Reconstructing palaeogeography and inter-island visibility in the Wallacean Archipelago during the likely period of Sahul colonization, 65 - 45,000 years ago. <i>Archaeological Prospection</i> , 24(3), 259-272.	28
Chapter 6. Least-cost pathway models indicate northern human dispersal from Sunda to Sahul	29
6.1. Authorship Declaration	29
6.2. Kealy, S., Louys, J., O'Connor, S. (2018). Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. <i>Journal of Human Evolution</i> , 125, 59-70.	29

Chapter 7. Phylogenetic relationships of the cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial ND2 gene	30
7.1. Authorship Declaration	30
7.2. Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S., Louys, J. (in review). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial ND2 gene. <i>Australian Mammalogy</i> .	33
Chapter 8. The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae)	66
8.1. Authorship Declaration	66
8.2. Kealy, S., Herrera, M., Aplin, K., Mitchell, K., Donnellan, S., Louys, J., & O'Connor, S. (in prep). The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).	69
Chapter 9. Conclusion	99
8.1. The Palaeogeography of Wallacea	100
8.2. Early Human Movement through Wallacea	101
8.2.1. The Model Results	101
8.2.2. The Archaeological Evidence	102
8.2.3. Validation by Proxy	103
8.3. Future Research Directions	104
8.3.1. A New Bathymetry for Wallacea	104
8.3.2. Calculating Island Uplift Rates for Wallacea	105
8.3.3. A Palaeocurrent Model for Wallacea	105
8.3.4. Cuscus Phylogenetics and Tracing Translocations	105
8.3.6. An Integrated Survey Effort	106
8.3.7. Testing the Northern Pathway	107
Exegesis References (Chapters 1, 2 & 9)	108
Appendix	125

List of Appendices

Appendix A: Procedure: Higher degree by research - thesis by compilation and thesis by creative works	125
Appendix B: Supplementary Information for: Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S., Louys, J. (in review). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial <i>ND2</i> gene. <i>Australian Mammalogy</i> .	132
Appendix C: Supplementary Information for: Kealy, S., Herrera, M., Aplin, K., Mitchell, K., Donnellan, S., Louys, J., & O'Connor, S. (in prep). The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).	133
Appendix D: O'Connor, S., Louys, J., Kealy, S., Mahirta. 2015. First record of painted rock art near Kupang, West Timor, Indonesia, and the origins and distribution of the Austronesian painting tradition. <i>Rock Art Research</i> , 32(2), 193-201.	134
Appendix E: Hawkins, S., O'Connor, S., Kealy, S. 2016. Late Quaternary hominin-bat (Chiroptera) interactions in the Asia-Pacific. <i>Archaeology in Oceania</i> , 51, 7-17.	135
Appendix F: Reepmeyer, C., O'Connor, S., Mahirta, Maloney, T., Kealy, S. 2016. Late Pleistocene/early Holocene maritime interaction in Southeastern Indonesia – Timor Leste. <i>Archaeological Science</i> , 76, 21-30.	136
Appendix G: Louys, J., Kealy, S., O'Connor, S., Price, G. J., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Mahirta, Tanudirjo, D. A., Santoso, W. D., Hidayah, A. R., Trihascaryo, A., Wood, R., Bevitt, J., Clark, T. 2017. Differential preservation of vertebrates in Southeast Asian caves. <i>International Journal of Speleology</i> , 46(3), 379-408.	137
Appendix H: Hawkins, S., O'Connor, S., Maloney, T. R., Lister, M., Kealy, S., Fenner, J. N., Aplin, K., Boulanger, C., Brockwell, S., Willan, R., Piotto, E., Louys, J. 2017. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. <i>Quaternary Science Reviews</i> , 171, 58-72.	138
Appendix I: O'Connor, S., Louys, J., Kealy, S., Samper Carro, S. 2017. Hominin dispersal and settlement east of Huxley's Line: The role of sea-level changes, island size, and subsistence behavior. <i>Current Anthropology</i> , 58(17), 567-582.	139
Appendix J: O'Connor, S., Mahirta, Samper Carro, S., Hawkins, S., Kealy, S., Louys, J., Wood, R. 2017. Fishing in life and death: Oldest evidence of Pleistocene fish-hooks from a burial context. <i>Antiquity</i> , 91(360), 1451-1468.	140
Appendix K: O'Connor, S., Mahirta, Tanudirjo, D., Ririmasse, M., Husni, M., Kealy, S., Hawkins, S., Alifah. 2018. Ideology, ritual performance and its manifestations in the rock art of Timor-Leste and Kisar Island, Island South East Asia. <i>Cambridge Archaeological Journal</i> , 28(2), 225-241.	141

Appendix L: O'Connor, S., Mahirta, **Kealy**, S., Louys, J., Kaharudin, H. A. F., Lebuan, A., Hawkins, S. 2018. Unusual painted anthropomorph in Lembata island extends our understanding of rock art diversity in Indonesia. *Rock Art Research*, 35(1), 79-84. 142

Appendix M: O'Connor, S., Mahirta, Louys, J., **Kealy**, S., Brockwell, S. 2018. New engraving finds in Alor Island, Indonesia extend known distribution of engravings in Oceania. *Archaeological Research in Asia*, 15, 116-128. 143

Appendix N: O'Connor, S., Mahirta, **Kealy**, S., Boulanger, C., Maloney, T., Hawkins, S., Langley, M., Kaharudin, H. A. F., Suniarti, Y., Husni, M., Ririmasse, M., Tanudirjo, D. A., Wattimena, L., Handoko, W., Alifah, Louys, J. 2018. Kisar and the archaeology of small island in the Wallacean Archipelago. *Journal of Island and Coastal Archaeology*. 144

Appendix O: Shipton, C., O'Connor, S., Jankowski, N., O'Connor-Veth, J., Maloney, T., **Kealy**, S., Boulanger, C. (*in review*). Conditions for continuity in human behaviour: A new sequence spanning 44,000 years from Asitau Kuru (Jerimalai), Timor-Leste, Wallacea. *Archaeological and Anthropological Sciences*. 145

List of Tables

Chapter 1

Table 1: Initial occupation dates for EMH Pleistocene archaeological sites in Wallacea (updated from Kealy et al., 2016: Table 1). **5**

Chapter 7

Table 1: Currently accepted classifications of the Phalangeridae as per Helgen and Jackson (2015). **55**

Table 2: Taxa included in the study with relevant gene sequences identified and GenBank accession numbers listed in corresponding order. **56**

Table 3: Divergence dates (in millions of years, to 2 d.p.) for select nodes from the calibrated phylogenetic analysis. **61**

Chapter 8

Table 1: Archaeological records for cuscus in comparison with initial human occupation on the island. **71**

Table 2: Current classifications of species considered in this study following Groves (2005) for pseudocheerid and burramys classifications, and Helgen and Jackson (2015) and Kealy et al. (in review) for classifications within Phalangeridae. **74**

Table 3: Divergence estimates (in millions of years, to 2 d.p.) for select nodes from the calibrated phylogenetic analysis, modified from Kealy et al. (in review: Table 3). **79**

Table 4: Comparison of biogeographic models run in BioGeoBEARS on the dated total evidence Phalangeridae phylogeny. **81**

List of Figures

Chapter 2

Figure 1: Diagram demonstrating the distance to the geometric horizon calculation using a right-angled triangle and Pythagoras' Theorem. **22**

Figure 2: Diagram demonstrating how a point which extends above the surface of the earth, extends visibility beyond the horizon. **22**

Chapter 7

Figure 1: Map showing distribution of the Phalangeridae and sampling localities for the novel sequences in this study. **63**

Figure 2: Undated ND2 phylogeny of the Phalangeridae. **64**

Figure 3: Time-calibrated phylogeny of the Phalangeridae. **65**

Chapter 8

Figure 1: Map showing distribution of the Phalangeridae (dark shading), with geographic regions used for the biogeographic analysis shaded in colours corresponding to Figure 3. **96**

Figure 2: Time-calibrated total evidence phylogeny of the Phalangeridae. **97**

Figure 3: Dispersal-Extinction-Cladogenesis with founder-event speciation (DEC+J) biogeographic model for Phalangeridae based on the calibrated total evidence analysis (Figure 2). **98**

Chapter 1. Introduction

1.1. Overview

Africa has long been established as the evolutionary place of origin of our species *Homo sapiens*. This is well supported by fossil, archaeological, and genetic records (Stinger, 2002; Stringer and Galway-Witham, 2017; Schlebusch and Jakobsson, 2018). The latest evidence suggests that *H. sapiens* had diverged from their common ancestor to become a separate, recognisable species by the Middle Pleistocene (Hublin et al., 2017; Posth et al., 2017). It is also well accepted that early modern humans (EMH; *H. sapiens*) along with archaic hominins (e.g. *H. erectus*, *H. neanderthalensis*) dispersed out of Africa at different intervals to colonise various parts of the globe (Bae et al., 2017a; Nielsen et al., 2017). However, the timing of initial dispersal of EMH out of Africa is one of the most contentious topics in anthropology, archaeology and genetic studies today. Most archaeologists agree that the initial dispersal of EMH out of Africa occurred sometime between 170 and 50 ka, based on a growing body of records from Asia (e.g. Westaway et al. 2017; Groucutt et al. 2018; Hershkovitz et al., 2018). The most conservative estimate is 50 ka, and is arrived at as the minimum age possible for dispersal in view of the fact that the ancestors of the Australian Aboriginal people had reached Australia by this time (Tobler et al., 2017; O'Connell et al., 2018).

The Australia+New Guinea continent (Sahul) has remained isolated by sea from the mainland continent of Southeast Asia (Sunda) for the entirety of human history (Hall, 2009). This isolation makes the dispersal event from Sunda to Sahul the earliest known (successful) sea crossing by *H. sapiens* anywhere in the world (Davidson and Nobel, 1992). Of particular interest to this dispersal event is the island archipelago which lies between the two continents of Sunda and Sahul, known as Wallacea. Occupation dates from Sahul provide the minimum age for the Sunda to Sahul sea crossing. Unfortunately, archaeological research in Wallacea has yet to recover any evidence of EMH occupation prior to the occupation dates recovered from Sahul (Kealy et al., 2016).

There is also debate around the chronology for initial Sahul occupation, with a date of ca. 65 ka recently obtained by OSL dating for Madjedbebe (Clarkson et al., 2017) being contended by some researchers who argue a 50 ka arrival date based on radiocarbon and molecular dating (O'Connell et al., 2018). Known EMH sites in Sunda older than those from Sahul are sparse, and the few that exist have had challenges to their chronologies (O'Connell et al., 2018). Thus, the date for out of Africa dispersal is often used as the maximum age boundary to bracket the Sunda-Sahul crossing, rather than dated sites in Southeast Asia itself (O'Connell et al., 2018; Skoglund and Mathieson, 2018). As noted above, the out of Africa *H. sapiens* dispersal event also continues to be extensively debated, in particular the dispersal which led to the eventual colonisation of Sahul. The latest genetic research posits this dispersal event occurring anywhere between 200 ka and just 50 ka ago (Fu et al., 2014; Kuhlwilm et al., 2016).

In addition to determining the timing of the Sunda to Sahul crossing event, the sparse and geographically patchy archaeological record of the Wallacean Archipelago also hinders investigations into the pattern of this dispersal. Of key interest is the identification of likely launch and landing locales on Sunda and Sahul, respectively, and the likely route/s taken through the islands of Wallacea. These route details have implications for a variety of studies

including investigations of human movement patterns throughout Sunda, Sahul, and Wallacea, responses to differences in palaeoenvironmental conditions, determining the likely technological capabilities of the first seafarers, and predictive indicators of regions with the highest archaeological potential for early EMH sites (Kealy et al., 2018a). In the absence of archaeological evidence, a number of hypothetical routes between Sunda and Sahul have been proposed as well as theoretical models of EMH movements and dispersal patterns (Birdsell, 1977; Sondaar, 1989; Clark, 1991; Morwood and Van Oosterzee, 2007; Allen and O'Connell, 2008). Until recently, however, there has been very little research conducted for the whole of Wallacea using digitised spatial data to implement dispersal models in a testable framework.

Here I present the results of my PhD research to investigate and model EMH movements and dispersal patterns through Wallacea in relation to the Sunda-Sahul initial crossing event. I begin with an outline of the research project and aims (1.2.) and an introduction to the geographical region of interest; Wallacea (1.3.). This is followed by a review of the latest literature concerning the bracketing dates (Minimum and Maximum Bound) for the Sunda-Sahul crossing; evidences for out of Africa dispersal and movement into Asia (and Sunda) (1.4.), as well as the different chronologies proposed for arrival in Sahul (1.5.). The impact of these variable chronologies is then explored in relation to the different hypotheses and models thus far proposed for EMH movement and dispersal through Wallacea (1.6.). In the following chapters I explicate my methodology and the results of my research into this earliest seafaring event.

1.2. Research Project and Aims

This research project was conducted as a part of the Australian Research Council Laureate Project (FL120100156): From Sunda to Sahul: Understanding modern human dispersal, adaptation and behaviour en route to Australia (henceforth Laureate Project), led by Chief Investigator Professor Sue O'Connor at the Australian National University. Focusing chiefly on human dispersal, my project aimed to explore initial human dispersal and subsequent interisland movements, through the Wallacean Archipelago.

Using modelling techniques, this PhD project investigated the movement of EMH through Wallacea and evaluated the results in light of the known archaeological record produced by the Laureate Project (see Chapter 4 and Appendices E-P) and other, external research endeavours. With the goal of modelling route/s through Wallacea and then testing the model outcome, the research was divided into six projects with the following aims:

1. To reconstruct the palaeogeography of Wallacea and the neighbouring coastlines of Sunda and Sahul for the periods of possible EMH arrival and dispersal (see Chapters 3, 5, & 6).
2. To model the intervisibility of islands within the Wallacean palaeo-archipelago, as they might have been viewed by EMHs (see Chapters 5 & 6).
3. To construct and run a least-cost surface model for human movement from Sunda to Sahul, based on the palaeogeographic reconstructions and intervisibility (see Chapter 6).
4. To develop a proxy model of EMH movement between islands based on the biogeography and possible human translocations of the Cuscus (*Phalanger*) (see Chapters 7 & 8).

5. To compare the least-cost model results with proxies for movement and the latest archaeological data from the region to test model validity and identify key regions for future archaeological focus (see Chapter 9).

1.3. Study Area: Wallacea

Wallacea is the biogeographical region between continental Australia-New Guinea (Sahul) and Southeast Asia (Sunda). Named after Sir Alfred Russel Wallace and his biogeographical line, Wallace's Line, which delineates the region's western extent (Wallace, 1860, 1876). Wallacea is significant to biogeographers and archaeologists alike as the islands of the archipelago have never been connected to the mainlands of either Sunda or Sahul, even during periods of lowest sea level (Kealy et al., 2016). This island isolation means that all organisms ever to occupy Wallacea, be they plants, animals, or humans, had to successfully complete sea crossings from the mainland in order to settle on these islands.

1.3.1. Geology and Biogeography

Wallace's Line, which runs north between the islands of Bali and Lombok, through the straits of Makassar between Borneo and Sulawesi and then east under the Philippines (Wallace, 1860, 1876), was modified by Huxley in 1868 to include the Philippines within the Wallacean Archipelago. As a result, researchers alternatively include or exclude the Philippines from their definitions of Wallacea depending on the selection of various biogeographical features of the Philippines, which are both similar and distinct from those of the rest of the Wallacean Archipelago (Wallace, 1860, 1876; Huxley, 1868; Dickerson et al., 1928; White and Bruce, 1986; Michaux, 2010; Lohman et al., 2011; Brown et al., 2013). Throughout this study I define Wallacea based on Wallace's original line, excluding the Philippines. This does not mean that the Philippines are excluded from the study, but are instead treated as a neighbouring region, following both Wallace (1860, 1876) and more recent studies (Lohman et al., 2011; Brown et al., 2013) which consider the Philippines to be its own unique biogeographic region. The eastern extent of Wallacea is bounded by Lydekker's Line which essentially follows the continental shelf of Sahul and has been relatively stable in its definition since it was first described (Lydekker, 1896; Merrill, 1923).

A geologically complex region, the islands of Wallacea owe their origins to a combination of uplift and volcanic arcs formed by the colliding forces of three major tectonic plates: the Eurasian Plate, India-Australian Plate, and the Pacific-Philippine Sea Plate. Thus, most islands consist of a core of metamorphosed Palaeozoic and Mesozoic formations or Tertiary (Paleogene + Neogene) volcanics, ringed by more recent (Quaternary) limestone deposits. The limestone frequently forms terraces as a result of uplift and sea-level changes (Koesoemadinata and Noya, 1989; Agustiyanto et al., 1994; Sudana et al., 1994; Noya et al., 1997). In some regions, particularly along the Banda Arc of southern Indonesia, continued volcanic activity has extended a number of islands through the formation of Quaternary volcanoes, some of which are still active today (e.g. Koesoemadinata and Noya, 1989). The major exception to this trend in geological composition is the island of Sulawesi.

Sulawesi is not only the largest island in Wallacea (and 11th largest in the world), but it is also the most geologically complex (Nugraha and Hall, 2018). The presence of continental rocks on Sulawesi, originating from Sahul, has often led to hypothesis of certain Australasian species owing their Sulawesi distribution to vicariance rafting events (Barker et al., 2007; Stelbrink et

al., 2012). This “raft” known as the Sula Spur, represents part of the north-westerly extent of the Australian continental plate, which collided with the North Sulawesi volcanic arc during the Early Miocene (Nugraha and Hall, 2018). This collision resulted in uplifting and the formation of a handful of islands which would eventually expand and merge over the next 20 Ma into the present-day configuration (see Nugraha and Hall, 2018 for a detailed analysis of the geological processes involved). It is important to point out that while the result of this collision led to the presence of Sahul continental rocks on Sulawesi, these would have been submerged before the collision, negating the possibility for a vicariance rafting event carrying Australian flora and fauna to Sulawesi (Barker et al., 2007; Stelbrink et al., 2012; Nugraha and Hall, 2018). All ecosystems on the islands of the Wallacean Archipelago therefore, comprise various amalgamations of over-water dispersing species originating from either continental Sunda or Sahul.

The Wallacean Archipelago is also notable for its records of early hominins and earliest evidence for sea-crossings by both *Homo sapiens* and an earlier hominin (possibly *H. erectus*). *H. erectus* is known from Java (Sunda) as early as 1.66 ± 0.4 Ma (Sémah et al., 2000; Bouteaux et al., 2007). East of Huxley’s Line, evidence from the Philippines for an unknown hominin presence at 777-631 ka has been recovered from Cagayan Valley, Luzon (Igicco et al., 2018). Early hominin occupation is recorded east of Wallace’s Line on Sulawesi (194-118 ka from Talepu; van den Bergh et al., 2016) and Flores ($>1.02 \pm 0.02$ Ma from Wolo Sege; Brumm et al., 2010), suggesting dispersal of this unidentified hominin into Wallacea by at least one million years ago. Concerning *H. sapiens* however, the oldest confirmed evidence for this over-water dispersal comes indirectly from the Australian archaeological record (see section 1.5. below).

Dispersal of the *H. floresiensis* ancestor and the unidentified early hominin to Flores and Sulawesi, respectively, have both been hypothesised as the result of chance or incidental drift dispersal (Dennell et al., 2014). The multitude of water crossings required to transverse the Wallacean Archipelago and reach Sahul however, makes a random chance hypothesis for this latter dispersal by EMH highly unlikely (Davidson and Noble, 1992; Bird et al., 2018). Additionally, genetics suggests that a significant number of individuals would have been necessary to comprise a successful colonising population for Sahul (Tobler et al., 2017; Bird et al., 2018); further reducing the likelihood of unintentional colonisation. This makes Wallace’s Line and the Wallacean Archipelago as a whole, the oldest known site in the world for deliberate maritime-crossings by humans.

1.3.2. The Archaeological Record of Wallacea

The vast majority of dates for the region have been obtained using the radiocarbon technique (Table 1; with the exception of the rockart in Sulawesi dated to ca. 40.7 ka by Aubert et al., 2014). Additionally, due to the poor preservation of organic remains encountered in the tropics (Louys et al., 2017; Morley, 2017), the oldest of these dates are rarely obtained from charcoal; instead relying on marine shell (Table 1). Radiocarbon dating of marine shell is, however, considered more problematic than other sources of radiocarbon such as charcoal, due to a greater number of uncertainties effecting the results.

Table 1: Initial occupation dates for EMH Pleistocene archaeological sites in Wallacea (updated from Kealy et al., 2016:Table 1). Radiocarbon dates are calibrated using OxCal v.4.3 (Ramsey, 2009) and the IntCal13^a (for charcoal) and Marine13 (for shells) calibration curves (Reimer et al. 2013). All ¹⁴C dates not obtained from marine shell are indicated with asterisk: *single charcoal, **bulk charcoal & bone, and ***freshwater shell.

ISLAND (IS. GROUP)	SITE NAME	¹⁴ C/U-SERIES DATE	CAL BP AGE 95.4%	REFS. ^b	
TIMOR	Jerimalai	41,572 ± 939	46,529 – 43,085	1	
	Laili	*40,417 ± 332	44,668 – 43,314	2	
	Lene Hara	38,207±610	42,998 – 41,251	3	
	Matja Kuru 2	32,200 ± 300	36,307 – 35,031	4	
	Bui Ceri Uato	26,520 ± 340	30,967 – 29,559	5	
	Uai Bobo 2	**13,400 ± 520	?17,680 – 14,470?	6	
ROTI (TIMOR)	Lua Meko	24,420 ± 250	28,603 – 27,676	7	
	Lua Manggetek	13,390 ± 430	16,802 – 14,089	7	
ALOR (NUSA TENGARA)	Gua Makpan	35,232 ± 427	40,342 – 38,508	8	
	Tron Bon Lei	17,630 ± 70	21,000 – 20,560	9	
KISAR (MALUKU BARAT DAYA)	Here Sorot Entapa	13,395 ± 33	15,730 – 15,327	10	
	Ratu Mali	13,129 ± 31	15,299 – 15,025	8	
FLORES (NUSA TENGARA)	Liang Bua	*42,500 ± 900	48,031 – 44,327	11	
SULAWESI	Leang Timpuseng	41,570 – 39,860 <i>Corrected U-Series</i>		12	
	Leang Bulu Bettue	40,000 – 39,600 <i>Laser ablation U-series</i>		13	
	Leang Jarie	39,990 – 39,350 <i>Corrected U-Series</i>		12	
	Leang Barugayya 2	53,100 – 35,700 <i>Corrected U-Series</i>		12	
	Leang Burung 2	***30,597 ± 323	^c 34,926 – 33,875	14	
	Leang Sampeang	33,360 – 31,840 <i>Corrected U-Series</i>		12	
	Gua Jing	32,600 – 29,100 <i>Corrected U-Series</i>		12	
	Leang Lompoa	30,500 – 28,200 <i>Corrected U-Series</i>		12	
	Leang Barugayya 1	32,300 – 26,000 <i>Corrected U-Series</i>		12	
	Leang Sakapao 1	25,390 ± 310	29,814 – 28,379	15	
	SALIBABU (TALAUD) MOROTAI (HALMAHERA)	Leang Sarru	30,850 ± 340	35,034 – 33,864	16
		Daeo 2	13,930 ± 140	16,767 – 15,889	17
	GEBE (HALMAHERA)	Golo Cave	32,210 ± 320	36,350 – 35,001	17

^aThe 'Northern Hemisphere' calibration curve is used here for all Wallacean dates as it is considered to provide a more reliable estimate than SHCal (the Southern Hemisphere Curve) for equatorial regions, including locations in the low latitudes of the Southern Hemisphere (Rachel Wood pers. comm.). ^bRefs.: 1 Shipton et al., in press; 2 Hawkins et al., 2017; 3 O'Connor et al., 2010; 4 O'Connor et al., 2014; 5 Selimiotis, 2006; 6 Glover, 1969; 7 Mahirta, 2003; 8 O'Connor et al., 2018e; 9 Samper Carro et al., 2016; 10 O'Connor et al., 2018a; 11 Sutikna et al., 2018; 12 Aubert et al., 2014; 13 Li et al., 2016; 14 Brumm et al., 2018; 15 Bulbeck et al., 2004; 16 Ono et

al., 2009; 17 Bellwood et al., 1998. °Calibrated with 50% Marine radiocarbon, pushing the calibration further towards atmospheric or marine alters the calibrated range by ca. ±150.

In particular, local marine reservoir (ΔR) effects, the “hard-water effect” for shells from limestone rich areas, and effects of recrystallisation (Douka et al., 2010) all detract from the accuracy of the final date. Shells selected for dating can be identified to species, enabling researchers to select suspension feeders over deposit feeders and thus, reduce the hard-water effect (Douka et al., 2010). Similarly, the use of fiegI staining (Dickson, 1966) and advances in pre-treatment processes has enabled radiocarbon laboratories to be quite confident in their assessment of recrystallisation (Douka et al., 2010). Unfortunately, a local reservoir effect has yet to be calculated for the Wallacean archipelago, causing all radiocarbon calibrations of marine shell dates for the region to be calculated without a ΔR offset (Table 1). Temporal errors can also occur in charcoal samples due to the ‘old wood’ effect (Kennett et al., 2002), however in the tropical environment of Wallacea this error range is unlikely to reach, and certainly not exceed, the local reservoir effect for shells. For investigations of earliest EMH occupation in Wallacea however, this currently unavoidable error range in the radiocarbon dates, of up to ca. 400 years, is negligible.

The oldest possible date for EMH occupation in Wallacea comes from Liang Bua, Flores, recently published in light of the reinterpreted stratigraphy in this cave (Sutikna et al., 2016, 2018). Sutikna et al. (2018) suggest EMH arrival on Flores ca. 48 – 44 ka based on changes in lithic raw material and a reduction in tool size in the deposits overlying the T3 tephra. This date range overlaps with both the Laili date of 44.7 – 43.3 ka (Hawkins et al., 2017) and the latest date recovered from the re-excavation of Asitau Kuru (previously known as Jerimalai), of ca. 47 – 43 ka (Shipton et al., in review), in Timor-Leste. The overlaps in the 95.4% confidence interval make any further determinations of the earliest known occupied site in the region not possible (Table 1). Regardless of the exact occupation order between these three sites, their combined results suggest that EMH had reached the islands of Flores and Timor, and central-south Wallacea generally, by at least 44 ka (Hawkins et al., 2017; Sutikna et al., 2018; Shipton et al., in review).

In addition to uncertainties surrounding the earliest known occupied site for Wallacea, the number and dates of sites on these islands are currently insufficient to discriminate any particular pathway from Sunda to Sahul (Table 1; Birdsell, 1977; Kealy et al., 2016, 2017, 2018a). However, the oldest EMH occupation dates for Wallacea come from Nusa Tenggara, in addition to a total of 13 additional sites with Pleistocene EMH occupation across five islands (Table 1), which would appear to support a southern route into Sahul (Birdsell, 1977). However, only nine Wallacean islands, out of the thousands that make up the archipelago, have a known Pleistocene occupation chronology (Table 1). Furthermore, all of the Wallacean date ranges are younger than 50 ka, the minimum accepted age for initial occupation of Australia (Table 1; O’Connell et al., 2018). Thus, while some might be tempted to use the older dates from Timor and Flores to support a southern entry into Australia, until a larger sample size throughout the region at both the inter- and intra-island level is achieved, the exact pattern and timing of Sahul colonisation will remain in question. The islands of northern Wallacea in particular have received only limited archaeological surveys and excavations. Significantly, more extensive archaeological investigation of these northern islands would be required before they could be comparable with data from the south (Kealy et al., 2018a,b).

1.4. The Maximum Bound: Out of Africa and into Asia

1.4.1. The Archaeological Record

The earliest evidence, globally, for anatomically modern human (AMH) *Homo sapiens* comes from Jebel Irhoud in Morocco, where remains have been recovered from a layer dated to 315 ± 34 ka (Hublin et al., 2017). These dates further support an African origin for our species (Stinger, 2002; Hublin et al., 2017; Stringer and Galway-Witham, 2017). Outside of Africa, recent findings from Misliya Cave in Israel suggests AMH had dispersed out of Africa and reached Israel by at least 194 – 177 ka ago (Hershkovitz et al., 2018). Qafzeh and Skhul Caves (120-90 ka), and Manot Cave (60-50 ka) in modern Israel, and Al Wusta (ca. 95-86 ka) in Saudi Arabia reflect later expansions of the geographical range of *H. sapiens* (Schwarcz et al., 1988; Stringer et al., 1989; Mercier et al., 1993; Hershkovitz et al., 2015; Groucutt et al., 2018). Following Oppenheimer's (2009, 2012a) early modern human (EMH) dispersal route out of Africa into India and Southeast Asia the archaeological record becomes substantially reduced both in the number of identified sites and the reliability of their AMH identification and date association (O'Connell et al., 2018).

Extensive research in India on various archaeological sequences containing stone tools, coupled with identification and concise dating of the Toba eruption in the deposit sequences, has been used to suggest that EMH may have been present in India as early as 77 ka (Haslam et al., 2010; Clarkson et al., 2012; Petraglia et al., 2012; Mark et al., 2014). Until human fossils are found and identified in association with these assemblages, however, the identity of the species of hominin responsible for their production will remain in question (Clarkson et al., 2018; Blinkhorn, 2018; O'Connell et al., 2018). Currently, the oldest confirmed evidence for EMH occupation of the Indian subcontinent comes from Fa Hien-lena rockshelter in Sri Lanka with a date of ca. 40 – 36 ka for the layer containing confirmed AMH *Homo sapiens* remains (Athreya, 2014; Premathilake and Hunt, 2018). This date could be extended back to ca. 48 – 45 ka should further analysis of the lower cultural deposits support an EMH origin (Premathilake and Hunt, 2018).

Moving further east, sites in China suggest EMH occupation possibly as early as 100 – 80 ka or even earlier (Shen et al., 2013; Bae et al., 2014; Cai et al., 2017). However, doubts remain as to either their assignment to *H. sapiens* or the association of the fossils with the dates (see Dennell et al., 2014; O'Connell et al., 2018). The earliest unequivocally EMH from China is the Tianyuandong partial skeleton from northern China, directly dated to 40 – 38 ka cal BP (34,430 ± 510 BA-03222; Shang et al., 2007) and supported by genetic sequencing (Fu et al., 2013). Similarly, dates for EMH presence in Laos between 70 – 46 ka (Shackelford et al., 2018) have had the early range of this age distribution questioned by O'Connell et al. (2018) based on the reliability of the U-series dates and context association between the remains and OSL dated sediments. It is the earlier end of this range (70 – 46 ka) which is however, favoured by Shackelford et al. (2018) based on saturation and bleaching features of the dated quartz grains.

At the southern extent of the Sunda continent, in present day Island Southeast Asia (ISEA), re-analysis and dating of the site of Lida Ajer in Sumatra has produced a date of 73-63 ka for what is argued to be a modern human fossil (Westaway et al., 2017). While O'Connell et al. (2018) also express doubts about the validity of this claim, in particular the association between the

EMH remains and the dated breccia deposit, Westaway et al. (2018) presented responding evidence to support the association and reliability of the Lida Ajer date. In nearby Borneo, the site of Niah has also produced early evidence for EMH occupation with a date of ca. 50 – 47 ka (Higham et al., 2009). Recent U-series dating of calcite bracketing painted rock art in central-east Borneo has also produced an estimate of 52 – 40 ka for art production (Aubert et al., 2018). The archaeological record therefore, suggests EMH had dispersed out of Africa by 177 ka and reached eastern Sunda by at least 52 ka, and likely 63 ka ago (Westaway et al., 2017; Aubert et al., 2018; Hershkovitz et al., 2018).

1.4.2. *The Genetic Record*

While the archaeological record for EMHs in Asia, Southeast Asia and Australia supports a pre-60 ka date for initial out of Africa dispersal (Dennell and Petraglia, 2012; Bae et al., 2017), genetic studies on the topic have produced very mixed results. Extensive research into early modern human (EMH) and archaic hominin genetic histories has been conducted in recent years using a wide variety of genetic data and techniques. These techniques include; mitochondrial DNA (mtDNA; e.g. Soares et al., 2012) and nuclear DNA (nDNA; e.g. Schiffels and Durbin, 2014) analyses using molecular clocks, through to whole genome analysis, and the calculation of generations since admixture events with non-*sapiens* hominins (e.g. Fu et al., 2014; Pagani et al., 2016). The latest studies differ in their dispersal estimates by almost 150 ka, with the earliest estimate suggesting out of Africa dispersal 200 – 100 ka ago (Kuhlwilm et al., 2016), and the most recent at just 50 ka (Fu et al., 2014). While archaeological evidence such as the findings from Misliya Cave supports a >100 ka date (Kuhlwilm et al., 2016; Hershkovitz et al., 2018), studies favouring the Fu et al. (2014) dates of 60 – 50 ka argue that if the dating of these earlier archaeological sites is accurate, they must represent EMH communities which contributed no genetic material to our present day populations (i.e. ‘failed dispersals’; Bae et al., 2017; Skoglund and Mathieson, 2018).

The study by Fu et al. (2014) considers the genome of the Ust’-Ishim specimen from Siberia, dated to 45 ka, to calculate the timing of an admixture event between Neandertal and EMH based on the breakdown rate of Neandertal DNA segments within the genome (Fu et al., 2014; Skoglund and Mathieson, 2018). Based on segment breakdown rate Fu et al. (2014) identified the number of generations separating the initial introduction of Neandertal DNA into the EMH genome and the Ust’-Ishim specimen. Multiplying this generation number by 29 years for an estimate of generation time, Fu et al. (2014) proposed a date of 60 – 50 ka for the admixture event. They further suggest that the proportion of Neandertal DNA in the Ust’-Ishim specimen (ca. 2%) is similar to all non-African modern populations, indicating that this admixture event must have occurred in a single time and place, just outside of Africa (Southwest Asia), and prior to the further dispersal of these peoples across the rest of the globe (Fu et al., 2014; Skoglund and Mathieson, 2018). The conclusions of these findings is that: a) EMH must have dispersed out of Africa as a single population, in a single event, which received an input of ca. 2% Neandertal DNA prior to their further dispersal into Asia and Europe; b) that this event must have occurred prior to 45 ka in order for the Ust’-Ishim specimen to reach Siberia; c) that EMH dispersed out of Africa only shortly before 60 – 50 ka and did not disperse beyond southwest Asia until after 60 – 50 ka in order for the Neandertal admixture event to occur; d) any pre-existing EMH populations outside of Africa were completely replaced by this 2% population (Fu et al., 2014; Skoglund and Mathieson, 2018).

However, the 60 – 50 ka ‘Neandertal segment breakdown’ theory (Fu et al., 2014; Skoglund and Mathieson, 2018) contrasts strongly with the archaeological data (see above), and some recent genetic studies (e.g. Kuhlwilm et al., 2016; Pagai et al., 2016). Furthermore, later studies by Fu et al. (2016) suggest that this ca. 2% Neandertal DNA in some modern populations is the result of gradual decline in percentages due to natural “selection against” the Neandertal sequences in EMH populations over time. They suggest declines over the last 45 ka from up to 6% Neandertal DNA down to ca. 2%. Fu et al.’s (2016) evidence for long-term natural selection operating on Neandertal-derived DNA within the *Homo sapiens* genome raises questions regarding their earlier calculation of generations-since-admixture of the Ust’-Ishim specimen (Fu et al., 2014), and the assumption of a single admixture event bracketing OoA dispersal (Skoglund and Mathieson, 2018). Additionally, some studies have suggested that this ca. 2% could have been achieved through latter admixtures between an earlier OoA EMH population with no Neandertal DNA and latter dispersers carrying higher percentages (Vernot and Akey, 2015).

Further supporting existence of an earlier EMH dispersal outside of Africa prior to the 60 – 50 ka admixture event, is the results of Pagani et al.’s (2016) study that found evidence for at least 2% ancestrally derived EMH admixture in the modern Papuan genome. Based on this Pagani et al. (2016) suggested an early EMH dispersal event after ca. 120 ka that largely died out and/or was replaced by the later “main” OoA dispersal event, but which has left small (ca. 2%) genetic traces in some modern populations. This hypothesis is significantly more congruent with the archaeological record, and somewhat supported by other genetic studies which support an earlier ‘Oceania’ dispersal prior to the rest of Eurasia (Malaspinas et al., 2016; Skoglund and Mathieson, 2018). The more recent discoveries regarding Neanderthal and EMH admixture have identified a Neanderthal population in the Altai Mountains, Siberia, that received genetic material from EMH outside of Africa ca. 100 ka (Kuhlwilm et al., 2016), further supporting the existence of EMH populations outside of Africa well before 60 ka.

As summarised by Sikora (2017) and Nielsen et al. (2017), current advances in genetic techniques and data availability is showing an increasingly complex history of EMH and archaic human dispersals and introgression out of Africa and throughout Asia over the last 200 ka (Posth et al., 2017). While genetic data is invaluable for understanding this complex history, many of the methods involved are still in the early stages of development, substantial datasets of comparable sequences from Australasian populations are still being compiled, and temporal estimates are heavily dependent on clocks whose rates are still under revision (Mallick et al., 2016; Pagani et al., 2016; Nielsen et al., 2017; Sikora, 2017; Tobler et al., 2017; Besenbacher et al., 2018). Thus, a variety of dispersal models have been proposed in an attempt to reconcile genetic and archaeological records in comparison to palaeoenvironmental and geographical factors (e.g. Bae et al., 2017a).

1.4.3. Modelling Movement Out of Africa and Through Asia

Investigations into out of Africa dispersals can be split into two different, although connected events: the immediate dispersal out of Africa into Southwest Asia (OoA) and the subsequent dispersal(s) from Southwest Asia (OoSA) throughout the rest of the world (Bae et al., 2017a,b; Sikora, 2017). The two most favoured models for the first event are a single OoA dispersal event at ca. 60-50 ka (MIS 3), or multiple dispersal events beginning during MIS 5 (130 – 71 ka; Lisiecki and Raymo, 2005) (Bae et al., 2017). Following the establishment of an out of Africa

population(s), models again favour either single or multiple dispersal events with further considerations regarding the number, timing and locations of different admixture events between EMH and archaic human populations (Sikora, 2017). Debate also surrounds the different paths these various dispersal events may have taken, with arguments for southern vs northern OoA dispersal (e.g. Vyas et al., 2017), as well as a coastal vs interior/terrestrial OoSA route(s) from Southwest Asia (see Groucutt et al., 2015).

As this project is primarily concerned with EMH arrival and dispersal through Wallacea and initial colonisation of Sahul, I focus here on models concerned with dispersal out of Southwest Asia and into Southeast Asia (Sunda). Looking at the timing and number of dispersals, three key models exist (Sikora, 2017): 1) an early OoA population which continued from Southwest Asia into Southeast Asia, followed by a separate, later OoA population which followed, mixed with, and eventually replaced the earlier population (Vernot and Akey, 2015; Pagani et al., 2016; Kuhlwiilm et al., 2016; Westaway et al., 2017; Hershkovitz et al., 2018); 2) an early “wave” of OoSA dispersal into Sunda and likely Sahul, separate to the later OoSA dispersal to the rest of the world (Rasmussen et al. 2011; Malaspinas et al., 2016); and 3) a single OoSA dispersal followed by later population divergence between Southeast Asians and northern Asians/Eurasians (Mallick et al., 2016).

The likelihood of any of these three Asian dispersals is clearly influenced heavily by what OoA dispersal model is favoured. Based on the current status of archaeological and genetic evidence (see above), the most parsimonious model for OoA dispersal appears to be the “MIS 5 – Multiple dispersal model” (Dennell and Petraglia, 2012; Bae et al., 2017a,b; Sikora, 2017). Despite discrepancies in the Sunda and Sahul archaeological records and incongruence between genetic studies, the presence of EMH populations outside of Africa by 177 – 90 ka ago (Stringer et al., 1989; Mercier et al., 1993; Hershkovitz et al., 2015; Groucutt et al., 2018) appears to be generally accepted by archaeologists and geneticists alike. The question, however, is if these early populations contributed any genetic material to modern human populations and if so, when and where did this introgression occur (Mallick et al., 2016; Pagani et al., 2016; Sikora, 2017). Pagani et al. (2016) provide strong support for the ‘EMH admixture’ model with evidence for an early EMH population that reached Sahul in advance of the later ‘wave’ of dispersal. Improved archaeological and genetic data, as well as advanced analytical tools, will be required to further unravel which of these dispersal models most likely resulted in our present day populations (Skoglund and Mathieson, 2018).

Regarding the southern vs northern routes out of Africa, palaeoclimate and dispersal models (e.g. Field and Lahr, 2005; Breeze et al., 2016) in addition to the archaeological record (Schwarcz et al., 1988; Stringer et al., 1989; Mercier et al., 1993; Hershkovitz et al., 2015) support the northern route across the Sinai Peninsula. The southern route, with its necessary water crossing of the Bab al Mandab Strait, is generally considered less likely due to the required rafting effort of at least 5 km (even at times of lowest sea level), when compared with the permanent land bridge of the Sinai (Bae et al., 2017a). However, such a crossing is not impossible, particularly when we consider that EMH likely possessed at least some level of maritime capability by the time they reached the Sunda coast (Bulbeck, 2007), and so should not be ruled out entirely (Breeze et al., 2016; Bae et al., 2017a). The determination of which route was used has implications for models concerning dispersal pathways from Southwest Asia through to the east coast of Sunda (Boivin et al., 2013).

While a southern dispersal route out of Africa leads into the long favoured coastal route to Sunda and Sahul (Bulbeck, 2007; Oppenheimer, 2009, 2012a,b), archaeological data from Southwest Asia and India increasingly support a more terrestrially focused strategy of EMH populations (Roberts et al., 2015, 2017; Blinkhorn et al., 2017). Supporters of the coastal route point to the necessary, long-term development of maritime technologies required for the eventual crossing of Wallacea (Bulbeck, 2007; Balme, 2013) and highlight the now-submerged continental shelves to explain the lack of coastal sites in the current landscape (Erlandson and Braje, 2015). Furthermore, coastal resources (e.g. shellfish) are considered a particularly energy efficient food source, favouring their exploitation by EMH populations (Mellars, 2006; Bulbeck, 2007), while flat coastal plains are favourable for easy dispersal (Field and Lahr, 2005; Field et al., 2007).

However, if we consider Roberts and Stewart's (2018) "generalist-specialist" model for human behavioural adaptation, particularly in light of the growing body of 'inland' archaeological evidence from South and Southeast Asia (Boivin et al., 2013; Blinkhorn et al., 2017; Roberts et al., 2017; Bacon et al., 2018), this eastward dispersal appears much more complex than initially thought (Oppenheimer, 2009). Evidence for specialisations to particular inland environments such as rainforests (Roberts et al., 2017), supports the 'generalist-specialist' model (Roberts and Stewart, 2018) and demonstrates EMH abilities to adapt to, and exploit an exceptionally wide range of resources without a restriction to a single habitat (e.g. coasts, Mellars, 2006). It has also been hypothesised that initial eastward dispersal through South Asia was focused on the interior with coastal environments populated by latter radiations (Blinkhorn et al., 2017). Future archaeological discoveries from South and Southeast Asia will be required for a clearer understanding of these dispersal patterns, however, as the models by Field et al. (2007) suggest both coastal and inland routes were likely employed in the initial EMH OoSA dispersal, as might be expected if EMH were generalist-specialists.

This inland vs coastal argument extends through Southeast Asia, right down to the eastern coast of Sunda where it has particular implications for models of EMH dispersal routes across Wallacea. For dispersal through Sunda these models tend to be classified as either a coastal route (Bulbeck, 2007; Oppenheimer, 2009, 2012a,b) or 'savanna corridor' (Bird et al., 2005). The coastal or 'beachcomber' route (Bulbeck, 2007; Oppenheimer, 2009, 2012a,b) follows the southern Eurasian coast east, all around the Indian Ocean to Bali (the most south-eastern extant of Sunda), before curling up north to follow the eastern Sunda coast to the northern tip of Borneo, and is therefore not considered to favour any particular launch point into Wallacea over another (Oppenheimer, 2012a). In contrast, the savanna corridor model suggests the presence of 'savanna' environments favourable to EMH exploitation and dispersal extending from the north through central and southern Sunda (Bird et al., 2005). This savanna corridor has been suggested by Bird et al. (2005, 2018) to support a southern (i.e. Bali) launch point and dispersal through Wallacea. However, the 'generalist-specialist' model of Roberts and Stewart (2018) and evidence for EMH occupation of rainforest environments in Sumatra (Westaway et al., 2017), cast doubts on the presumption of a savanna focus by EMH and the channelling effect the savanna corridor might have had on EMH dispersal routes. Least-cost models of EMH movement through Sunda support an interchanging coastal and inland pathway with support for both southern and northern launch points into Wallacea (Field and Lahr, 2005; Kealy et al., 2018a)

1.5. The Minimum Bound: Initial Occupation of Sahul

1.5.1. *The Conundrum of Madjedbebe*

To the east of Wallacea lies Sahul, the conjoined continent of Australia and New Guinea which emerges when sea levels drop below present levels by ca. 20 m. As Wallacean occupation dates comparable with or earlier than those from Sahul have yet to be discovered (Table 1; Kealy et al., 2016), accurate determinations of the timing and location of earliest human occupation on Sahul is of significant importance for inferring when and where people first moved through Wallacea. To this end the archaeological site of Madjedbebe (previously known as Malakunanja II) located in Mirarr Country at the western edge of the Arnhem Land plateau, Northern Territory, has been of great significance to both Australian and Australasian archaeology (and also more broadly to global studies of human evolution and dispersal). Based on optical luminescence dating (OSL) techniques, the latest date recovered for the initial occupation of Madjedbebe is $65.0 \pm (3.7, 5.7)$ ka (Clarkson et al., 2017).

The Madjedbebe date of ca. 65 ka predates other early occupation sites in Sahul by at least 15 ka (Turney et al., 2001; Bird et al., 2002; Bowler et al., 2003; Hamm et al., 2016; Wood et al., 2016; Delannoy et al., 2017; Veth et al., 2017; Maloney et al., 2018b; McDonald et al., 2018) and this, among other reasons, has led to a questions on the validity of these dates (O'Connell et al., 2018). O'Connell et al. (2018) also point to problems with the site's stratigraphy, suggesting Madjedbebe has been significantly disturbed with substantial downward movement of artefacts, resulting in marked overestimations of the date of occupation. They suggest an alternative initial occupation date for Sahul of ca. 50 ka (O'Connell et al., 2018) based largely on the recent mitochondrial genome analysis of Tobler et al. (2017), and generally supported by radiocarbon dates recovered from a number of sites throughout Australia and New Guinea.

A proposed explanation for the disparity in occupation dates between Madjedbebe in the north and dates throughout the rest of Australia is the "initial adaptation phase" hypothesis proposed by Maloney et al. (2018b). This hypothesis suggests that the initial colonising population of Australia may have undergone an "adaption" period whereby population dispersal was stalled in northern Australia until technologies and population numbers had built up sufficiently for greater expansion (Maloney et al., 2018b). Palaeovegetation models also suggest a distinct change from general savanna/dry vegetation-type conditions of Wallacea and New Guinea and the different environments of Australia, to occur along the very northern tip of Australia (Hope et al., 2004). Based on these models, Madjedbebe is located on one of the few remaining (above water) regions of Australian Sahul where palaeovegetation conditions matched those of Wallacea. This latitudinal change in vegetation types may have also contributed to stalling southward dispersal and the necessity of an "initial adaptation phase" (Hope et al., 2004; Maloney et al., 2018b). The possibility of dispersal throughout the rest of Australia beginning from a northern Australian population after initial human arrival is also tentatively supported by the Tobler et al. (2017) phylogeny. Tobler et al.'s (2017) phylogeography strongly suggest a Northern Australian founding population as the origin point for the rest of Australia's indigenous populations.

1.5.2. Occupation of Australia based on Regional Genetics

It should be noted that the Tobler et al. (2017) study focused on regionalism within Australia, including 25 Melanesian samples and no outgroup data from Africa or Asia. Furthermore, the calibrations of the molecular clock used by Tobler et al. (2017) relied largely on rate data compiled from European studies focused on the last ca. 25 ka, with a single tip date of ca. 1.25 ka based on estimates of the WHL4 skeleton age from Lake Mungo (Heupink et al., 2016). Recent mutation rate studies have also suggested significantly slower annual rates than previously estimated (Sally, 2016; Besenbacher et al., 2018). While these studies are based on genome wide calculations, and not focused on mitochondrial DNA (Tobler et al., 2017), continued changes in our understanding of mutation rates has substantial implications for studies relying on molecular clocks and the divergence estimate which they produce (Moorjani et al., 2016; Sikora, 2017). Furthermore, while the molecular calibration methodology used by Tobler et al. (2017) may be suitable for post-colonisation interpretations of regionalism, the earlier, initial divergence estimates may be affected by time dependency differences not reflected in the clock rates (Ho et al., 2011).

While the Tobler et al. (2017) study has the potential to recover accurate divergence estimates for Australian colonisation, the current uncertainties in our knowledge of clock rates encourages very careful consideration of the results. In particular, the initial evolution rates could be out as a result of temporal dependency on events such as possible population bottlenecks during dispersal across Wallacea and the initial colonisation event of Sahul (Malaspina et al., 2016). Furthermore, when we consider the dated phylogeny recovered by Tobler et al. (2017), the 95% HPD intervals for their five “Aboriginal-Australian-Only” (AAO) clades cover an estimated divergence period of between 61.3 ka to 31.6 ka. These five clades also place within more deeply diverging clades, comprising either AAO samples or both Australian and Melanesian samples, whose mean divergence estimates extend beyond 50 ka (Tobler et al., 2017). O’Connell et al. (2018)’s use of the Tobler et al. (2017) study to support Australian colonisation at ca. 50 ka appears to be a slight misinterpretation of the phylogenetic results. Rather, the Tobler et al. (2017) study suggests the presence of regional populations in Australia from about 50 ka, encouraging the hypothesis of initial arrival prior to this date.

When considering the radiocarbon evidence for initial occupation of Australia (Turney et al., 2001; Bowler et al., 2003; Bird et al., 2002; Hamm et al., 2016; Wood et al., 2016; Delannoy et al., 2017; Veth et al., 2017; Maloney et al., 2018b; McDonald et al., 2018), the Signor-Lipps effect (Signor and Lipps, 1982; Raup, 1986), the “initial adaption phase” hypothesis (Maloney et al., 2018b), and regional genetics (Tobler et al., 2018), a pre-50 ka arrival date appears likely. In light of this, the Madjedbebe date of ca. 65 ka with a minimum “conservative estimate” of 59.3 ka for initial human occupation of northern Australia (Clarkson et al., 2017) seems less extreme or improbable than initial interpretation may suggest (O’Connell et al., 2018). However, the 10 – 15 ka gap between the Madjedbebe dates and the rest of Australia seems particularly long for an “adaptation phase”, and such an early date is poorly supported by the genetics (Tobler et al., 2017). Extensive investigations into the chronology and stratigraphy at Madjedbebe over the last few years by Clarkson et al. (2015, 2017, 2018), have provided strong support for the stratigraphic integrity of the site and its ca. 65 ka occupation date. Thus, a disparity between Madjedbebe and the rest of Sahul and Wallacea remains. Future archaeological investigations throughout northern Australia as well as Wallacea and New Guinea will be required to determine the validity and cause of this current temporal gap in our

records of Sahul colonisation. Until further data is recovered, the initial human occupation of Sahul is therefore considered here as ca. 65 – 50 ka (Clarkson et al., 2017; Tobler et al., 2017; O’Connell et al., 2018).

1.6. Modelling Movement into and around Wallacea

A model is a similar but simplified representation of a thing (e.g. organism, object, phenomenon) (Maria, 1997). In science, models are used to systematically represent real-world processes or phenomena, and in so doing, enable their detailed investigation (Maria, 1997; Börner et al., 2012). In particular, scientific models enable the prediction of a future event or change in a present system as well as the investigation of past systems which may no longer exist. It is important to note that while scientific models aim for accuracy, they also aim to simplify and reduce the real world into a set of elements and fundamental laws (Maria, 1997; Börner et al., 2012). A model is best when simplification reduces complexity with limited parameters to enable easy experimentation and interpretation, while also representing the actual system and the majority of its salient features as best as possible (Maria, 1997).

Scientific models come in a variety of forms depending on the system being investigated and methods used (Börner et al., 2012). In the study of past human movements, the models employed by scientists can be divided into two main types. 1) Theoretical models: whereby the researcher(s) investigate a number of parameters/variables which would affect moveability and direction, and discuss their hypothetical result, sometimes with the aid of hand drawn maps illustrating their favoured path. 2) Simulated models: whereby the parameters/variables of the theoretical model are converted into mathematical values which can be a mix of fixed, probabilistic, static and dynamic variables. This mathematical model is then configured into an operational one (usually through the use of computer software and programming), whereby this ‘simulated’ system can be reconfigured and experimented upon at will. While theoretical and simulated models may often appear to produce the same results, it is important to realise that the results of a theoretical model are *unvalidated*. In order to validate a model, it must be simulated, and those simulated results compared with the empirical data (Maria, 1997; Börner et al., 2012). As theoretical models do not produce simulated results, they remain a useful but unvalidated source of information.

1.6.1. Hypothetical Routes and Theoretical Models

The earliest detailed effort to plot likely dispersal routes from Sunda to Sahul was the seminal work by Joseph Birdsell, begun in 1957 and finalised in his 1977 publication. Based on factors of island visibility, crossing distance, and target size (island width), Birdsell (1977) drew two main, hypothetical routes through Wallacea with a total of five variations. Route 1, also known as the ‘northern route’ into Sahul launches from the extended Borneo coast near the present-day Balabalagan islands across the Makassar Strait to Sulawesi. East of Sulawesi route 1 is split into three alternatives; A, B, and C, with Sahul landings near the present-day Raja Ampat islands, Misool Island, and Aru islands, respectively (Birdsell, 1977). Route 2, or the ‘southern route’ launches from Bali, crossing the Lombok Strait into the Nusa Tenggara archipelago of southern Wallacea. Route 2 has two alternative landing options, A at the Aru islands alongside the route 1C termination point, and B with a southern crossing directly from Timor to northern Australia. The only significantly different alternative route to Birdsell’s (1977) model, is the northern entry from the Philippines down to Sulawesi and into Wallacea proposed by Sondaar

(1989) and Morwood and Van Oosterzee's (2007) (see Kealy et al., 2016: Figure 2). A final variation is the additional southern arm of Sondaar's (1989) "China Giant Rat" route which continues south from Sulawesi to the island of Flores, Nusa Tenggara. A southward migration from Sulawesi is also supported by hypotheses regarding stegodon and the *H. floresiensis* ancestor dispersals (see Dennell et al., 2014), and increased island connectivity throughout the Flores Sea due to lowered sea levels (see Kealy et al., 2016).

Other theoretical models of EMH movement through Wallacea have been less focused on identifying particular routes and more concerned with the drivers behind movement and the various adaptations dispersal requires (Clark, 1991; Chappell, 1993; Bulbeck, 2007; Allen and O'Connell, 2008; O'Connell et al., 2010; Balme, 2013). The 'cultural adaptation' models have incorporated various climate and optimal foraging parameters to produce hypothetical scenarios whereby EMH populations were either 'pushed' or 'pulled' across the seascape due to changing sea levels and resource availability. Unlike Birdsell (1977) and Oppenheimer (2009) who considered lowest sea levels to be the most favourable for dispersal based on a 'shortest distance theory', Chappell (1993), Clark (1991), and O'Connell et al. (2010), all suggest that rising sea levels likely acted as a driver behind dispersal. In addition to this 'push' mechanism behind rising sea levels encouraging population dispersal (Clark, 1991), the 'pull' factor of 'untouched' ecosystems on distant islands has been proposed as an encouragement behind dispersal to new areas based on the principals of optimal foraging (Allen and O'Connell, 2008). Furthermore, periods of higher sea levels have been hypothesised to increase estuarine resource availability, increasing this 'pull' factor during higher sea levels (Bulbeck, 2007; Erlandson and Braje, 2015).

As for the out of Africa studies, genetics has also been used to investigate population movements and dispersal patterns throughout Wallacea and its neighbouring regions. Unfortunately, Wallacea (as well as Southeast Asia and Oceania) has an extremely complex history of multiple, latter dispersal events which, through processes of admixture and replacement have resulted in minimal genetic signatures for the 'initial' populations remaining throughout the region today (Hill et al., 2007; Reich et al., 2011; Hudjashov et al., 2017; Lipson et al., 2018; McColl et al., 2018). Compounding this problem is the lack of aDNA data for Wallacea, a result of the region's extremely poor climactic conditions for DNA preservation (Hofreiter et al., 2015), and skeletal remains more generally (Louys et al., 2017; O'Connor et al., 2017a). Thus, much of the genetic dispersal patterns for initial EMHs in Wallacea are inferred from studies of Sunda and Sahul. The latest studies of interest in this regard are the work by McColl et al. (2018) and Lipson et al. (2018) on Southeast Asian dispersals using aDNA, and Tobler et al. (2017) on the mitochondrial phylogenetics of Australia and New Guinea based on historical samples. These studies suggest initial dispersal from Sunda around 60 ka ago, reaching Sahul by at least 50 ka, followed by permanent genetic isolation of Aboriginal Australians from four later dispersals of Hoabinhians (Southeast Asian hunter-gatherer descendants of the initial EMH dispersal), Neolithic farmers of East and Southeast Asia, and the Austronesian islanders (Tobler et al., 2017; Lipson et al., 2018; McColl et al., 2018).

1.6.2. Models in Practice

The largest scale simulation for modelling human dispersal is the STEPPINGOUT program developed by Mithen and Reed (2002). This model considers the entirety of the earth's surface (with the exception of the Americas) with regards to hominin dispersals between 2 Ma to 500

ka, and includes multiple variables of colonisation rates, palaeoenvironment, topography, and dietary preferences. While the STEPPINGOUT simulation is a fantastic tool for testing global-scale models of hominin dispersal, unfortunately the resolution does not enable similar testing of smaller scale dispersals such as the one from Sunda to Sahul. STEPPINGOUT divides the world (minus the Americas) into seven pentagons; containing 14 hexagons which are further split into a grid of 7406 triangular cells, where each cell equates to ca. 45,000 km² of the earth's surface (Mithen and Reed, 2002). Such a resolution means areas larger than the island of Timor are reduced to a single cell.

A much higher resolution model developed by Field and Lahr (2005), considered an area radius of 60 km to simulate EMH least-cost pathways out of Africa based on only three variables (slope, rivers, and deserts). Field and Lahr (2005) suggest that a higher resolution model with fewer variables offers a better approximation of real-world conditions, with easier comparisons and testing of the results, than the broader STEPPINGOUT model (Mithen and Reed, 2002; Field and Lahr, 2005). Unfortunately, while the Field and Lahr (2005) and later Field et al. (2007) least-cost models provided an excellent framework for testing EMH out of Africa dispersals, their classification of sea water as an impermeable barrier forced the models to halt upon reaching the east coast of Sunda (Field and Lahr, 2005).

Interestingly, there is perhaps a greater proportion of simulated models relative to theoretical ones for over-sea travel than for land. This difference is perhaps due to the more complex interactions of ocean crossing parameters which make their interpretation by eye significantly more difficult. The extensive research surrounding the origin question of the Pacific islanders has also encouraged greater developments of computer simulation in this area. While early models such as Birdsell (1977) and Irwin (1989) were theoretical-only models of sea crossings, both these models have since been tested via computer simulations (Irwin et al., 1990; Davies and Bickler, 2014; Kealy et al., 2018a). The Pacific and Irwin's (1989) "across the wind" model has received much more extensive and varied simulations (see Davies and Bickler, 2014 for a summary), than for the Wallacean region. With the exception of a single study in the Timor Sea (Wild, 1986), there had been no simulation models developed for the crossing from Sunda to Sahul until 2018 (Bird et al., 2018; Kealy et al., 2018a; Norman et al., 2018).

Sea crossing models for Wallacea can be divided into two main varieties; those concerned with drift and sailing, as effected by variables of wind and current (e.g. Wild, 1986; Bird et al., 2018), and those concerned with distance and visibility (e.g. Kealy et al., 2018a; Norman et al., 2018). While these different variables are all interconnected and are jointly incorporated (to varying degrees) in models for the Pacific (Irwin et al., 1990; Davies and Bickler, 2014), there are a number of factors which have limited the potential of their combined application in Wallacea. Firstly, the period of likely colonisation of Wallacea and Sahul is significantly earlier than that of the Pacific (Green et al., 2008; Clarkson et al., 2017). The period of expansion into the Pacific (ca. 3.3 – 2.9 ka; Green et al., 2008; Kirch, 2010) occurs well after the extremes in climate variability and sea level changes of the Pleistocene (Lambeck and Chappell, 2001). With global ocean patterns stabilising in the Holocene to ones we recognise today, and minimal sea level changes effecting bathymetry (Lambeck and Chappell, 2001), the currents and winds of the Pacific ca. 3 ka ago likely bear a close resemblance to those of the present, enabling modellers to employ modern current data (e.g. Callaghan and Fitzpatrick, 2008). Additionally, the significant ocean gaps between the islands of the Pacific cause any bathymetric changes to have a very limited impact on overall currents (Gingele et al., 2002; Kawamura et al., 2006).

In Wallacea, on the other hand, the significant antiquity of the period in question, marked sea level fluctuations during the pre-LGM, tectonic changes, and nearness of islands resulting in significant changes to channel bathymetry, all make the incorporation of wind and current data significantly more difficult. While global models of ocean currents have included Wallacea (e.g. Weaver et al., 2001), the low resolution makes the data for specific inter-island models virtually meaningless. An alternative adopted by a number of modellers uses modern current data (e.g. Wild, 1986; Morwood and van Oosterzee, 2007; Bird et al., 2018, in review; Norman et al., 2018). Irrespective of the unknown effects of bigger, global changes in palaeocurrents that would have contributed to the Wallacean region (e.g. Prell et al., 1980), there are pitfalls in the use of modern currents for models of palaeo-Wallacea.

As the majority of modern current applications have simply reconstructed their palaeogeography for the period under investigation, and then overlain modern current data, a clear problem is seen when a modern current runs into the “wall” of a mega-island’s coast, formed from the merging of two islands as a result of lowered sea levels. While some studies seem content to leave the model at that, the reconstruction of a current simply disappearing as it reaches the coast is highly unlikely. It should be further pointed out that ocean currents are extremely complex, interconnected systems, whereby the narrowing and/or shallowing of some channels and closing of others would precipitate a multitude of (literally) flow-on effects throughout the entire system. Thus, until a high-resolution model of Wallacean palaeo-currents is developed (and simulated), accurate models which incorporate currents into their simulations will remain elusive. This can be seen in the model by Norman et al. (2018), who relied on factors of visibility, island connectivity and population demographics for their agent-based model simulation and only considered their current models in the theoretical sense. A recent study by Bird et al. (in review) has attempted to combine these visibility and current variables to model drift and purposeful voyaging between select points along the northern and southern routes. In order to include current data in their study, Bird et al. (in review) were forced to base their models on a number of assumptions regarding minimal differences between modern current patterns and the palaeo-currents of Wallacea, which so far remain untested.

1.5.3. Proxies for Human Movement

Proxies for human movement come in two distinct forms: substitution proxies whereby the movements of something else (e.g. a different mammal species) is used to hypothesise similar movements by humans, or proxy indicators whereby objects or organisms can be directly linked to human activities and thus indicate movement. An example of the first proxy is the work by Sondaar (1989) who used dispersal patterns of giant rats and stegodons to infer possible paths followed by EMH into Sahul. While his stegodon analysis largely concerned connectivity between just Sulawesi and Flores, his work on giant rat distributions led Sondaar (1989) to propose two routes to Sahul, the China Giant Rat Route, and the Sunda Giant Rat Route. While Sondaar’s (1989) research informs further on the general connectivity of the Wallacean islands, his routes differ little from the overall results of Birdsell’s (1977) model (see Kealy et al., 2016: Figure 2) and their generalised nature provided little or no information concerning the smaller islands of the region (Sondaar, 1989).

Proxy indicators for human movement are objects or organisms which are foreign to the location of interest and identified as owing their arrival to human agencies. A simple proxy

might be the presence of marine shells in a cave site some distance from the coast, indicating that its inhabitants had access to, or traded with peoples who had access to, the sea (e.g. Hawkins et al., 2017). The further identification of the initial arrival of the foreign object and its source location provide archaeologists with a wealth of information regarding early human movement patterns, community connectivity, and technology levels at different points in time. Examples of useful proxies for inter-island movement in Wallacea include rodents, obsidian, pottery, dogs, and cuscuses.

While these movement proxies have received notable attention in the regions of Near Oceania and the wider Pacific (see Storey et al., 2013 for a summary), their applications in Wallacea, particularly for Pleistocene movements, has been very limited. Only a single study has so far found proxy evidence for Pleistocene human movement between Wallacean islands, that of Reepmeyer et al. (2016) who used obsidian sourcing to identify the presence of obsidian from the same (as yet unidentified) source on both Timor and Alor islands. While this study indicates an obsidian network connecting Alor and Timor islands ca. 14 – 12 ka, the lack of local sources on Timor and replacement of known local sources on Alor at this time strongly suggests at least one other island (the source) was involved in this trade network (Reepmeyer et al., 2016).

At around 3.5 ka we see much more extensive evidence for inter-island movements in Wallacea based on obsidian networks between the Talauds, Borneo, and the Philippines (Reepmeyer et al., 2011), the arrival of pottery throughout the region, and dogs and cuscus on Timor (O'Connor, 2015); all indicating a significant increase in inter-island interactions. However, our understanding of the directionalities of even these more recent movements is very poorly constrained. Obsidian sources remain unidentified (Reepmeyer et al., 2011, 2016), mtDNA studies of the early Timor dog have failed to identify a likely (immediate) source population (Greig et al., 2018), and molecular phylogenetics of the Timor cuscus supports the general assumption of a New Guinea origin, however, significant gaps in sampling makes further investigations unavailable at this time (Kealy et al., in review, in prep). Recent aDNA analysis of black rats on the Talaud islands have been used to infer dispersal from Sulawesi rather than the Philippines (Louys et al., 2018). Further archaeological investigations in Talaud, and DNA research of rats throughout the surrounding region are required, however, to confirm this hypothesis and pinpoint the source locality (Louys et al., 2018). Improving our understanding of these inter-island movements, even for more recent times, can greatly assist in model developments and interpretations of model outputs. In particular, the determination of directionality is of great significance as it provides us with solid evidence for successful movement between two points, which can be used for the future calibration and testing of our models of human movement.

1.6. Thesis Structure

This thesis is a “Thesis by Compilation”, whereby the chapters contained within consist of independent research papers that are published, under revision, or in preparation for submission to peer-reviewed academic journals (Chapters 3 – 8), and an encompassing exegesis (Chapters 1, 2 and 9) which has not been submitted elsewhere. Following the ANU guidelines for “Thesis by Compilation” (Appendix A), Chapters 3–8 are styled and formatted in accordance with the requirements of the journal to which they were submitted, and corresponding signed authorship declarations which detail the contribution of each author are included at the beginning of each of these chapters.

Chapter 3 explores the state of the EMH archaeological record for Wallacea and surrounds at the beginning of the project and the effects lowered sea levels have on the seascape of the palaeo-archipelago. Chapter 4 details the fieldwork methodology developed and implemented throughout the course of this research project and the greater Laureate Project to expand the quantity and spatial distribution of known archaeological sites in Wallacea (see also Appendices E – P). Chapter 5 depicts the palaeogeographical reconstructions of the Wallacean archipelago for the broad period of likely human arrival (65 – 45 ka), and calculates the extent of intervisibility between islands for these time slices. Chapter 6 builds on the work in the previous chapters to compile a cost surface dataset to model EMH dispersal routes from Sunda to Sahul using a ‘least-cost pathway’ model. Chapter 7 takes a step away from direct archaeological or model investigations of human movement to explore the relationships and dispersal timings of a possible proxy for human movement, the cuscus (*Phalanger*). Chapter 8 combines the results of Chapter 7 and the known archaeological and modern records for cuscus throughout Wallacea and Sahul to develop a biogeographical model for testing the likelihood and directionality of possible human translocations of cuscus in palaeo-Wallacea.

Chapter 2. Methods

In this chapter key concepts and methodologies which underpin the thesis are discussed. Methods specific to individual research projects are described in the published and unpublished papers, and not covered in this chapter to avoid repetition. Instead, this chapter provides background on the various datasets, assumptions, and calculations upon which the research is based, and specific methods developed.

2.1. Palaeogeographic Reconstruction of Wallacea

This research project relies upon palaeogeographic reconstructions of the Wallacean archipelago and its surrounding regions. The palaeogeographic reconstructions modelled in this thesis are formed from three key datasets, detailed below.

2.1.1. *The General Bathymetric Chart of the Oceans (GEBCO)*

GEBCO is the leading authority on global, publicly-available bathymetric datasets, operating under joint support from the International Hydrographic Organization (IHO) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO (Smith and Sandwell, 1997). The most recent and updated GEBCO grid was released in 2014 and is a combination of sounding data and satellite-based interpolation. Approximately 18% of the GEBCO_14 Grid consists of multibeam and single-beam soundings, with interpolation between these sounding points guided by satellite-derived gravity data (Weatherall et al., 2015). The GEBCO_14 Grid has a relatively coarse resolution of 30 arc seconds per cell, which equates to approximately 950 m pixels for the Wallacean region. While for Wallacea as a whole the GEBCO_14 30 arc second grid is the best currently available, datasets with significantly improved resolution do exist for select regions of the globe.

Bird et al. (2018) used one of these finer resolutions for their reconstructions of the region between Timor and Australia and suggested that the coarser resolution of the GEBCO_14 grid would lead to underestimations of island elevation in palaeogeographic reconstructions. Inaccuracies in the GEBCO_14 dataset also become apparent when compared with ship sounding data collected by Dutch traders at the end of the 19th Century and charted by the hydrography department of the Netherlands (Department of Hydrography, Netherlands, 1902). In particular, narrow channels between islands such as Halmahera and Morotai recover differences in the order of hundreds of metres between the GEBCO_14 and Dutch sounding measurements. This comparison suggests that the scale of the GEBCO_14 dataset is resulting in averaging across these small channels, leading to overestimations of island size and connectivity (Department of Hydrography, Netherlands, 1902).

Nevertheless, the GEBCO_14 Grid dataset is currently the most accurate and detailed bathymetric chart of Wallacea available. As Weatherall et al. (2015) point out, it would require another 900 years of ship surveying efforts to completely map the world's ocean floors. The use of a single bathymetric dataset which seamlessly covers the entire region of interest also ensures consistency in the resolution of all data and resulting analyses. Thus, the GEBCO_14 Grid is used for all the palaeogeographic reconstructions in this thesis.

2.1.2. The Sea-Level Change Model

Throughout this thesis I have used the sea level palaeoclimate model of Lambeck and Chappell (2001) for reconstructions of relative sea level heights. The Lambeck and Chappell (2001) sea-level change model is based on records from the Huon Peninsula in Papua New Guinea. More recent sea-level models than the one by Lambeck and Chappell (2001) are available such as the Siddall et al. (2003) and Grant et al. (2014) Red Sea-based models, and the Waelbroeck et al. (2002) and Böhm et al. (2015) North Atlantic models. However, as the multi-site sea level study by Kopp et al. (2009) illustrates, none of these other records covering the last interglacial are as close to the Wallacean region as the Huon Peninsula record. Additionally, while there are climate records recovered from sites in Wallacea itself, such as the speleothem record of Ayliffe et al. (2013) on Flores, this record only extends back to 31 ka. The Huon Peninsula record however, preserves region-specific relative sea-level data for the last 100,000 years, making it best suited to studies of early human occupation of Wallacea ca. 70 – 45 ka (Lambeck and Chappell, 2001).

2.1.3. An Average Rate of Uplift for Wallacea

The tectonic activity of Wallacea, resulting from the colliding forces of three tectonic plates, has produced notable degrees of uplift throughout the region. Average uplift rates of up to 1.4 m rise every thousand years have been recorded (Roosmawati and Harris, 2009), however, there is considerable variability between uplift rates on the different Wallacean islands. Of the thousands of islands in Wallacea, only eight (Timor, Semau, Rote, Savu, Sumba, Alor, Kisar, and Sulawesi) have had their uplift investigated (Chappell and Veeh, 1978; Jouannic et al., 1988; Pirazzoli et al., 1993; Hantoro et al., 1994; Sumosusastro et al., 1989; Cox, 2009; Roosmawati and Harris, 2009; Major et al., 2013; Nexer et al., 2015).

Uplift is an important variable to consider in palaeogeographic reconstructions as it can have significant impacts on reconstructed island extent. A lack of consideration for uplift can result in significant overestimation on palaeo-island size. Thus, until a greater percentage of Wallacean islands have documented uplift rates, the known rates were used to calculate a regional average. The result of this calculation was an average Wallacean uplift rate of 0.5 m/ka (see Kealy et al., 2017; Chapter 5), which was used for palaeogeographic reconstructions throughout this project. To implement this rate into the palaeogeographic reconstructions, the sea-level values from Lambeck and Chappell's (2001) model were adjusted. Thus, for the period 60 ka ago, Wallacea is assumed to be 30 m lower than its present uplifted height. As Lambeck and Chappell (2001) model a sea level of 59 m below present for 60 ka, when adjusted for this average uplift, the resulting palaeogeographic reconstruction places the 60 ka sea-level at the -29 m bathymetric mark, or 29 m below the present shore-line. See Chapter 4 and Appendix J for further details of the methodology and outcomes.

2.2. Visibility and Intervisibility in an Island Archipelago

Visibility of an object or landmark is effected by six factors: object size, distance from the viewer, atmospheric transparency/obscuring elements, contrast between the object and its background, the position of the sun, and the viewer's visual acuity. When measuring the extent of visibility we rely on distance-to-the-horizon calculations, that are based on Pythagoras' theorem (French, 1982).

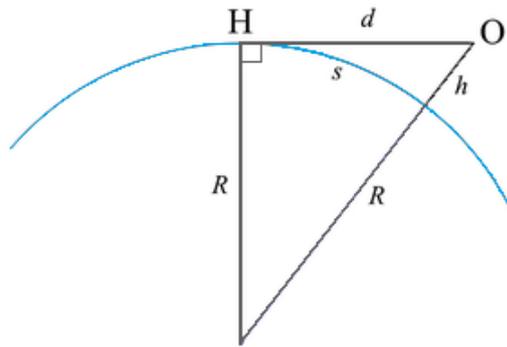


Figure 1: Diagram demonstrating the distance to the geometric horizon calculation using a right-angled triangle and Pythagoras' Theorem. s = surface of the earth, O = observer, H = horizon, d = distance from O to H , h = height of the observer, R = radius of the earth.

The diagram in Figure 1 illustrates how lines drawn between the centre of the earth and an observer's eye located h above the surface of the earth forms a right-angled triangle when linked with the geometric horizon. Thus, the distance to the horizon can be calculated by the following:

$$d^2 = (R + h)^2 - R^2$$

$$d^2 = 2Rh + h^2$$

$$d = \sqrt{2Rh + h^2}$$

However, as $h \ll R$ it is customary to neglect the additional h^2 in the equation (French, 1982). Thus; $d \approx \sqrt{2Rh}$. Taking into account the standard radius of the earth ($R = 6378$ km), this equation can be further refined to $d = 3.57 \times \sqrt{h}$.

When viewing an object (or island), we must also take into account the object height to determine how far it extends above the horizon, thus extending the distance at which it is visible to the observer.

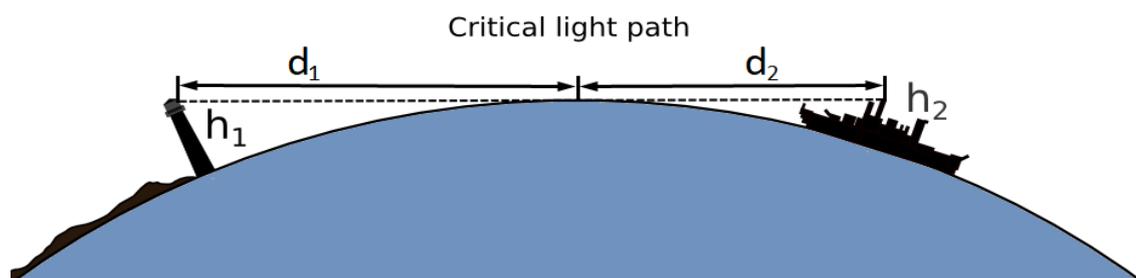


Figure 2: Diagram demonstrating how a point which extends above the surface of the earth, extends visibility beyond the horizon. To calculate this, each distance-to-the-horizon measurement is calculated for the observer and for the object being viewed, and then combined to determine the total visibility.

To do this we must calculate the distance to the horizon for the observer and the emerging object and then add them together to get our total distance of visibility (see Figure 2). Thus, the equation becomes; $d_{12} = (3.57 \times \sqrt{h_1}) + (3.57 \times \sqrt{h_2})$ or $d_{12} = 3.57(\sqrt{h_1} + \sqrt{h_2})$. In this way we can calculate the maximum distance at which an observer can view an object emergent above the horizon. In the case of an island archipelago and a possible early

human disperser, this can be expressed as $h_1 = 0.5$ m (an estimated eye height for an observer seated in a simple watercraft such as a canoe or raft), and $h_2 =$ maximum island height (in metres). This equation notably does not account for atmospheric refraction which bends light following the curvature of the earth, allowing the observer to see slightly beyond the distance calculated here. Calculating the degree of atmospheric refraction is, however, extremely complicated as it is dependent on atmospheric composition and density that are in turn heavily affected by differences in temperature, particularly over bodies of water. Thus, an observer may find refraction extending their vision only marginally and then substantially, respectively, over two consecutive days. Due to the difficulty in calculating the effect of refraction, in addition to the inverse effect of contrast reduction caused by incoherent atmospheric scatter (French, 1982; Bohren and Fraser, 1986), a refraction constant is not included in the visibility equation used here (see Chapter 3 for further details and intervisibility reconstructions).

A variety of phenomena exist that can negatively affect visibility. These include: precipitation, mist, fog, haze, dust, volcanic ash, and smoke. Similarly, a number of phenomena exist that can form above an island and that may indicate its presence to an observer, even if the island itself is not visible above the horizon. These include: cloud formations, smoke, looming (a type of mirage which raises the visibility of objects beyond the horizon), cloud reflection and sea birds (Lewis, 1971; Bednarik, 2001). The unpredictability of these phenomena, however, prohibits any calculation of their effect on measures of visibility distance. Thus, while the visibility calculation expressed above does not take these various additional factors into account, when considering the temporal scale of the project, it acts as a sound average measure of visibility throughout the region.

2.3. Phylogeography and its Application to Questions in Archaeology

Phylogeography aims to determine the origin of the current geographical configuration within and among related species across a landscape based on patterns in the organism's evolutionary history (Emerson et al., 2011; Wiley and Lieberman, 2011). Phylogeographical analyses can be used to determine likely mechanisms driving these patterns of evolution and biogeography through comparisons with models of palaeoenvironment, palaeoclimate, palaeogeology, and archaeology. Of particular relevance to this project is the use of phylogeography to investigate the impacts of early human colonisers on island ecosystems and the possibility of species translocations.

While no marsupial species is known to have ever successfully crossed over Wallace's Line, a number of marsupials are known from the islands of Wallacea, indicating successful dispersal west of Lydekker's Line (Heinsohn, 2011). Some of these marsupials have been recovered in archaeological excavations in Wallacea and their island distribution in the region attributed to human translocations (Heinsohn, 2010; O'Connor, 2015). In light of limited archaeological evidence and direct dates on these, phylogenetics can be used to inform on patterns and timings of events in the evolutionary history of a species, which can in turn inform on the likelihood of natural vs. anthropogenic dispersing agents. Furthermore, determining the existence (or not) of past human translocation activities can implicate directional movement of early humans between islands.

2.3.1. *Morphological, Molecular, and Total Evidence Phylogenetics*

Modern phylogenetic analyses use explicit character matrices and computerised, algorithm-based methods that attempt to reconstruct the evolutionary relationships of organisms according to a specific optimality criterion, such as maximum parsimony or maximum likelihood (Donoghue et al. 1989; Wiley and Lieberman 2011). Although in principle any datatype (e.g., behavioural, biochemical) can be used in phylogenetic analyses, most studies use morphological data, molecular data or a combination of the two. Molecular data is advantageous due to the high number of characters (as every single nucleotide base potentially represents a different character, and genomes can be billions of base pairs long) and high objectivity (molecular characters are easily defined, thus improving reliability of the individual character scores). Where molecular data falters, however, and morphological data becomes particularly important, is in the inclusion of fossil taxa for which molecular data is generally unavailable (Hillis 1987; Wiens 2004). Phylogenies based solely on morphological data, however, are often poorly resolved (Ruedas and Morales, 2005; Kealy and Beck, 2017; Kealy et al., in prep) and incongruent with the molecular phylogenies (Osborne and Christidis, 2002; Ruedas and Morales, 2005; Crosby, 2007; Kealy and Beck, 2017). Thus, most researchers (e.g. Asher et al. 2004; Wiens 2004; Wiens et al. 2010) suggest that both datatypes should be employed for resolving phylogenetic relationships of groups which include modern and fossil taxa. This can be done through separate comparisons between the different analyses with calibrations to the molecular datasets relying on the results of the morphological phylogenies. Or alternatively, it can be achieved by combining molecular and morphological data into a single dataset for what is known as a 'total evidence' phylogenetic analysis (Wiens, 2009; Kealy and Beck, 2017). The inclusion of morphological data with molecular data can provide 'hidden' support for molecular clades and help resolve relationships where the phylogenetic signal in molecular data is weak. Importantly, this method also enables the use of 'tip and node dating' to recover the most accurate estimates of divergence times within the phylogeny. Tip and node dating is where minimum age constraints of selected nodes are specified by a priori fossil calibrations, and maximum age constraints for nodes result from the interaction between the node calibrations and dates on the fossil 'tips' of individual taxa (Kealy and Beck, 2017).

2.3.2. *Biogeography: Natural Dispersal vs Human Translocation*

Beginning with Wallace in the 1860s and '70s, biogeography has remained a fundamental discipline in the study of evolutionary biology and natural history. Evolutionary patterns reconstructed using phylogenetics can be applied to test evolutionary processes and determine the effects of biotic and abiotic factors on the distribution of life on earth (Wiley and Lieberman, 2011). A key question asked by archaeologists and biologists concerns the impact that prehistorical humans had on their environments, in particular on present-day distributions of plants and animals. While such questions remain nearly impossible to test at continental scales, the isolated nature of island ecosystems provides scientists with a unique setting for investigating natural dispersal versus human translocations. As the Wallacean archipelago and islands of New Guinea and the Bismarks represent the earliest region of island occupation by modern humans, they represent a unique opportunity for studies of this topic.

Recent advances in probabilistic modelling of geographical range evolutions has enabled the investigation of biogeographical questions using model-based maximum-likelihood (ML) and Bayesian methodologies (Matzke, 2012). The R statistical program software package;

BioGeoBEARS (Matzke, 2013) enables the analysis of biogeographic patterns including dispersal, vicariance, and founder events between taxa in a phylogenetic tree. The BioGeoBEARS package operates off a dated, phylogenetic tree with corresponding (present-day) geographical distribution data, inputted in R and analysed using Bayesian statistics under a series of evolutionary parameters (see Matzke, 2012). The results of this model and their corresponding statistical likelihood values can be used to interpret the probability of particular 'natural' relocation events, while also highlighting areas where these events are unlikely, suggesting possible anthropogenic intervention. The specifics of BioGeoBEARS implementation in this project are discussed in Chapter 8.

The results of the biogeographic model can then be compared with the palaeogeographic history and archaeological record of the region to develop hypotheses regarding early interactions between island communities and directional movement between islands. Combined with other proxy models for inter-island movement (e.g. Reepmeyer et al., 2016; Louys et al., 2018) these known crossings can be compared with route models for validation purposes and future development planning (see Chapter 9).

Chapter 3. Islands Under the Sea: A Review of Early Modern Human Dispersal Routes and Migration Hypotheses Through Wallacea

Authors: Shimona Kealy, Julien Louys, Sue O'Connor

Publication: Journal of Island and Coastal Archaeology

Current Status: Published

Citation: Kealy, S., Louys, J., & O'Connor, S., 2016. Islands under the sea: a review of early modern human dispersal routes and migration hypotheses through Wallacea. *Journal of Island and Coastal Archaeology*, 11(3), 364-384.

Link to Paper: <https://doi.org/10.1080/15564894.2015.1119218>

Shimona Kealy: developed the research question, reviewed the literature, conducted the analysis, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

Signed:



Shimona Kealy

Julien Louys: assisted with the development of the research question, edited and reviewed the manuscript.

Signed:



Julien Louys

Sue O'Connor: secured funding for the Laureate project, edited and reviewed the manuscript.

Signed:



Sue O'Connor

Chapter 4. A Geological and Spatial Approach to Prehistoric Archaeological Surveys on Small Islands: Case Studies from Maluku Barat Daya, Indonesia

Authors: Shimona Kealy, Lucas Wattimena, Sue O'Connor

Publication: *Kapata Arkeologi*

Current Status: Published

Citation: Kealy, S., Wattimena, L., O'Connor, S., 2018. A geological and spatial approach to prehistoric archaeological surveys on small islands: case studies from Maluku Barat Daya, Indonesia. *Kapata Arkeologi*, 4(1), 1-14.

Link to Paper: <http://dx.doi.org/10.24832/kapata.v13i2.458>

Shimona Kealy: jointly developed the research question, conducted the remote survey, undertook fieldwork, recorded and mapped sites, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

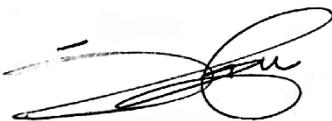
Signed:



Shimona Kealy

Lucas Wattimena: undertook fieldwork, assisted with recording and mapping of sites, translated Indonesian publications for reference, edited and reviewed the manuscript.

Signed:



Lucas Wattimena

Sue O'Connor: secured funding for the Laureate project, jointly developed the research question, undertook fieldwork, edited and reviewed the manuscript.

Signed:



Sue O'Connor

Chapter 5. Reconstructing Palaeogeography and Inter-island Visibility in the Wallacean Archipelago During the Likely Period of Sahul Colonization, 65–45000 Years Ago

Authors: Shimona Kealy, Julien Louys, Sue O'Connor

Publication: Archaeological Prospection

Current Status: Published

Citation: Kealy, S., Louys, J., & O'Connor, S., 2017. Reconstructing palaeogeography and inter-island visibility in the Wallacean Archipelago during the likely period of Sahul colonization, 65 - 45,000 years ago. *Archaeological Prospection*, 24(3), 259-272.

Link to Paper: <https://doi.org/10.1002/arp.1570>

Shimona Kealy: developed the research question, conducted the analysis, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

Signed:



Shimona Kealy

Julien Louys: edited and reviewed the manuscript.

Signed:



Julien Louys

Sue O'Connor: secured funding for the Laureate project, edited and reviewed the manuscript.

Signed:



Sue O'Connor

Chapter 6. Least-cost pathway models indicate northern human dispersal from Sunda to Sahul

Authors: Shimona Kealy, Julien Louys, Sue O'Connor

Publication: Journal of Human Evolution

Current Status: Published

Citation: Kealy, S., Louys, J., O'Connor, S. (2018). Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. *Journal of Human Evolution*, 125, 59-70.

Link to Paper: <https://doi.org/10.1016/j.jhevol.2018.10.003>

Shimona Kealy: developed the research question, developed the variables, conducted the analysis, tested and interpreted the model outcomes, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

Signed:



Shimona Kealy

Julien Louys: assisted with model tests, edited and reviewed the manuscript.

Signed:



Julien Louys

Sue O'Connor: secured funding for the Laureate project, edited and reviewed the manuscript.

Signed:



Sue O'Connor

Chapter 7. Phylogenetic relationships of the cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial *ND2* gene

Authors: Shimona Kealy, Steve C Donnellan, Kieren J Mitchell, Michael Herrera, Ken Aplin, Sue O'Connor, Julien Louys

Publication: Australian Mammalogy

Current Status: In Review

Citation: Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S., Louys, J. (in review). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial *ND2* gene. *Australian Mammalogy*.

Note: The Supplementary Information files referred to in this manuscript can be found in Appendix B of this thesis.

Shimona Kealy: developed the research question, collected surface samples in the field, secured partial funding for DNA sequencing, obtained relevant, pre-existing sequences from the online database GenBank, identified evolutionary-rate models for all partitions, identified dates for model calibration, conducted the phylogenetic analysis, interpreted the model outcomes, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

Signed:



Shimona Kealy

Steve Donnellan: extracted and sequenced the majority of the new MT-ND2 sequences, aligned Mt-ND2 sequences, secured funding for ARC Discovery Project (DP140103650) which funded personnel costs in the laboratory, edited and reviewed the manuscript.

Signed:



Steve C Donnellan

Kieren Mitchell: developed the probe-set for sequence enrichment, co-developed the DNA library, mapped mtDNA sequences, co-wrote the sequencing section of the methods and supplementary information, edited and reviewed the manuscript.

Signed:



Kieren J Mitchell

Michael Herrera: extracted and sequenced the Mt-ND2 Timor sequences, co-developed the DNA library, co-wrote the sequencing section of the methods and supplementary information, edited and reviewed the manuscript.

Signed:



Michael Herrera

Ken Aplin: collected tissue samples for sequencing, advised on species identifications, edited and reviewed the manuscript.

Signed:

Ken Aplin

Sue O'Connor: secured funding for the Laureate project, edited and reviewed the manuscript.

Signed:



Sue O'Connor

Julien Louys: collected surface samples in the field, edited and reviewed the manuscript.

Signed:

A handwritten signature in black ink, consisting of several overlapping loops and a long horizontal stroke, set against a light gray rectangular background.

Julien Louys

1 Phylogenetic relationships of the cuscuses (Diprotodontia: Phalangeridae) of Island
2 Southeast Asia and Melanesia based on the mitochondrial *ND2* gene.

3 Shimona Kealy^{1,2*}, Steve C Donnellan^{3,4}, Kieren J Mitchell^{3,5,6}, Michael Herrera^{3,7}, Ken
4 Aplin^{1,4}, Sue O'Connor^{1,2}, Julien Louys^{1,8}

5 ¹ Archaeology and Natural History, College of Asia and the Pacific, The Australian
6 National University, Acton, 2601, ACT, Australia

7 ² ARC Centre of Excellence for Australian Biodiversity and Heritage, The Australian
8 National University, Canberra, 2601, ACT, Australia

9 ³ School of Biological Sciences, University of Adelaide, Adelaide, SA, 5005, Australia

10 ⁴ South Australian Museum, Adelaide, SA, 5000, Australia

11 ⁵ ARC Centre of Excellence for Australian Biodiversity and Heritage, University of
12 Adelaide, Adelaide, SA, 5005, Australia

13 ⁶ Australian Centre for Ancient DNA, University of Adelaide, Adelaide, SA, 5005,
14 Australia

15 ⁷ Archaeological Studies Program, University of the Philippines, Diliman, Quezon City,
16 1101, Manila, Philippines

17 ⁸ Australian Research Centre for Human Evolution, Environmental Futures Research
18 Institute, Griffith University, Nathan, QLD, 4111, Australia

19 *Corresponding author: shimona.kealy@anu.edu.au

20 **Running Head:** Phylogenetic relationships of the cuscuses

21

22 **ABSTRACT**

23 The species-level systematics of the arboreal marsupial family Phalangeridae,
24 particularly the genus *Phalanger*, are poorly understood. This is partly the result of the
25 taxon's wide distribution across Australia, New Guinea, eastern Indonesia, and
26 surrounding islands. In order to refine the species-level systematics of Phalangeridae,
27 and improve our understanding of their evolution, we generated 36 novel mitochondrial
28 *ND2* DNA sequences from multiple species and sample localities. We combined our
29 new data with previously available sequences and produced the most comprehensive
30 molecular phylogeny for Phalangeridae to date. The results of our analyses strongly
31 support the monophyly of the three phalangerid subfamilies: Trichosurinae,
32 Ailuropinae, Phalangerinae. However, our results also suggest the need to re-examine
33 all specimens currently identified as '*Phalanger orientalis*'. We further suggest the
34 elevation of the Solomon Island *P. orientalis* subspecies to species level - *P. breviceps* -
35 and highlight the need for further work on the different island populations of this
36 species. In addition, samples from the Timor *P. orientalis* population formed a
37 monophyletic clade, consistent with introduction by humans from a single source
38 population. Further research on the east Indonesian population of *P. orientalis* will be
39 required to locate the source population for Timor *P. orientalis* and determine whether
40 it merits subspecies classification.

41 **Keywords:** *Phalanger*, New Guinea, Indonesia, Timor, molecular

42

43 **Introduction**

44 The Phalangeridae are a family of arboreal marsupials found throughout eastern
45 Indonesia, Timor-Leste, New Guinea, Melanesia, and Australia (Fig. 1; Flannery 1994;
46 Crosby 2002). With a total of 29 currently recognised species in six genera, the
47 Phalangeridae is the most diverse of the extant possum families (Helgen and Jackson
48 2015). In addition, they have the broadest longitudinal range of any marsupial group
49 and the type species - *Phalanger orientalis* Pallas, 1766 - has the distinction of being
50 the first Australidelphian marsupial encountered by Europeans (Calaby 1984; Helgen
51 and Jackson 2015). The Phalangeridae is also one of very few marsupial families to owe
52 part of its present distribution to purposeful translocation by humans during the late
53 Holocene (Flannery and White 1991; Heinsohn 2010). Despite their early scientific
54 identification, diversity, profusion, broad geographic distribution, and fascinating
55 history of human interaction, the evolution and systematics of Phalangeridae have
56 remained poorly understood, with a remarkably unstable taxonomy (Ruedas and
57 Morales 2005; Crosby 2007; Helgen and Jackson 2015).

58 While the family level classification of Phalangeridae is well established (e.g. Beck
59 2008; Meredith *et al.* 2009; Mitchell *et al.* 2014), the decades-long debate over
60 subfamily groupings has only recently been clarified by Helgen and Jackson (2015).
61 They divided the Phalangeridae into three subfamilies: Trichosurinae (*Wyulda* and
62 *Trichosurus*), Ailuropinae (*Strigocuscus*, and *Ailurops*), and Phalangerinae (*Phalanger*
63 and *Spilocuscus*), with the Australasian cuscuses (Ailuropinae and Phalangerinae)
64 recognised as a sister group to the Australian scaly- and brush-tailed possums
65 (Trichosurinae; Table 1; Helgen and Jackson 2015). This classification was first
66 suggested by Ruedas and Morales (2005), however, a lack of congruence between
67 morphological and molecular phylogenies, in addition to limited taxonomic coverage in
68 molecular studies (Flannery *et al.* 1987; George 1987; Hamilton and Springer 1999;
69 Kirsch and Wolman 2001; Osborne and Christidis 2002; Crosby and Norris 2003;
70 Ruedas and Morales 2005; Raterman *et al.* 2006; Crosby 2007; Meredith *et al.* 2009;
71 Mitchell *et al.* 2014), resulted in a delay of formal recognition (Helgen and Jackson
72 2015). Helgen and Jackson (2015) also resolved many of the uncertainties surrounding
73 genus level classifications in the family but highlighted the significant lack of resolution
74 in species level taxonomy.

75 Part of the underlying uncertainty of phalanger species stems from their scattered island
76 distribution, with numerous populations and taxa isolated by ocean barriers. Species
77 such as *Phalanger pelengensis*, *P. ornatus*, *P. gymnotis*, and *P. mimicus* have all had
78 subspecies and even species classifications suggested for their various isolated
79 populations. Some of these classifications were later ratified, while others still require
80 further and more extensive taxonomic investigation (Helgen and Jackson 2015). For
81 example, studies on the type species of *Phalanger* - *P. orientalis* - have noted
82 significant morphological variation between populations (Flannery 1994). The
83 widespread range of this species (the second-widest in the Phalangeridae), has
84 encouraged further taxonomic revisions (Menzies and Pernetta 1986; Norris and Musser
85 2001; Groves 2005; Leary *et al.* 2016a; Helgen and Jackson 2015). Moreover, the six
86 subspecies of *P. orientalis* proposed by Menzies and Pernetta in 1986, based on metric
87 and non-metric features of the skull and dentition, have received limited scientific
88 attention. Of the three subspecies that have received further study, two (*P.*
89 *intercastellanus* and *P. mimicus*) were raised to species level while the other (*P. o.*
90 *breviceps*) is the only currently recognised subspecies distinct from *P. o. orientalis*
91 (Flannery 1994, 1995; Helgen and Jackson 2015). There has been no further taxonomic
92 research conducted on the Timor or Bougainville island populations (*P. o. timorensis*
93 and *P. o. kori*). The sixth subspecies proposed by Menzies and Pernetta (1986; *P. o.*
94 *vulpecula*) has been suggested to be part of *P. intercastellanus* (Colgan *et al.* 1993).
95 There have however, been no molecular investigations into the ‘highland’ and ‘lowland’
96 populations of this possible subspecies divided by the 750 m contour line (Menzies and
97 Pernetta 1986).

98 Currently the only available molecular data for the various *P. orientalis*-group
99 populations includes 5 nuclear gene sequences from a single *P. orientalis* sample
100 (Amrine-Madsen *et al.* 2003) collected from an unknown location on New Guinea
101 (Mark Springer *pers. comm.*), a *12S rRNA* mitochondrial gene sequence from a single
102 sample of *P. mimicus* (Springer *et al.* 1995), and a single *ND2* MT-DNA sequence for
103 *P. o. breviceps* (Osborne and Christidis 2002). Furthermore, the *P. orientalis* population
104 from the type locality of Ambon island has yet to be sampled for any molecular
105 analysis, limiting the phylogenetic validation of sequences currently identified as *P.*
106 *orientalis*. A similar lack of data for different populations, subspecies, and possible
107 subspecies also exists for the rest of the Phalangeridae (Helgen and Jackson 2015).

108 In addition to intra-specific uncertainties, many previous phylogenetic studies of the
109 Phalangeridae have limited their sampling to only a single species per genus, and in
110 some cases omitted certain genera entirely (Hamilton and Springer 1999; Kirsch and
111 Wolman 2001; Ruedas and Morales 2005). The most inclusive molecular study
112 produced thus far considered only 12 of the 29 recognised phalangerid species (Osborne
113 and Christidis 2002). Historic and current uncertainties surrounding species and genus
114 level classifications within the Phalangeridae have also led to multiple re-identifications
115 of various vouchered specimens. Not only does this have implications for previous
116 studies using those specimens, but has also led to a lack of reliability of some publicly
117 available molecular sequences, as the corresponding metadata is not always updated on
118 the online database. For example, the '*P. orientalis*' specimen (AMS M18526) from
119 which Springer *et al.* (1995) sequenced the *12S rRNA* gene was later reclassified as *P.*
120 *intercastellanus* following reevaluation of the *P. orientalis* species group by Norris and
121 Musser (2001; see Ruedas and Morales 2005), yet GenBank still continues to list the
122 species ID of the *12S rRNA* sequence (U33496) as *P. orientalis*. This misattribution has
123 resulted in studies such as that of Kavanagh *et al.* (2004), where U33496 was combined
124 with another *P. orientalis* sequence in order to expand the intraspecific genetic
125 coverage, creating a "chimeric" taxon. To further complicate matters, the specimen
126 from which sequence U33496 was derived has since been revised to *P. mimicus*,
127 according to the Online Zoological Collections of Australian Museums Database
128 (OZCAM).

129 Thus, while the family and subfamily classifications of the Phalangeridae may now be
130 well established, there remains significant work to be carried out at the inter- and intra-
131 specific levels within the family, with particular respect to differences between island
132 populations (Menzies and Pernetta 1986; Norris and Musser 2001; Groves 2005; Helgen
133 and Jackson 2015; Leary *et al.* 2016a). To this end, here we present the most
134 taxonomically comprehensive molecular phylogeny of the Phalangeridae, with a focus
135 on the genus *Phalanger*. We rely on just a single gene (*ND2*) without combining any
136 pre-existing data to remove the risk of multi-species combinations from mis-
137 identifications. We also include 36 novel *ND2* sequences, including multiple samples
138 and sample localities of the same species, in order to investigate the validity of current
139 identifications, and to explore relationships between isolated populations and subspecies
140 of cuscus.

141 **Materials and Methods**142 *Species analysed*

143 We included 53 samples from 21 species, of which 18 belong to the family
144 Phalangeridae and three are outgroups (Table 2). Species and samples selected relied on
145 specimens available in the Australian Biological Tissue Collection (ABTC), South
146 Australian Museum (SAM) and previously published *ND2* sequences on the online
147 database GenBank. Selection of samples was conducted to maximizing numbers of
148 species included, and also to include multiple samples per species (where possible) to
149 validate specimen identification (see Table 2 and Fig. 1). For outgroup taxa, one species
150 from each genus within the phalangerid sister family Burramyidae was selected, and
151 one representative species from the Superfamily Petauroidea was selected to incorporate
152 other phalangeriforms (Table 2).

153 *DNA extraction*

154 DNA was extracted from the tissue samples using a DNeasy Blood and Tissue Kit
155 (Qiagen, Hilden, Germany), following manufacturer's instructions, but with the
156 following modifications: the tissue digestion step (buffer ATL plus Proteinase K) was
157 conducted overnight at 55 °C with the addition of dithiothreitol (DTT) (Supplementary
158 Information S1.1).

159 *DNA sequencing*

160 Following extraction using a DNeasy Blood & Tissue kit (QIAGEN), DNA from the
161 Timor *P. orientalis* DNA samples was sheared to an average 200 base pair (bp) sized
162 fragment using a Covaris S220 machine (Woburn, MA). DNA polishing,
163 phosphorylation, adapter ligation and polymerase 'fill-in' reactions were done
164 sequentially to create fully double-stranded adaptor-tagged DNA libraries for each of
165 the samples (Meyer and Kircher 2010). Custom adapters that featured internal barcode
166 sequences were used to allow multiplexing of individuals and downstream de-
167 multiplexing (Supplementary Information S1.1). Capture-based enrichment was
168 performed after the creation of the barcoded libraries via hybridization to biotinylated
169 RNA baits synthesized by Arbor Biosciences (MI, USA). The RNA baits were designed
170 using various marsupial mitochondrial sequences. One round of hybridization was
171 performed following manufacturer's protocol (MYbaits, v2 manual) with indicated

172 modifications (S1.1). The quality of the hybridized-enriched libraries was checked
173 using the TapeStation 2200 (Agilent Technologies, Santa Clara, USA) and sequenced on
174 an Illumina NextSeq at the Australian Genome Research Facility in Adelaide.
175 Sequencing data were demultiplexed according to barcode sequences and filtered based
176 on quality. We assembled a mitochondrial genome sequence using reads from the
177 highest-quality sample (ABTC62229) and then used this assembly as the reference for
178 mapping data from the other samples. Final 75% majority consensus sequences were
179 then generated for each library.

180 DNA from all other tissue samples in the present study was extracted using a Puregene
181 DNA Isolation Kit (Gentra Systems, Minneapolis, Minnesota, USA) and subjected to
182 PCR amplification of the mitochondrial *ND2* gene followed by Sanger sequencing
183 (Supplementary Information S1.2). See Supplementary Information (S1) for a detailed
184 description of DNA sequencing and data processing methods.

185 *Alignment and partitions*

186 The *ND2* sequences were aligned with MUSCLE (Edgar 2004) as implemented in
187 Geneious v11, resulting in a master alignment of 999 bp for a total of 53 taxa. As *ND2*
188 is a protein-coding gene, the sequences were aligned to account for codons and cross
189 referenced in MEGA v.7.0.26 (Kumar *et al.* 2016) with the alignment algorithm
190 MUSCLE for codons. Following alignment codon positions were designated so that an
191 appropriate partitioning scheme and nucleotide substitution model for each partition
192 could be identified with PartitionFinder v2.1.1 (Lanfear *et al.* 2016). For the
193 PartitionFinder analysis, we restricted comparisons to models implemented by
194 MrBayes, with the assumption of linked branch lengths, the “all” search algorithm, and
195 with the Bayesian Information Criterion used for model selection, as suggested by
196 Lanfear *et al.* (2012). The best-fitting partitioning scheme and nucleotide substitution
197 models identified by PartitionFinder were then implemented in the phylogenetic
198 analysis (Supplementary Information S2.1).

199 *Undated phylogenetic analysis*

200 We performed an undated, model-based Bayesian phylogenetic analysis on our *ND2*
201 dataset, implemented in Mr. Bayes v.3.2.6 (Ronquist *et al.* 2012) run on the CIPRES
202 Science Gateway (Miller *et al.* 2010). The analysis comprised four runs of four chains
203 (one cold, three heated) each, sampling trees every 5000 generations, and run for 10

204 million generations. The post-burn-in trees were summarized using 50% majority rule
205 consensus, with mean Bayesian posterior probabilities (BPPs) as support values.

206 *Calibrated phylogenetic analysis*

207 To estimate divergence times within Phalangeridae, three node calibrations
208 (Phalangeroidea, Burramyidae, and Phalangeridae) in addition to a root calibration,
209 were incorporated into the Bayesian analysis in MrBayes (Supplementary Information
210 S2.2). We used a single Independent Gamma Rates (IGR) clock model, implementing a
211 fossilized birth-death tree branching prior that assumed “diversity” sampling (Zhang *et*
212 *al.* 2016) and a sample probability of 0.6 for our modern taxa; this value is slightly less
213 than the proportion of named phalangerid species in our matrices (0.64), but allows for
214 the existence of a few additional undescribed species. As our molecular analysis
215 includes only modern taxa, the fossilization prior was fixed as 0. Node calibrations were
216 specified as uniform distributions with “hard” minimum and maximum bounds
217 reflecting the uncertainty within the fossil record. The Bayesian analysis was then run
218 as for the undated dataset. The resulting consensus tree was then analysed in FigTree
219 v.1.4.3 (FigTree 2016) to extract divergence estimates.

220 **Results**

221 *Undated phylogenetic analysis*

222 Our undated *ND2* analysis of Phalangeridae produced a consensus tree with high
223 support values (BPP > 0.95) for most clades (Fig. 2). The results of our undated analysis
224 show strong support (BPP = 1) for monophyly of the family Phalangeridae and each of
225 the three subfamilies (Table 1; Ailuropinae, Phalangerinae, Trichosurinae). In addition,
226 our results strongly support the position of the subfamily Trichosurinae (*Trichosurus*
227 and *Wyulda*) as the sister lineage to a clade comprising Ailuropinae and Phalangerinae.
228 Within Phalangerinae, both *Spilocuscus* and *Phalanger* were recovered as monophyletic
229 with strong support (BPP = 1).

230 A basal *Phalanger* clade comprising *P. gymnotis* and *P. matanim* receives moderate
231 support from our results (BPP = 0.86). Within the rest of *Phalanger*, our results strongly
232 support a clade comprising the Woodlark Island cuscus (*P. lullulae*), *P. mimicus*, *P.*
233 *intercastellanus*, and three *P. orientalis* samples as the outgroup to the remaining
234 *Phalanger* samples (BPP = 1).

235 The silky cuscus (*P. sericeus*) was recovered as a monophyletic species with strong
236 support (BPP = 1). In contrast, *P. carmelitae* appears to be polyphyletic: Osborne and
237 Christidis's (2002) sample is strongly supported as part of a clade including *P.*
238 *orientalis breviceps* (BPP = 0.95). This *P. o. breviceps* clade also includes a single *P.*
239 *orientalis* sample from New Britain with strong support (BPP = 1).

240 The remaining *Phalanger carmelitae* samples and *P. vestitus* form a strongly supported
241 clade (BPP = 0.99) in which the single *P. vestitus* sample from Chimbu Province forms
242 a subclade with the two new *P. carmelitae* samples. This subclade is in turn sister to a
243 subclade comprising the rest of the *P. vestitus* samples, both with strong support (BPP =
244 1). The remaining *P. orientalis* sequences are recovered as a monophyletic species with
245 strong support (BPP = 1). Almost all the *P. orientalis* samples from West Sepik
246 Province form a strongly supported clade (BPP = 0.99), with the exception of a single
247 West Sepik *P. orientalis* sample that is more closely related to the two *P. orientalis*
248 samples from Madang (although with low support; BPP = 0.23). All the *P. orientalis*
249 samples from Timor are recovered in a single strongly supported clade (BPP = 1)
250 although relationships among the samples within the Timor clade, as well as between
251 the Timor clade and its sister clade (Madang + one West Sepik sample), are poorly
252 resolved.

253 *Calibrated phylogenetic analysis*

254 The calibrated phylogenetic analysis produced a tree with a topology matching that of
255 the undated analysis (Fig. 3). Similarly, strong support (BPP = 1) was also recovered for
256 the monophyly of all phalangerid subfamilies and genera represented in the analysis.

257 By conducting a calibrated phylogenetic analysis on our *ND2* dataset, we produced
258 estimates of the divergence times for the different groups within Phalangeridae (Table
259 3). Our median node age estimates fall within the range estimates for comparable clades
260 from recent *Phalanger*-specific studies (Ruedas and Morales 2005; Raterman *et al.*
261 2006), except for the dates recovered for crown Phalangerinae and *Phalanger* by
262 Ruedas and Morales (2005). Apart from crown Phalangeroidea, all our median
263 divergence estimates are older than the ranges recovered in the phylogeny of Meredith
264 *et al.* (2009). The 95% Highest Posterior Densities (HPD) recovered by our study do,
265 however, overlap with all the comparable estimates shown in Table 3 (including
266 Meredith *et al.* 2009, with the exception of crown Phalangerinae), and the age of deeper

267 clades (i.e. Phalangeroidea and Phalangeridae) are also found to be congruent with those
268 reported by other broader scale studies (i.e. Beck 2008).

269 **Discussion**

270 *Classifications and divergence times within Phalangeridae*

271 We have presented the most comprehensively sampled molecular phylogeny of
272 Phalangeridae to date. Overall the relationships among taxa are congruent with recent
273 molecular phylogenetic studies, both mitochondrial (i.e. Ruedas and Morales, 2005) and
274 nuclear (i.e. Raterman *et al.* 2006; Meredith *et al.* 2009). Accepted families, subfamilies
275 and genera (as per Helgen and Jackson 2015) are all recovered as monophyletic and
276 with strong support.

277 We do not find any support for the inclusion of *Strigocuscus* within Trichosurinae as
278 previously suggested by morphological studies (Flannery *et al.* 1987; Crosby 2002).
279 *Strigocuscus celebensis* appears to be sister taxon to *Ailurops ursinus* within the
280 subfamily Ailuropinae. However, the current lack of mitochondrial sequences for *St.*
281 *sangirensis* (the only other species recognised in the genus; Helgen and Jackson 2015)
282 and *A. melanotis* and *A. furvus* means the relationships of the other species within this
283 subfamily remain uncertain. The lack of additional sequences for Ailuropinae also
284 limits our interpretations of divergence times for this subfamily.

285 Our time-calibrated phylogeny suggests that dispersal of the common ancestor of
286 Ailuropinae and Phalangerinae (the cuscuses) out of Australia occurred during the late
287 Oligocene to early Miocene, corresponding to the emergence of the New Guinea Bird's
288 Head, in turn resulting from the collision of the Australian and Pacific plates (Hall
289 2009). The Early Miocene collision of the Sula Spur and the North Sulawesi volcanic
290 arc, which resulted in mountainous regions over 1000 m on palaeo-Sulawesi for the first
291 time (Nugraha and Hall 2018), also supports our estimate for an early Miocene dispersal
292 of the ancestral Ailuropinae. The diversification events within the Phalangerinae,
293 following its divergence from Ailuropinae, likely reflect the various sea level
294 fluctuations and geological upheavals experienced by the New Guinea and east
295 Indonesian region during the Miocene (Hall 2009).

296

297

298 *On classifications within Phalanger*

299 Our study focuses largely on relationships within the genus *Phalanger*, particularly the
300 identifications of different '*P. orientalis*' specimens. In agreement with current
301 classifications, we recover *P. gymnotis*, *P. matanim*, and *P. sericeus* as monophyletic in
302 our MT-ND2 phylogeny with good support. However, no other *Phalanger* species
303 included in our study is recovered as monophyletic. *P. orientalis* in particular is
304 recovered as extremely polyphyletic based on current identifications. Our phylogeny
305 recovers three distinct 'orientalis-morphotype' clades where specimens identified as *P.*
306 *orientalis* are recovered; the *P. mimicus*-*P. intercastellanus* clade, *P. o. breviceps* clade,
307 and the West Sepik-Madang-Timor clade. We recover the Timor cuscus population as
308 monophyletic, supporting all previous studies which suggest it constitutes a single
309 species belonging to the *P. orientalis* species group (Menziés and Pernetta 1986; Helgen
310 and Jackson 2015). For the purposes of clarification, we assume that the *P. orientalis*
311 specimens from Timor are 'true' members of the *P. orientalis* species, and only the
312 New Guinea *P. orientalis* samples which are recovered in monophyly with the Timor
313 clade belong in *P. orientalis*. Confidence in this classification however, will require the
314 future sequencing and comparison with cuscus samples taken from the *P. orientalis* type
315 locality of Ambon island. All *P. orientalis* samples which are not recovered as
316 monophyletic to the West Sepik-Madang-Timor clade are consequently considered here
317 as misidentifications of different species.

318 The New Britain '*P. orientalis*' sample forms a clade with the *P. o. breviceps* samples,
319 strongly suggesting that this is a misidentified *P. o. breviceps* sample (Fig. 1 and 2). The
320 re-identification of the New Britain '*P. orientalis*' sample as *P. o. breviceps* is
321 supported by Thomas' (1888, 1895) original classification of the New Britain
322 populations with the Solomon Island populations, and more recently by Helgen and
323 Jackson's (2015) proposed species distributions. The location of the *P. o. breviceps*
324 clade in our phylogeny, polyphyletic with respect to the 'true' *P. orientalis* clade,
325 further supports this re-identification (Fig. 2). Furthermore, as the *P. o. breviceps* clade
326 is not closely related to the *P. orientalis* clade, we suggest that this subspecies be raised
327 to a full species: *P. breviceps*. This revision supports Thomas's (1895) taxonomy,
328 although it is contrary to Menziés and Pernetta (1986) and current accepted
329 classifications (Helgen and Jackson 2015).

330 We recovered the pre-existing *P. carmelitae* sequence from the study by Osborne and
331 Christidis (2002) as a basal member of the *P. breviceps* clade and polyphyletic with
332 respect to our other *P. carmelitae* samples (Fig. 2). The provenance of the Osborne and
333 Christidis (2002) sample, in the northeastern Oro Province (Fig. 1 and 2), suggests it
334 likely represents a descendent of the ‘mainland’ (New Guinean) source for the island *P.*
335 *breviceps* populations. The early divergence estimates of this Oro sample+*P. breviceps*
336 clade further supports the elevation to species rank of *P. breviceps* (Fig. 3). Additional
337 research into the various known and probable *P. breviceps* populations throughout the
338 Bismarck Archipelago and the Solomon Islands will be required to further clarify the
339 evolutionary history of this clade. In particular, the archaeological record of ‘*P.*
340 *orientalis*’ in the region suggests human introductions of *P. breviceps* (or its ancestor)
341 to New Ireland as early as ca. 22.5-23.6 ka ago (Leavesley *et al.* 2002; Leavesley and
342 Chappell 2004; Summerhayes 2007) and Buka Island (Solomons) at ca. 8.5-9 ka
343 (Wickler 2001; Helgen and Jackson 2015). Improved identifications of the
344 archaeological material, possibly with the use of ancient DNA, along with direct dating
345 of the specimens would also play an important role in improving our understanding of
346 this species-group and its fascinating dispersal history.

347 While samples such as the New Britain ‘*P. orientalis*’ sequence in this study can be
348 confidently revised to *P. breviceps*, other specimens, such as those placed with the *P.*
349 *lullulae*+*P. mimicus*+*P. intercastellanus* group, cannot be revised any further than ‘not-
350 *P. orientalis*’ due to the lack of monophyly of the species recovered within this clade.
351 When Norris and Musser (2001) first identified *P. mimicus* as a species separate from *P.*
352 *orientalis* and *P. intercastellanus*, they also identified distinct geographic ranges for
353 each species. When these geographic ranges are compared with our sample locations
354 (Fig. 1 and 2; Norris and Musser, 2001: Fig. 1) the ‘*P. orientalis*’ sequence from
355 Morobe Province falls within the *P. intercastellanus* geographic range, while all the
356 closely related Southern Highland Province sequences (including the ‘*P.*
357 *intercastellanus*’ sequence) are actually within the range of *P. mimicus*. Further analysis
358 of the samples used in this study, in addition to those reviewed by Norris and Musser
359 (2001) is required to resolve the relationships within this clade and identifications of
360 these samples.

361 *Phalanger vestitus* is currently known from four separate localities on New Guinea, and
362 it has been proposed that the taxonomy of these separate populations be investigated

363 (Leary *et al.*, 2016b). In this study however, we only included sequences from the
364 central-east New Guinea population. These *P. vestitus* sequences are recovered in a
365 clade with *P. carmelitae* (with the exception of the previously published sequence from
366 Oro Province), a relationship supported by the electrophoretic study of Colgan *et al.*
367 (1993). Our *P. vestitus*+*P. carmelitae* clade can be further split into two sister clades: a
368 '*P. carmelitae*' clade and a *P. vestitus* clade (Fig. 2). A single '*P. vestitus*' sample from
369 Chimbu Province is recovered with the *P. carmelitae* sequences, and we tentatively
370 suggest that this sample is a misidentified *P. carmelitae* based on the BPP support for
371 its position in the phylogeny and the Pliocene divergence estimate (Fig. 3). However,
372 thorough examination of the other three *P. vestitus* populations in addition to *P.*
373 *carmelitae* samples from eastern Papua New Guinea will be required to further
374 understand the relationships between, and classifications of these two species.

375 *The origin of Phalanger orientalis on Timor*

376 We recover the *P. orientalis* sequences from Timor as a single monophyletic group,
377 supporting biological and archaeological conclusions that only a single species inhabits
378 the island (Fig. 2; Glover 1986; Flannery 1994; Heinsohn 2001, 2005; O'Connor 2015).
379 Our analysis also supports the hypothesis that this population shares a close relationship
380 with the modern New Guinean *P. orientalis*. While our analysis suggests a close
381 relationship to *P. orientalis* populations in western Papua New Guinea (central New
382 Guinea island), it should be noted that populations from Indonesian Papua further to the
383 west (and closer to Timor) were not available. Menzies and Pernetta (1986) proposed a
384 separate subspecies for Timor; *P. o. timorensis*, which is somewhat supported by our
385 phylogeny. Further genetic research, however, on both the Ambon type population and
386 cuscus populations from Indonesian Papua, will be required to determine if the Timor
387 clade merits recognition as a distinct subspecies.

388 Our estimates for the timing of the divergence of the Timor *P. orientalis* from its sister
389 clade range from approximately 820 to 570 thousand years ago (Table 4, Fig. 3).

390 Whether or not this divergence happened on Timor is not revealed by our analyses.

391 While divergence dates for other taxa recovered from our analysis agree with previous
392 molecular dating studies (Table 4), a 0.82 Ma date for the establishment of a Timor
393 cuscus population runs contrary to both the fossil and archaeological records, the latter
394 of which suggest an introduction date of approximately 3 ka (Glover 1986; O'Connor
395 2015).

396 Two scenarios could account for this disparity if our estimated divergence times are
397 correct. Firstly, this could indicate natural dispersal into Timor and subsequent omission
398 from all paleontological and archaeological sites until approximately 3,000 years ago.
399 Such a scenario would be consistent with the fact that the earliest records for humans in
400 the region are significantly younger than our divergence estimate (Summerhayes *et al.*
401 2010; Clarkson *et al.* 2017; Hawkins *et al.* 2017) and may be accounted for
402 archaeologically by a change of hunting technologies 3,000 years ago. However, we
403 consider this scenario much less likely than the alternative, principally because the
404 extensive archaeological records and the more moderate paleontological records have
405 failed to recover a single phalangerid fossil despite thousands of similarly-sized, and
406 likely ecologically convergent, giant rodent fossils (Aplin and Helgen 2010; Louys *et al.*
407 2017). The alternative scenario would require people to have translocated *P.*
408 *orientalis* from an as yet unsampled source population whose inclusion in the
409 phylogenetic analysis would push the divergence date of the Timor population closer to
410 the present. As with the classification difficulties discussed above, further work to
411 identify potential source populations and relationships to populations of *P. orientalis* on
412 neighbouring islands (i.e. western New Guinea, Ambon, Seram, Babar, Wetar;
413 assuming biological surveys for other Lesser Sunda and Moluccan island are accurate)
414 will require additional geographical sampling. It should also be noted that we may have
415 overestimated recent divergence times (e.g. the divergences among Timor *P. orientalis*
416 individuals) due to the time-dependency of rates previously reported for mitochondrial
417 data (see Ho *et al.* 2005), as our study was calibrated by constraining the age of nodes
418 deep in the phylogenetic tree. Thus, while we can be confident in our species (and
419 higher level) divergence estimates, there is the distinct possibility that our divergence
420 estimates within the Timor *P. orientalis* clade are significantly older than the ‘true’
421 dates. Further research into the palaeontological and archaeological record of these
422 species and the incorporation of this data into future phylogenetic analysis will improve
423 our understanding of the evolution of these taxa.

424 **Conclusion**

425 Despite being amongst the first Australidelphian marsupials ever encountered by
426 Europeans, the majority of known cuscus species in the Phalangeridae have received a
427 surprising lack of attention in modern genetic research. The most comprehensive
428 molecular phylogeny, until our study, included only 12 of the 29 recognized

429 Phalangeridae species. Furthermore, despite being the type species for the genus,
430 *Phalanger orientalis* has received minimal genetic attention and suffers from extensive
431 classification and specimen identification problems. Here we presented a
432 comprehensive *ND2* gene sequence molecular phylogeny for the Phalangeridae, with a
433 particular focus on identifications of *P. orientalis* samples and the inclusion (for the first
434 time) of the *P. orientalis* populations on Timor. Our study indicates the necessity of
435 future research to refine and clarify the identifications and classification of *P. orientalis*
436 and emphasises the caution with which researchers should approach '*P. orientalis*'
437 specimens and sequences for inclusion in future studies of phalangerids.

438 Our phylogenetic results for the Phalangeridae, and estimated divergence dates, are
439 congruent with previous molecular analyses and palaeogeography. *Phalanger*
440 *orientalis*, *P. mimicus*, *P. intercastellanus*, *P. vestitus*, and *P. carmelitae* are identified
441 as species requiring further investigation, both for sampling populations in the field but
442 also a greater investigation of specimens held in museum collections. *P. orientalis* in
443 particular requires careful re-analysis of specimens before their inclusion in studies of
444 the Phalangeridae. Our study revealed that the Solomon Island cuscus, previously
445 considered a subspecies of *P. orientalis*, forms a polyphyletic clade with respect to other
446 *P. orientalis* samples and should be considered a distinct species, *P. breviceps*, with an
447 ancestral source population likely located in New Guinea's Oro Province. Additionally,
448 support is recovered for the Menzies and Pernetta (1986) classification of a distinct
449 subspecies - *P. orientalis timorensis* - for the Timor cuscus, however further research is
450 required to ratify this classification. Based on fossil and archaeological evidence we
451 propose that introduction of *P. orientalis* to Timor, almost certainly by humans,
452 occurred from an original source population of *P. orientalis* on the island of New
453 Guinea. Future sampling of *P. orientalis* populations in Indonesian Papua (west New
454 Guinea) and the Ambon type population will be required to clarify the immediate source
455 population of the Timor population and its subspecies status. Our study highlights the
456 need to thoroughly evaluate the Phalangeridae across its various geographic ranges on
457 New Guinea and throughout the islands of Melanesia and Indonesia. This will have
458 significant impacts not only for our understanding of cuscus evolution and
459 biogeography but also for the conservation of these species, as further studies will likely
460 reveal cryptic species/subspecies and reduced, or more isolated geographic ranges than
461 currently recorded.

462 **Acknowledgments**

463 This research was partially funded by an Australian Archaeology Association Student
464 Research Grant awarded to S.K., an ARC Laureate awarded to S.O. (FL120100156), an
465 ARC Discovery grant (DP140103650) awarded to SCD, KA and PP, PhD student
466 research funds provided to S.K. by the School of Culture, History and Language,
467 College of Asia and the Pacific, ANU, and Archaeology and Natural History at ANU
468 student research funding awarded to S.K. We thank Dr Alejandro Velasco Castrillon for
469 performing the Sanger sequencing and everyone at the Australian Centre for Ancient
470 DNA (University of Adelaide) for their assistance. The authors thank the two
471 anonymous reviewers whose comments improved our manuscript.

472 **Supplementary Information**

473 Additional information on methods of DNA extraction and sequencing (S1) and
474 sequence partitions, nucleotide substitution models, and node calibrations (S2) are in the
475 supplementary document. For Nexus files of the undated and calibrated matrixes see the
476 supplementary nexus file. All new *ND2* sequences are available on GenBank under the
477 accession numbers listed above; see <https://www.ncbi.nlm.nih.gov/genbank/>.

478 **Conflicts of Interest**

479 The authors declare there are no known conflicts of interest.

480 **References**

- 481 Amrine-Madsen, H., Scally, M., Westerman, M., Stanhope, M. J., Krajewski, C., and
482 Springer, M. S. (2003). Nuclear gene sequences provide evidence for the monophyly of
483 australidelphian marsupials. *Molecular Phylogenetics and Evolution* **28**(2), 186-196.
- 484 Aplin, K. P., and Helgen, K. M. (2010). Quaternary murid rodents of Timor Part I: new
485 material of *Coryphomys buehleri* Schaub, 1937, and description of a second species of
486 the genus. *Bulletin of the American Museum of Natural History* **341**, 1-80.
- 487 Beck, R. M. D. (2008). A dated phylogeny of marsupials using a molecular supermatrix
488 and multiple fossil constraints. *Journal of Mammalogy* **89**(1), 175-89.

- 489 Burk, A., and Springer, M. S. (2000). Intergeneric relationships among Macropodoidea
 490 (Metatheria: Diprotodontia) and the chronicle of kangaroo evolution. *Journal of*
 491 *Mammalian Evolution* **7**(4), 213-237.
- 492 Calaby, J. H. (1984). Foreword. In 'Possums and Gliders'. (Eds A. P. Smith and I. D.
 493 Hume.) Pp. iii–iv. (Surrey Beatty & Sons with Australian Mammal Society: Sydney)
- 494 Clarkson, C., Jacobs, Z., Marwick, B., Fullagar, R., Wallis, L., Smith, M., Roberts, R.
 495 G., Hayes, E., Lowe, K., Carah, X., Florin, S. A., McNeil, J., Cox, D., Arnold, L. J.,
 496 Hua, Q., Huntley, J., Brand, H. E. A., Manne, T., Fairbairn, A., Shulmeister, J., Lyle, L.,
 497 Salinas, M., Page, M., Connell, K., Park, G., Norman, K., Murphy, T., and Pardoe, C.
 498 (2017). Human occupation of northern Australia by 65,000 years ago. *Nature* **547**, 306-
 499 310.
- 500 Colgan, D. J., Flannery, T. F., Trimble, J., and Aplin, K. P. 1993. Electrophoretic and
 501 Morphological Analysis of the Systematics of the Phalanger-Orientalis (Marsupialia)
 502 Species Complex in Papua-New-Guinea and the Solomon-Islands. *Australian Journal*
 503 *of Zoology*, **41**(4), 355-378.
- 504 Crosby, K. (2002). Studies in the diversity and evolution of phalangeroid possums
 505 (Marsupalia; Phalangerida; Phalangeroidea). PhD Thesis, University of New South
 506 Wales, Sydney.
- 507 Crosby, K. (2007). Rediagnosis of the fossil species assigned to *Strigocuscus*
 508 (Marsupialia, Phalangeridae), with description of a new genus and three new species.
 509 *Alcheringa: An Australasian Journal of Palaeontology* **31**(1), 33-58.
- 510 Crosby, K., and Norris, C. (2003). Periotic Morphology in the Trichosurin Possums
 511 *Strigocuscus celebensis* and *Wyulda squamicaudata* (Diprotodontia, Phalangeridae) and
 512 a Revised Diagnosis of the Tribe Trichosurini. *American Museum Novitates* **3414**, 1-14.
- 513 Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and
 514 high throughput. *Nucleic Acids Research* **32**(5), 1792–1797.
- 515 FigTree. (2016). FigTree v1.4.3. Available at <http://tree.bio.ed.ac.uk/software/figtree/>
 516 [accessed January 2018].
- 517 Flannery, T. (1994). 'Possums of the World: A Monograph of the Phalangeroidea.'
 518 (Australian Museum/Geo Productions: Sydney.)

- 519 Flannery, T. F., and White, J. P. (1991). Animal translocation. *National Geographic*
 520 *Research and Exploration* **7**(1), 96-113.
- 521 Flannery, T., Archer, M., and Maynes, G. (1987). The phylogenetic relationships of
 522 living phalangerids (Phalangerioidea: Marsupialia) with a suggested new taxonomy. In
 523 'Possums and Opossums: Studies in evolution, V.II'. (Ed. M. Archer.) Pp. 477-506.
 524 (Surrey Beatty & Sons and the Royal Zoological Society of New South Wales: Sydney.)
- 525 George, G. G. (1987). Characterisation of the living species of cuscus (Marsupialia:
 526 Phalangeridae). In 'Possums and Opossums: Studies in evolution, V.II'. (Ed. M.
 527 Archer.) Pp. 507-526. (Surrey Beatty & Sons and the Royal Zoological Society of New
 528 South Wales: Sydney.)
- 529 Glover, I. (1986). 'Archaeology in Eastern Timor, 1966–67.' *Terra Australis* **11**.
 530 (Australian National University: Canberra.)
- 531 Groves, C. P. (2005). Order Diprotodontia. In 'Mammal Species of the World: A
 532 Taxonomic and Geographic Reference. 3rd Edition'. (Eds. D. E. Wilson and D. M.
 533 Reeder) Pp. 43-70. (The Johns Hopkins University Press: Baltimore, MD.)
- 534 Hamilton, A. T., and Springer, M. S. (1999). DNA sequence evidence for placement of
 535 the ground cuscus, *Phalanger gymnotis*, in the tribe Phalangerini (Marsupialia:
 536 Phalangeridae). *Journal of Mammalian Evolution* **6**, 1-17.
- 537 Hawkins, S., O'Connor, S., Maloney, T. R., Litster, M., Kealy, S., Fenner, J. N., Aplin,
 538 K., Boulanger, C., Brockwell, S., Willan, R., Piotto, E., and Louys, J. (2017). Oldest
 539 human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum
 540 foraging responses to late Pleistocene environments. *Quaternary Science Reviews* **171**,
 541 58-72.
- 542 Heinsohn, T. E. (2001). Human influences on vertebrate zoogeography: animal
 543 translocation and biological invasions across and to the east of Wallace's Line. In
 544 'Faunal and Floral Migrations and Evolution in SE Asia-Australasia'. (Eds I. Metcalfe,
 545 J. M. B. Smith, M. Morwood and I. Davidson.) Pp. 153-170. (A.A. Balkema: Lisse.)
- 546 Heinsohn, T. E. (2005). Den sites and habitats utilised by the northern common cuscus
 547 *Phalanger orientalis* (Marsupialia: Phalangeridae) in East Timor. *Australian*
 548 *Mammalogy* **27**, 99-101.

- 549 Helgen, K. M., and Jackson, S. M. (2015). Family Phalangeridae (Cuscuses, Brush-
550 tailed Possums and Scaly-tailed Possum). In 'Handbook of The Mammals of the World,
551 Vol. 5: Monotremes and Marsupials'. (Eds D. E. Wilson and R. A. Mittermeier.) Pp.
552 456-497. (Lynx Edicions: Barcelona.)
- 553 Ho, S.Y., Phillips, M.J., Cooper, A., and Drummond, A.J. (2005). Time dependency of
554 molecular rate estimates and systematic overestimation of recent divergence times.
555 *Molecular Biology and Evolution* **22**(7), 1561-1568.
- 556 Kavanagh, J. R., Burk-Herrick, A., Westerman, M., and Springer, M. S. (2004).
557 Relationships among families of Diprotodontia (Marsupialia) and the phylogenetic
558 position of the autapomorphic honey possum (*Tarsipes rostratus*). *Journal of*
559 *Mammalian Evolution* **11**(3-4), 207-22.
- 560 Kirsch, J. A. W., and Wolman, M. A. (2001). Molecular relationships of the bear
561 cuscus, *Ailurops ursinus* (Marsupialia: Phalangeridae). *Australian Mammalogy* **23**, 23-
562 30.
- 563 Kumar, S., Stecher, G., and Tamura, K. (2016). MEGA7: molecular evolutionary
564 genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*
565 **33**(7), 1870-1874.
- 566 Lanfear, R., Calcott, B., Ho, S. Y., and Guindon, S. (2012). PartitionFinder: combined
567 selection of partitioning schemes and substitution models for phylogenetic analyses.
568 *Molecular Biology and Evolution* **29**(6), 1695-1701.
- 569 Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2016).
570 PartitionFinder 2: new methods for selecting partitioned models of evolution for
571 molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*
572 **34**(3), 772-773.
- 573 Leary, T., Singadan, R., Menzies, J., Helgen, K., Wright, D., Allison, A., Hamilton, S.,
574 Salas, L., and Dickman, C. (2016a). *Phalanger orientalis*. The IUCN Red List of
575 Threatened Species 2016:e.T16847A21951519.
- 576 Leary, T., Singadan, R., Menzies, J., Helgen, K., Wright, D., Allison, A., Aplin, K.,
577 Salas, L., and Dickman, C. (2016b). *Phalanger vestitus*. The IUCN Red List of
578 Threatened Species 2016:e.T16850A21950723.

- 579 Louys, J., Kealy, S., O'Connor, S., Price, G. J., Hawkins, S., Aplin, K., Rizal, Y., Zaim,
580 J., Tanudirjo, D. A., Santoso, W. D., and Hidayah, A. R. (2017). Differential
581 preservation of vertebrates in Southeast Asian caves. *International Journal of*
582 *Speleology* **46**(3), 379-408.
- 583 Menzies, J. I., and Pernetta, J. C. (1986). A taxonomic revision of cuscuses allied to
584 *Phalanger orientalis* (Marsupialia: Phalangeridae). *Journal of Zoology* **1**(3), 551-618.
- 585 Meredith, R. W., Westerman, M., and Springer, M. S. (2009). A phylogeny of
586 Diprotodontia (Marsupialia) based on sequences for five nuclear genes. *Molecular*
587 *Phylogenetics and Evolution* **51**, 554-571.
- 588 Meyer, M., and Kircher, M. (2010). Illumina sequencing library preparation for highly
589 multiplexed target capture and sequencing. *Cold Spring Harbor Protocols* **2010**(6), 1-
590 10.
- 591 Miller, M. A., Pfeiffer, W., and Schwartz, T. (2010). Creating the CIPRES Science
592 Gateway for inference of large phylogenetic trees. In 'Proceedings of the Gateway
593 Computing Environments Workshop (GCE), New Orleans, LA, 14-14 Nov. 2010', Pp.
594 1-8.
- 595 Mitchell, K. J., Pratt, R. C., Watson, L. N., Gibb, G. C., Llamas, B., Kasper, M., Edson,
596 J., Hopwood, B., Male, D., Armstrong, K. N., Meyer, M., Hofreiter, M., Austin, J.,
597 Donnellan, S. C., Lee, M. S. Y., Phillips, M. J., and Cooper, A. (2014). Molecular
598 phylogeny, biogeography, and habitat preference evolution of marsupials. *Molecular*
599 *Biology and Evolution* **31**(9), 2322-2330.
- 600 Munemasa, M., Nikaido, M., Donnellan, S., Austin, C. C., Okada, N., and Hasegawa,
601 M. (2006). Phylogenetic analysis of diprotodontian marsupials based on complete
602 mitochondrial genomes. *Genes and Genetic Systems* **81**(3), 181-191.
- 603 Nilsson, M. A., Arnason, U., Spencer, P. B., and Janke, A. (2004). Marsupial
604 relationships and a timeline for marsupial radiation in South Gondwana. *Gene* **340**(2),
605 189-96.
- 606 Norris, C. A., and Musser, G. G. (2001). Systematic revision within *Phalanger*
607 *orientalis* complex (Diprotodontia, Phalangeridae): a third species of lowland gray
608 cuscus from New Guinea and Australia. *American Museum Novitates* **3356**, 1-20.

- 609 O'Connor, S. (2015). Rethinking the Neolithic in Island Southeast Asia, with particular
610 reference to the archaeology of Timor-Leste and Sulawesi. *Archipel* **90**, 15-47.
- 611 Osborne, M. J., and Christidis, L. (2002). Molecular relationships of the cuscuses,
612 brushtail and scaly-tailed possums (Phalangerinae). *Australian Journal of Zoology* **50**,
613 135-149.
- 614 Pestell, A. J., Cooper, S. J., Saint, K., and Petit, S. (2007). Genetic structure of the
615 western pygmy possum, *Cercartetus concinnus* Gould (Marsupialia: Burramyidae)
616 based on mitochondrial DNA. *Australian Mammalogy* **29**(2), 191-200.
- 617 Phillips, M. J., Lin, Y. H., Harrison, G., and Penny, D. (2001). Mitochondrial genomes
618 of a bandicoot and a brushtail possum confirm the monophyly of australidelphian
619 marsupials. *Proceedings of the Royal Society of London B: Biological Sciences*
620 **268**(1475), 1533-1538.
- 621 Raterman, D., Meredith, R. W., Ruedas, L. A., and Springer, M. S. (2006). Phylogenetic
622 relationships of the cuscuses and brushtail possums (Marsupialia: Phalangeridae) using
623 the nuclear gene BRCA1. *Australian Journal of Zoology* **54**, 353-361.
- 624 Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S.,
625 Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). MrBayes 3.2:
626 efficient Bayesian phylogenetic inference and model choice across a large model space.
627 *Systematic Biology* **61**(3), 539-542.
- 628 Ruedas, L. A., and Morales, J. C. (2005). Evolutionary relationships among genera of
629 Phalangeridae (Metatheria: Diprotodontia) inferred from mitochondrial DNA. *Journal*
630 *of Mammalogy* **86**, 353-365.
- 631 Summerhayes, G. R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A., and
632 Fullagar, R. (2010). Human adaptation and plant use in highland New Guinea 49,000 to
633 44,000 years ago. *Science* **330**(6000), 78-81.
- 634 Thomas, O. (1888). 'Catalogue of the Marsupialia and Monotremata in the collection of
635 the British Museum.' (British Museum (Natural History):London.)
- 636 Thomas, O. (1895). On some mammals collected by Mr. Albert Meek on Fergusson
637 Island, D'Entrecasteaux Group. *Novitates Zoologicae* **2**, 163-165.

- 638 Zhang, C., Stadler, T., Klopstein, S., Heath, T. A., and Ronquist, F. (2016). Total-
639 evidence dating under the fossilized birth–death process. *Systematic Biology* **65**(2),
640 228–249.

641 **Tables**

642 Table 1: Currently accepted classifications of the Phalangeridae as per Helgen and
643 Jackson (2015).

Order Diprotodontia Owen, 1866

Family Phalangeridae Thomas, 1888

Subfamily Trichosurinae Flynn, 1911

Trichosurus Lesson, 1828

Wyulda Alexander, 1918

Subfamily Ailuropinae Flannery, Archer and Maynes,
1987

Ailurops Wagler, 1830

Strigocuscus Gray, 1862

Subfamily Phalangerinae Thomas, 1888

Phalanger Storr, 1780

Spilocuscus Gray, 1862

644

645

646 Table 2: Taxa included in the study with relevant gene sequences identified and GenBank accession numbers listed in corresponding order.

Species	Common Name	Collection Locality	Location Code ^a	Museum Voucher ^b	Tissue Sample ^c	GenBank accession	Refs ^d
<i>*Pseudocheirus peregrinus</i>	Common Ringtail Possum	Australia		-		AJ639870	1
<i>*Cerartetus nanus</i>	Eastern Pygmy Possum	Australia				AY135178	2
<i>*Burrhamys parvus</i>	Mountain Pygmy Possum	Bogong High Plains, Vic., Australia		NMV C31228		KJ868103	3
<i>Trichosurus vulpecula</i>	Common Brushtail Possum	New Zealand		-		AF357238	4
<i>Trichosurus caninus</i>	Mountain Brushtail Possum	Alstonville, NSW, Australia		ABTC1397		KJ868163	3
<i>Trichosurus arnhemensis</i>	Northern Brushtail Possum	Melville Is., Australia		ABTC29990		AF343890	2
<i>Wyulda squamicaudata</i>	Scaly-tailed Possum	Mitchell Plateau, Australia		ABTC07724		KJ868165	3
<i>Ailurops ursinus</i>	Bear Cuscus	Sulawesi, Indonesia		NK80066		KJ868096	3
<i>Strigocuscus celebensis</i>	Small Sulawesi Cuscus	Sulawesi, Indonesia		NK103527		KJ868161	3
<i>Spiloglossus maculatus</i>	Common Spotted Cuscus	Baumina, Madang Prov., Papua New Guinea (PNG)	Ma	AMS M21024	ABTC49143	KJ868160	3
<i>Spiloglossus maculatus</i>	Common Spotted Cuscus	Waro, Southern Highlands, PNG	SH	AMSM18358	ABTC46929	TBA	9

<http://www.publish.csiro.au/journals/am>

<i>Spilocuscus rufoniger</i>	Black-spotted Cuscus	Mr Boobiari, Sandaun, PNG	WS	AMS M13519	ABTC42601	AF343888	5
<i>Spilocuscus rufoniger</i>	Black-spotted Cuscus	Kobobip, Sandaun, PNG	WS	AMS M13520	ABTC42634	TBA	9
<i>Spilocuscus kraemeri</i>	Admiralty Island Cuscus	Admiralty Islands, Manus, PNG	???	???	ABTC43058	TBA	9
<i>Phalanger carmelitae</i>	Mountain Cuscus	Oro Prov., PNG	Or	AMS M19104	???	AF343887	2
<i>Phalanger carmelitae</i>	Mountain Cuscus	Nong River, Sandaun, PNG	WS	AMS M14695	ABTC44257	TBA	9
<i>Phalanger carmelitae</i>	Mountain Cuscus	Bobole, Southern Highlands, PNG	SH	AMS M16263	ABTC45676	TBA	9
<i>Phalanger gymnotis</i>	Ground Cuscus	Bobole, Southern Highlands, PNG	SH	AMS M18485	ABTC44950	KJ868142	6
<i>Phalanger gymnotis</i>	Ground Cuscus	Wigote, Sandaun, PNG	WS	AMS M14698	ABTC44156	TBA	9
<i>Phalanger intercastellanus</i>	Common Cuscus	Namosado, Southern Highlands, PNG	SH	AMS M18362	ABTC46670	TBA	9
<i>Phalanger lullulae</i>	Woodlark Cuscus	Woodlark Is., PNG	FC79	???	???	AF343882	7
<i>Phalanger matanin</i>	Telefomin Cuscus	Nong River, Sandaun, PNG	WS	AMS M14702	ABTC44274	TBA	9
<i>Phalanger matanin</i>	Telefomin Cuscus	Sol River, Sandaun, PNG	WS	AMS M14186	ABTC47168	TBA	9
<i>Phalanger mimicus</i>	Southern Common Cuscus	Doido, Chimbu, PNG	Ch	AMS M13870	ABTC43820	TBA	9
<i>Phalanger mimicus</i>	Southern Common Cuscus	Namosado, Southern Highlands, PNG	SH	AMS M18526	ABTC46179	TBA	9

<i>Phalanger orientalis</i>	Northern Common Cuscus	Tibi, Sandaun, PNG	WS	AMS M13472	ABTC42543	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Wigote, Sandaun, PNG	WS	AMS M15996	ABTC44078	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Telefolip, Sandaun, PNG	WS	AMS M16687	ABTC47202	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Munbil, Sandaun, PNG	WS	AMS M16684	ABTC47242	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Telefomin Valley, Sandaun, PNG	WS	AMS M16686	ABTC47419	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Kiera, Morobe, PNG	Mo	No voucher	ABTC44854	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Namosado, Southern Highlands, PNG	SH	AMS M17898	ABTC46322	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Waro, Southern Highlands, PNG	SH	AMS M17152	ABTC46803	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Karkar Is., Madang, PNG	Ma	AMS M19068	ABTC49357	TBA	9
<i>Phalanger orientalis</i>	Northern Common Cuscus	Bundi, Madang, PNG	Ma	AMS M19996	ABTC49364	TBA	9

<i>Phalanger orientalis</i>	Northern Common Cuscus	Nakanai Mtns, West New Britain, PNG	W.NB	ANWC M30930	ABTC122409	TBA	9
<i>Phalanger orientalis breviceps</i>	Solomon subspecies	Choiseul Is., Solomon Islands		AMS M23014	ABTC50540	AF343881	2
<i>Phalanger orientalis breviceps</i>	Solomon subspecies	Choiseul Is., Solomon Islands		AMS M23375	ABTC50531	TBA	9
<i>Phalanger orientalis timorensis</i> **	Timor possible subspecies	Gunung Mutis, West Timor, Indonesia		WAM M34811	ABTC62226	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Gunung Mutis, West Timor, Indonesia		WAM M34812	ABTC62227	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Gunung Mutis, West Timor, Indonesia		WAM M34813	ABTC62228	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Gunung Mutis, West Timor, Indonesia		WAM M34814	ABTC62229	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Gunung Mutis, West Timor, Indonesia		WAM M34816	ABTC62231	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Panite, West Timor, Indonesia		WAM M35001	ABTC62232	TBA	9
<i>Phalanger orientalis timorensis</i> '	Timor possible subspecies	Panite, West Timor, Indonesia		WAM M35002	ABTC62233	TBA	9
<i>Phalanger sericeus</i>	Silky Cuscus	Central Prov., PNG	Ce	AMS M12869	???	AF343884	2
<i>Phalanger sericeus</i>	Silky Cuscus	Mt. Albert Edward, Central Prov., PNG	Ce	AMS M12868	ABTC42500	TBA	9
<i>Phalanger sericeus</i>	Silky Cuscus	Bobole, Southern Highlands, PNG	SH	AMS M16268	ABTC45089	TBA	9
<i>Phalanger sericeus</i>	Silky Cuscus	Sol River, Sandaun, PNG	WS	AMS M16688	ABTC47180	TBA	9
<i>Phalanger vestitus</i>	Stein's Cuscus	Bobole, Southern Highlands, PNG	SH	AMS M16274	ABTC46631	AB241057	8

	<i>Phalanger vestitus</i>	Stein's Cuscus	Ofektaman, Sandaun, PNG	WS	AMS MI3497	ABTC42666	TBA	9
	<i>Phalanger vestitus</i>	Stein's Cuscus	Nong River, Sandaun, PNG	WS	AMS MI4704	ABTC44016	TBA	9
	<i>Phalanger vestitus</i>	Stein's Cuscus	Doido, Chimbu, PNG	Ch	AMS MI5307	ABTC43786	TBA	9
647	^a Location code corresponding to Fig. 1C. ^b Museum Codes: NMV: Museum Victoria; AMS: Australian Museum, Sydney; WAM: Western Australian Museum; ABTC: Australian Biological Tissue Collection, South Australian Museum; ANWC: Australian National Wildlife Collection; NK: Museum of Southwestern Biology, University of New Mexico. ^c The studies where the original sequences were published are referenced. * indicates outgroup taxa. **The possible P. orientalis subspecies from the island of Timor is named in parenthesis as this classification has not been formally recognized. Refs: 1 Nilsson et al. 2004; 2 Osborne and Christidis 2002; 3 Mitchell et al. 2014; 4 Phillips et al. 2001; 5 Burk and Springer 2000; 6 Pestell et al. 2007; 7 Hamilton and Springer 1999; 8 Munemasa et al. 2006; 9 current study (these sequences will be uploaded to GenBank and their accession numbers made available following review of this manuscript).							
648								
649								
650								
651								
652								
653								
654								

655 Table 3: Divergence dates (in millions of years, to 2 d.p.) for select nodes from the
 656 calibrated phylogenetic analysis.^a

Clade	95% HPD ^b (Ma)	Median Age (Ma)	Ruedas and Morales (2005)	Raterman <i>et al.</i> (2006)*	Meredith <i>et al.</i> (2009)
Burramyidae – Phalangeridae split (= crown Phalangeroidea)	51.18 – 31.14	40.84	n/a	n/a	49.4 – 36.6
Trichosurinae (<i>Trichosurus</i> + <i>Wyulda</i>) – Ailuropinae+Phalangerinae split (= crown Phalangeridae)	35.54 – 18.57	26.74	27.3 – 24.7	36.2 – 17.55	21.7 – 13.6
Ailuropinae (<i>Ailurops</i> + <i>Strigocuscus</i>) – Phalangerinae (<i>Phalanger</i> + <i>Spilocuscus</i>) split	30.39 – 15.55	22.49	23.2 – 21.1	32.47 – 13.95	17.9 – 10.7
Crown Phalangerinae	24.42 – 11.93	17.72	16.1 – 14.6	19.43 – 6.00	11.6 – 6.2**
<i>Phalanger</i>	19.12 – 9.16	13.94	13.8 – 12.5	16.18 – 4.07	10.5 – 5.4***
<i>Phalanger orientalis</i>	4.07 – 1.13	2.37	n/a	n/a	n/a
<i>Phalanger orientalis</i> Timor samples	1.5 – 0.35	0.82	n/a	n/a	n/a

657 ^aCompared with most recent estimates from molecular phylogenies of Phalangeridae
 658 (*Ruedas and Morales 2005; Raterman et al. 2006; Meredith et al. 2009*). ^bHPD =
 659 Highest posterior density. **Raterman et al., (2006) date ranges are the compound*
 660 *ranges of both their Multidivtime and BEAST estimates. **Analysis included*
 661 *Strigocuscus pelengensis which is absent from our study. ***Following George’s*
 662 *(1987) classification of P. pelengensis in Phalanger, as supported by Meredith et al.*
 663 *(2009).*

664

665 **Figure Captions**

666 Fig. 1: Map showing distribution of the Phalangeridae and sampling localities for the
667 novel sequences in this study. A) Map of Australasia with distribution of Phalangeridae
668 species shaded in grey. Insets B and C indicated. B) Island of Timor with collecting
669 sites indicated by red triangles. C) Papua New Guinea and the Solomon Islands with the
670 provinces and islands sampled highlighted and labelled (see Table 2 for label codes).

671 Fig. 2: Undated *ND2* phylogeny of the Phalangeridae. Nodes coloured according to
672 mean Bayesian posterior probabilities (BPP), black = >0.91 , orange = 0.80-0.91, red =
673 <0.80 . Scale bar represents 0.06 substitutions/site. Phalangerinae samples are
674 highlighted according to sampling localities, with colours corresponding to Fig. 1C and
675 key in top left.

676 Fig. 3: Time-calibrated phylogeny of the Phalangeridae. Mean Bayesian posterior
677 probabilities (BPP) are indicated by coloured nodes, as per Fig. 2. Branch lengths are
678 proportional to time and correspond to the scale at the base, in millions of years before
679 present. Bars at nodes represent 95% Highest Posterior Densities (HPD).

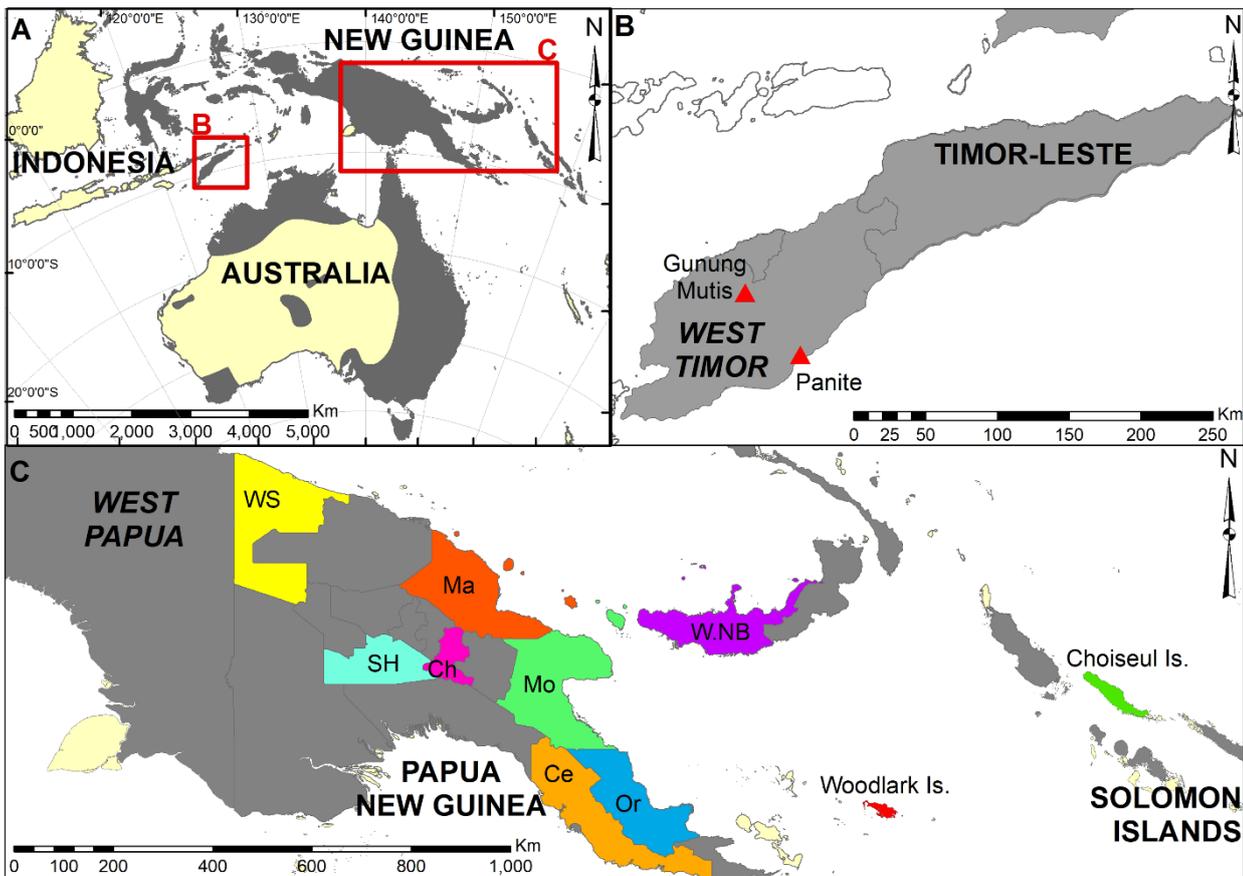


Fig. 1: Map showing distribution of the Phalangeridae and sampling localities for the novel sequences in this study. A) Map of Australasia with distribution of Phalangeridae species shaded in grey. Insets B and C indicated. B) Island of Timor with collecting sites indicated by red triangles. C) Papua New Guinea and the Solomon Islands with the provinces and islands sampled highlighted and labelled (see Table 2 for label codes).

(300 x 300 DPI)

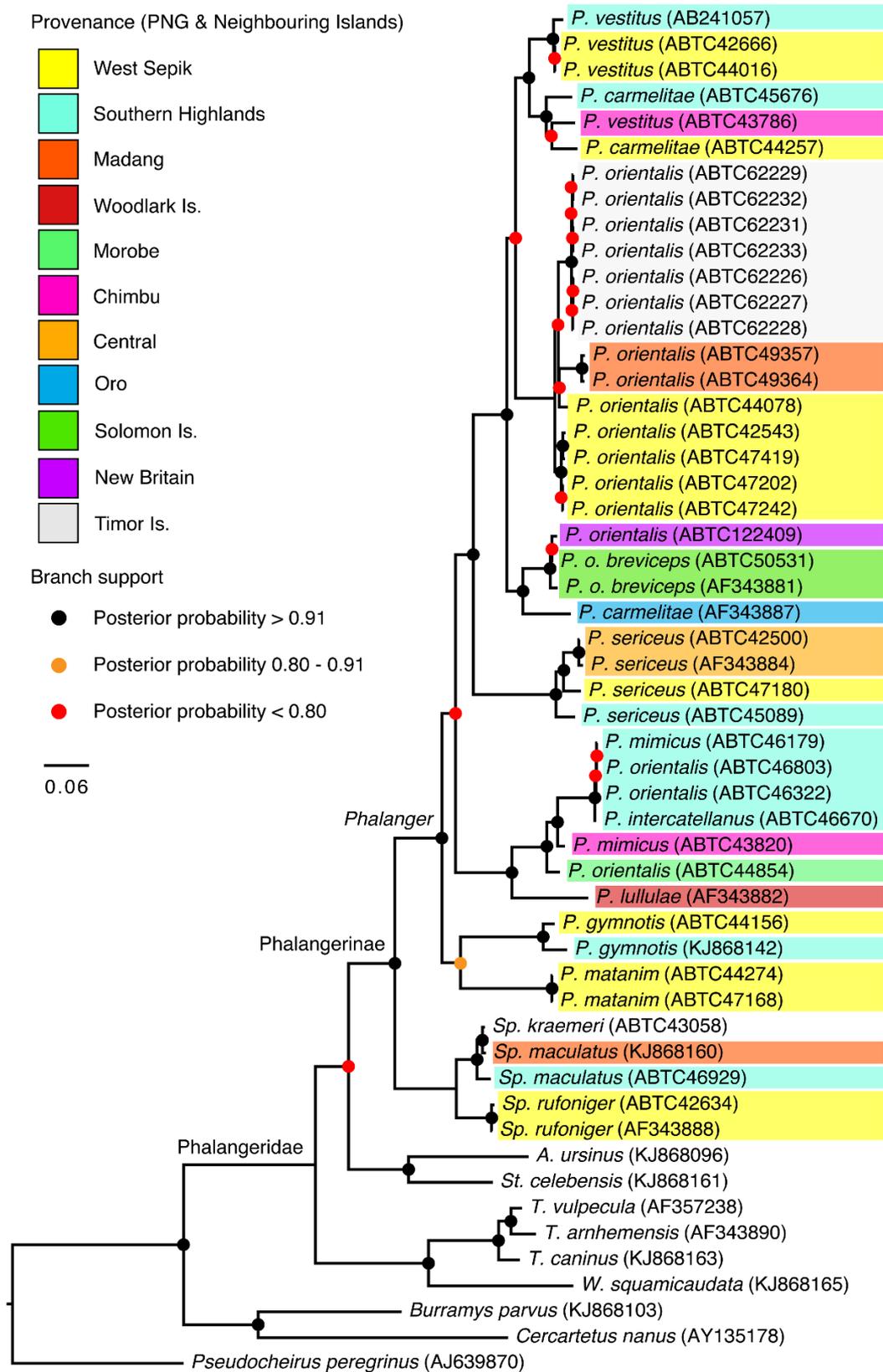


Fig. 2: Undated ND2 phylogeny of the Phalangeridae. Nodes coloured according to mean Bayesian posterior probabilities (BPP), black = >0.91, orange = 0.80-0.91, red = <0.80. Scale bar represents 0.06 substitutions/site. Phalangerinae samples are highlighted according to sampling localities, with colours corresponding to Fig. 1C and key in top left.

(300 x 300 DPI)

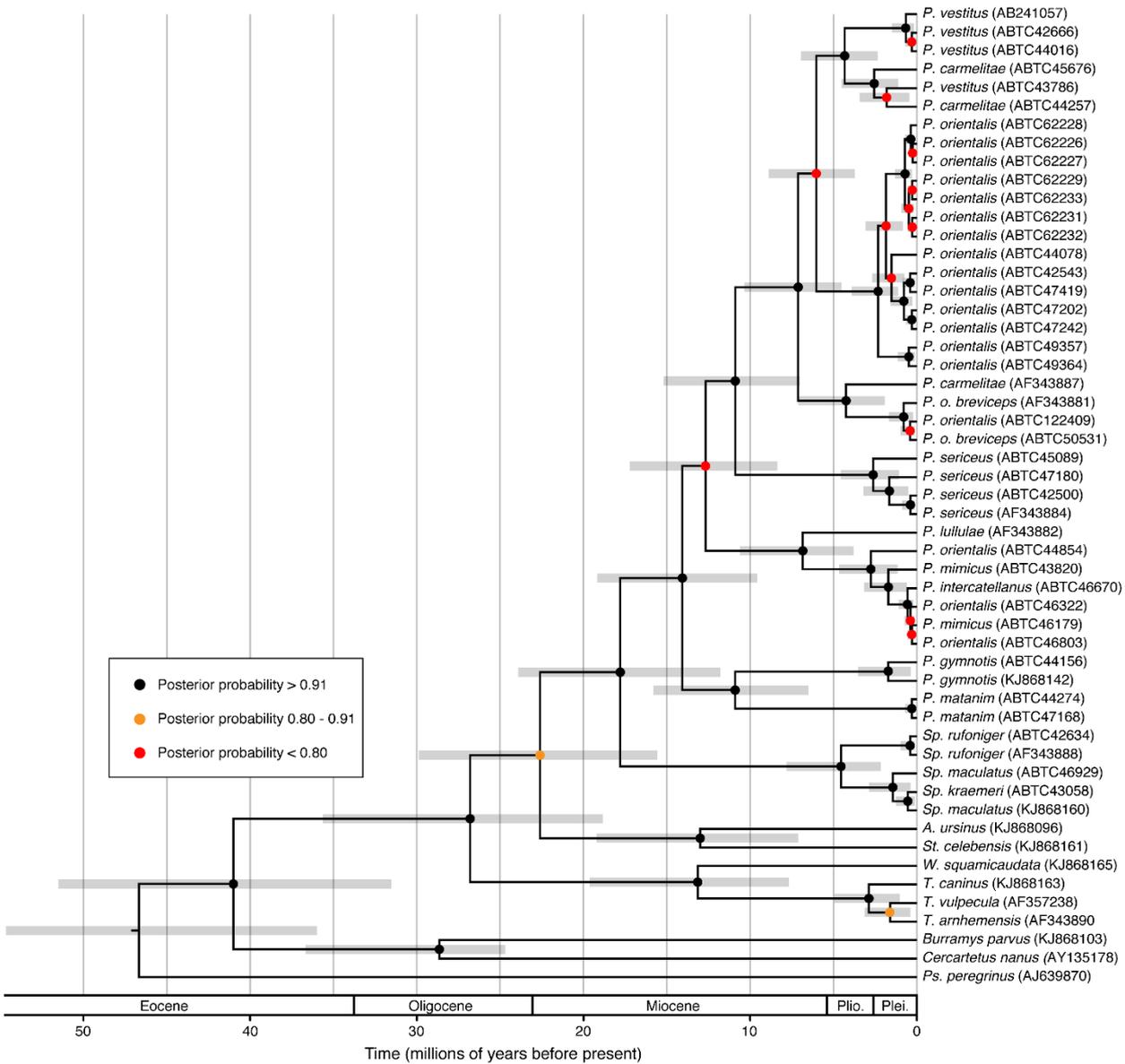


Fig. 3: Time-calibrated phylogeny of the Phalangeridae. Mean Bayesian posterior probabilities (BPP) are indicated by coloured nodes, as per Fig. 2. Branch lengths are proportional to time and correspond to the scale at the base, in millions of years before present. Bars at nodes represent 95% Highest Posterior Densities (HPD).

(300 x 300 DP)

Chapter 8. The applications of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).

Authors: Shimona Kealy, Michael Herrera, Ken Aplin, Kieren J Mitchell, Steve C Donnellan, Julien Louys, Sue O'Connor

Publication: Undecided

Current Status: In Preparation

Citation: Kealy, S., Herrera, M., Aplin, K., Mitchell, K., Donnellan, S., Louys, J., & O'Connor, S. (in prep). The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).

Note: The Supplementary Information files referred to in this manuscript can be found in Appendix C of this thesis.

Shimona Kealy: developed the research question, collected archaeological samples in the field and from pre-existing collections, secured partial funding for aDNA sequencing, obtained relevant, pre-existing sequences from the online database GenBank, aligned DNA sequences, identified and extracted secondary structures, identified evolutionary-rate models for all partitions, revised morphological characters, compiled morphological matrix, conducted the phylogenetic analysis, conducted the biogeographic analysis, interpreted the model outcomes, drew up the figures, drafted the manuscript, edited and reviewed the manuscript.

Signed:



Shimona Kealy

Michael Herrera: extracted and sequenced ancient and modern mtDNA, developed the DNA library, jointly mapped aDNA sequences, co-wrote the sequencing section of the methods and supplementary information.

Signed:



Michael Herrera

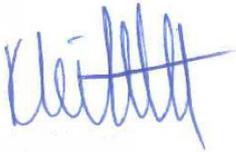
Ken Aplin: collected skeletal and tissue samples for sequencing, advised on species identifications.

Signed:

Ken Aplin

Kieren Mitchell: developed the probe-set for sequence enrichment, mapped mtDNA sequences, jointly mapped aDNA sequences, co-wrote the sequencing section of the methods and supplementary information.

Signed:



Kieren Mitchell

Steve Donnellan: secured funding for ARC Discovery Project (DP140103650) which funded personnel costs in the laboratory.

Signed:



Steve Donnellan

Julien Louys: collected archaeological samples in the field, assisted with biogeography model development, edited and reviewed the manuscript.

Signed:



Julien Louys

Sue O'Connor: secured funding for the Laureate project, edited and reviewed the manuscript.

Signed:

A handwritten signature in blue ink, appearing to read "Sue O'Connor". The signature is written in a cursive style with a large initial "S" and "O".

Sue O'Connor

The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).

Shimona Kealy, Michael Herrera, Ken Aplin, Kieren J Mitchell, Steve C Donnellan, Julien Louys, Sue O'Connor

ABSTRACT

The Phalangeridae are a family of arboreal marsupials found throughout Australia, New Guinea, Indonesia and Melanesia. Commonly referred to as cuscuses, the Asia-Pacific phalangerid species have had a number of their island distributions attributed to prehistoric anthropogenic translocations. While some of these possible translocations are supported by archaeological evidence, most are lacking such data and questions regarding the timing and directionality of all these translocations remain. Here we propose a novel method to investigate the likelihood and directionality of these possible cuscus translocations based on phylogeography. We constructed the first dated, total evidence (molecular and morphological) phylogeny of the Phalangeridae incorporating modern, archaeological, and fossil taxa. This phylogeny was then run through the R package BioGeoBEARS to produce a model of the family's biogeographic history. This biogeographic model, in addition to the divergence estimates obtained from the phylogenetic analysis, were then compared with the archaeological records and palaeogeographical reconstructions to determine the likelihood of anthropogenic translocations vs. natural dispersals. We recovered good support for anthropogenic translocations of *Phalanger breviceps* and *P. orientalis* to New Ireland and Timor, respectively. We also found strong evidence to suggest that all other island populations of *P. breviceps* originated from the New Ireland population, not from additional translocations out of New Guinea. We find good support for a natural dispersal of *P. ornatus* to the Halmahera island group, rather than anthropogenic translocation. This study demonstrates the potential of this method for future investigation of prehistoric translocations on islands. A number of gaps in the available cuscus data were identified as key areas for future research.

KEYWORDS: Biogeography, Phalanger, Phylogenetics, Translocation, Introduction

1 INTRODUCTION

Cuscus is the common name given to the arboreal marsupials grouped within two subfamilies (Phalangerinae and Ailuropinae) of the possum family Phalangeridae (Kealy et al., in review). The geographic range of the cuscuses spans northern Australia to New Guinea, and west from the Solomon Islands to Sulawesi and the Talaud Archipelago. The Phalangeridae consists of 30 currently recognised species, 23 of which are found outside of Australia. It is the most geographically widespread of the Australasian marsupial families and the most species-rich of the possums (Figure 1; Helgen and Jackson, 2015).

The cuscuses are also significant in being one of only a few groups of marsupials (along with members of the Macropodidae, Petauridae and Peramelidae) whose present distribution may partially be the result of prehistoric human-assisted translocations (Spriggs, 1997; Heinsohn, 2001, 2010). Some of these possible cuscus translocations, if correct, would represent the oldest evidence for intentional human translocation of animals anywhere in the world (Flannery and White, 1991, Spriggs, 1997, Summerhayes, 2007). The evidence for these translocations is limited. With the exception of some New Ireland and New Britain populations that have a historical record for their translocation (Flannery and White, 1991; Heinsohn, 1998, 2004, 2010), other island populations translocations have variable support ranging from archaeological records (e.g. O'Connor, 2015) to simply the assumption that marsupials are poor swimmers and thus must require human assistance to reach their island localities (e.g. Flannery, 1995).

Within Phalangeridae and on the various islands of Salebabu, Timor, Leti, Wetar, Sanana, Selayar, Buru, Ambon, Seram, Banda, Kai, Gebe, Morotai, Mussau Islands, Bismarck Archipelago, Solomon Islands, Alcester, Long, Manus, Unea (Bali), and Witu (Heinsohn, 2010), *Ailurops melanotis* (Flannery, 1994; 1995), *Strigocuscus celebensis* (Groves, 1976), *Spilocuscus maculatus* (Groves, 1976; Whitten et al., 1987; Kirch, 1988), *Sp. kraemari* (Flannery, 1995; Heinsohn, 1997; Spriggs, 1997), *Phalanger orientalis* (Glover, 1986; Spriggs, 1997; O'Connor 2006; 2015), *P. ornatus* (Bellwood et al., 1998), and *P. lullulae* (Flannery, 1994, 1995) have all had some portion of their geographical distribution attributed to early human activities. Much of this has been speculative, and stems largely from a perceived 'aqua-phobic' nature of marsupials (Calaby, 1984; Heinsohn, 2010). Historic observances of human transportation have been noted (Groves, 1976), though only a few studies provide any archaeological evidence (Table 1).

Notable exceptions include the work in Melanesia by Spriggs (1997), Heinsohn (1997), and Leavesley (2005); and in Timor by Glover (1986) and O'Connor (2015). Cuscus remains have been recovered from archaeological deposits on New Ireland dating back 23.6-22.5 ka (Flannery and White, 1991, Spriggs, 1997, Summerhayes, 2007), Timor (3.4-3.2 ka; O'Connor, 2015), north Solomons (9-8.5 ka, Wickler, 2001; Summerhayes, 2007), Mussau (3.7-3.2 ka; Kirch, 1988; Kirch et al., 1991), Manus (14.5013 ka; Spriggs, 1997, Summerhayes, 2007), Halmahera (5.6 – 5 ka, Bellwood et al., 1998), Gebe (13-12.6 ka, Bellwood et al., 1998), and Morotai (16-15.1 ka; Bellwood et al., 1998) (Table 1). Additionally, Long Island has an oral history record of cuscus translocation in the 19th century (Mayr and Diamond, 2001). The evidence for translocations is still circumstantial, however, and there is increasingly tentative evidence to support the possibility of cuscus translocations prior to the Holocene (Heinsohn, 2001, 2010; O'Connor, 2015). Studies such as Bellwood et al. (1998) suggest possible human

introductions based on the first appearance of cuscus remains alongside with cultural material in archaeological assemblages. A closer look at this record however, shows that layers below the first appearance of cuscus are completely free of any bone whatsoever (Bellwood et al., 1998; Pasveer and Bellwood, 2004), suggesting the correlation may be an artefact of preservation.

Table 1: Archaeological records for cuscus in comparison with initial human occupation on the island. Material dated is indicated in brackets, ‘shell’ refers to marine shell unless otherwise stated. Radiocarbon dates were calibrated using IntCal13 (for charcoal) and Marine13 (for marine shell) calibration curves (Riemer et al., 2013) using OxCal v.4.3 Online (Ramsey, 2009).

Island (Is. Group)	Initial Human Occupation		Earliest Record for Cuscus		Refs.
	Radiocarbon Date (ka)	95.4% cal BP age	Radiocarbon Date (ka)	95.4% cal BP age	
Buka (Solomons Is.)	28.34 ± 0.28 (shell)	32,624 - 31,214	7.93 ± 0.11 – 9.46 ± 0.15 (charcoal)	9,079 - 8,477	1
Eloaua (St Matthias Is.)	3.26 ± 0.09 (charcoal)	3,702 - 3,252	3.26 ± 0.09 (charcoal)	3,702 - 3,252	2; 3
Manus (Admiralty Is.)	12.4 ± 0.08 (charcoal)	14,938 - 14,128	11.73 ± 0.28 (charcoal)	14,450 - 13,011	4; 5
New Ireland	39.09 ± 0.55; 38.76 ± 0.1; 40.09 ± 0.57 (shell)	42,782 - 42,341 (combined calibration)	19.54 ± 0.25 (shell)	23,629 - 22,495	6; 7
Halmahera (Halmahera Is.)	5.12 ± 0.1 (estuarine shell)	5,581 - 4,979 (100-50% marine curve)	5.12 ± 0.1 (estuarine shell)	5,581 - 4,979 (100-50% marine curve)	8; pers. obs.
Morotai (Halmahera Is.)	13.39 ± 0.14 (shell)	15,970 - 15,145	13.39 ± 0.14 (shell)	15,970 - 15,145	8; pers. obs.
Gebe (Halmahera Is.)	32.221 ± 0.32 (shell)	36,360 - 35,010	11.31 ± 0.08 (shell)	12,962-12,626	8; 9
Timor-Leste (Timor)	41,572 ± 939 (shell)	46,529 – 43,085	3.111 ± 0.029 (Cuscus bone) 5.52 ± 0.06 (charcoal)	3,386 - 3,240 (direct date) 6,435 - 6,207	10; 11; 12

References: 1 Wickler, 2001; 2 Kirch, 1988; 3 Kirch et al., 1991; 4 Fredericksen et al., 1993; 5 Williams, 1999; 6 Leavesley and Chappell, 2004; 7 Leavesley et al., 2002; 8 Bellwood et al., 1998; 9 Irwin et al., 1999; 10 Shipton et al., in review; 11 O’Connor, 2015; 12 Glover, 1969

Only on Timor, which is the sole island with direct dates on cuscus remains and an extensive archaeological (and zooarchaeological) record which pre-dates the first records of cuscus alongside other cultural material, is the evidence for cuscus translocations reliable (Table 1; O’Connor 2015). Islands with cuscus records that correspond with initial human arrival (e.g. St Matthias Islands; Kirch, 1988) do not disprove translocation hypotheses (as cuscus may have been introduced simultaneously with human colonisation), however the lack of earlier faunal records means these records are unable to act as support for translocation. Similarly, while associated dates for cuscus remains which post-date human arrival provide stronger support

for translocation, associated dates can be substantially different to the 'true' (direct) date of the remains (see O'Connor, 2015), making their interpretation as translocation less reliable. Despite multiple sites on Timor with faunal records extending into the Pleistocene that support pre-Holocene absence of cuscus (e.g. O'Connor et al., 2002, 2014; O'Connor, 2007; O'Connor and Aplin, 2007; Hawkins et al., 2017; Louys et al. 2017; Meijer et al., 2019), these data are, however, currently unable to provide any insights into the original source populations for the Timor cuscus.

The family and subfamily level groupings of the phalangerids is well established (Meredith et al., 2009; Helgen and Jackson, 2015), although classifications at other taxonomic levels within Phalangeridae still suffer differing degrees of uncertainty (Helgen and Jackson, 2015; Kealy et al., in review). This uncertainty has been amplified by significant disparities between the morphological and molecular phylogenies, numerous taxonomic changes, and inconsistencies in both museum specimen and GenBank sequence identifications (Kealy et al., in review). The recent taxonomically comprehensive phylogeny of the Phalangeridae produced by Kealy et al. (in review) using the *ND2* mitochondrial gene found strong support for the 'molecular' subfamily classification (as suggested by Ruedas and Morales, 2005 and ratified by Helgen and Jackson, 2015). This classification places the Australian *Trichosurus* and *Wyulda* in a separate, basal clade of the phalangerids (subfamily Trichosurinae), with the cuscuses divided into two additional subfamilies: Ailuropinae (*Ailurops* and *Strigocuscus*) and Phalangerinae (*Phalanger* and *Spiloguscus*) (Table 1; Kealy et al., in review). These results conflict with the morphology-based classifications but are supported by multiple molecular studies and a seemingly more parsimonious biogeographic distribution (Flannery et al., 1987; Norris, 1994; Hamilton and Springer, 1999; Kirsch and Wolman 2001; Osborne and Christidis, 2002; Crosby and Norris, 2003; Crosby et al., 2004; Ruedas and Morales, 2005; Raterman et al., 2006; Crosby, 2007; Meredith et al., 2009; Mitchell et al., 2014; Kealy et al., in review).

The *ND2* study by Kealy et al. (in review) also recovered substantial evidence for specimen identification problems and taxonomic issues, in particular regarding cuscuses currently listed as *Phalanger orientalis*. *P. orientalis*, as it is currently classified, covers the broadest longitudinal range of the cuscuses and is the species most commonly mentioned as undergoing human translocation (Glover, 1986; Spriggs, 1997; Wickler, 2001; Leavesley et al., 2002; Leavesley and Chappell, 2004; O'Connor, 2006, 2015; Summerhayes, 2007; Helgen and Jackson, 2015). However, further examinations of this taxon has often resulted in splitting the *P. orientalis* hypodigm into several species (Colgan et al., 1993; Norris and Musser, 2001; Kealy et al., in review). For example, Kealy et al. (in review) clearly demonstrate that the islands to the east of New Guinea are populated by a distinct *Phalanger* species. This has significant implications for our interpretations of the archaeological record and efforts for unravelling the evolutionary, dispersal, and possible translocation history of this taxon.

For example, when the Bismarck and Solomon cuscus was considered a subspecies of *P. orientalis*, its origin was considered the result of translocations of *P. orientalis* from New Guinea, with subspecies differentiation following their island isolation (Summerhayes, 2007; Helgen and Jackson, 2015). However, the reclassification of the Bismarck and Solomon cuscus as a unique species, and the identification of a possible source population in the province of Oro, northeastern Papua New Guinea (Kealy et al., in review), has implications for directionality of the possible translocation. It significantly reduces the likelihood of multiple translocations or dispersals east from New Guinea, suggesting movement between the islands

of the Bismark and Solomons in relative isolation. Further investigations into the archaeology and records of cuscus arrival on these islands, and throughout the Asia-Pacific more generally, is required before a reliable dispersal hypothesis can be developed.

Given the scarce archaeological evidence, we propose an alternative method to investigate the biogeography of the Phalangeridae family, and test some of the translocation hypotheses for the group. Here, we report the results of this method with a particular focus on the origin of *P. orientalis* on Timor, and *P. ornatus* in the Halmahera island group. By conducting the first total evidence (morphological and molecular) phylogenetic study of the phalangerids, calibrated with fossil and archaeological dates, and the first available cuscus ancient DNA (aDNA) sequence, we aim to improve our understanding of the evolutionary relationships of this group and investigate their biogeographic history. The statistical program BioGeoBEARS was employed to model biogeographic history and interpret the most likely pattern of dispersal for Phalangeridae into six key geographic zones (Australia, New Guinea, Moluccas, Sulawesi, Timor and Melanesia).

2 MATERIALS AND METHODS

2.1 Species Analysed

We included 26 taxa representing 20 species in our final total evidence and biogeographic study (Table 2). Of these 20 species, 17 belong to the family Phalangeridae and three were outgroup species. Seven different samples of *Phalanger orientalis* from Timor were obtained from the South Australian Museum (SAM) and their complete mitochondrial genome sequenced. Five surface or sub-surface cuscus specimens collected from Timor-Leste and one archaeological specimen from North Maluku were also successfully sequenced for mitochondrial aDNA (see Supplementary Information Table S1)

Additional species and specimens incorporated into the total evidence analysis were selected based on the results of three separate phylogenies: the Kealy et al. (in review) *ND2* tree, a novel molecular dataset which combined some of the species from Kealy et al. (in review) with additional mitochondrial and nuclear sequences (see 2.3, 2.5.1), and a revised morphological dataset based on the Crosby (2002) study (see 2.4, 2.5.2). Species were selected with the aim of maximising diversity but minimising taxonomic and identification inconsistencies, with a focus on the Phalangerinae.

Based on the results of the Kealy et al. (in review) phylogeny, only species or populations which were recovered as monophyletic were used in the combined molecular analysis. Additionally, only sequences from samples in the same geographic range as the Kealy et al. (in review) samples were combined in the dataset. Thus, species such as *Phalanger carmelitae* were excluded from this study while species such as *P. sericeus* were not combined with any of the additional GenBank sequences. Based on the results of the combined molecular phylogeny developed here (see Supplementary Information S1-3, Figure S4), for the total evidence analysis, representation of New Guinea *P. orientalis* specimens was reduced to a single taxon, modern representatives of Timor *P. orientalis* were reduced to three taxa (reflecting the slightly separate geographic populations), and sub-recent *P. orientalis* specimens from Timor were reduced to three taxa (based on both phylogenetic results and maximum data coverage). As the morphological phylogeny failed to provide any further resolution to the classifications of conflicted species (see Supplementary Information S5-7, Figure S8), only species also

represented in the combined molecular analysis were selected for incorporation of their morphological data into the total evidence analysis. The two exceptions to this were the fossil species *Trichosurus dicksoni* and *Onirocuscus reidi*, which were included for clock calibration purposes.

Table 2: Current classifications of species considered in this study following Groves (2005) for pseudocheerid and burramys classifications, and Helgen and Jackson (2015) and Kealy et al. (in review) for classifications within Phalangeridae. The two fossil species are indicated with a “†” with classifications based on Crosby (2007), other extinct species assigned to Phalangeridae are not listed here. Species incorporated into the phylogenetic analysis are indicated in **bold**.

Classification	Species
<u>Family Pseudocheiridae Winge, 1893</u>	
Genus <i>Pseudocheirus</i> Ogilby, 1837	<i>Pseudocheirus peregrinus</i> Boddaert, 1785
<u>Family Burramyidae Broom, 1898</u>	
Genus <i>Cercartetus</i> Gloger, 1841	<i>Cercartetus nanus</i> Desmarest, 1818; <i>C. concinnus</i> Gould, 1845; <i>C. caudatus</i> Milne-Edwards, 1877; <i>C. lepidus</i> Thomas, 1888
Genus <i>Burramys</i> Broom, 1896	<i>Burramys parvus</i> Broom, 1896
<u>Family Phalangeridae Thomas, 1888</u>	
<u>Subfamily Trichosurinae Flynn, 1911 - ‘Brushtail and Scaly-tailed Possums’</u>	
Genus † <i>Onirocuscus</i> Crosby, 2007	† <i>Onirocuscus reidi</i> Flannery and Archer, 1987
Genus <i>Trichosurus</i> Lesson, 1828	<i>Trichosurus vulpecula</i> Kerr, 1792; <i>T. caninus</i> Ogilby, 1836; <i>T. johnstonii</i> Ramsay, 1888; † <i>Trichosurus dicksoni</i> Flannery and Archer, 1987; <i>T. cunninghami</i> Lindenmayer, Dubach and Viggers, 2002
Genus <i>Wyulda</i> Alexander, 1918	<i>Wyulda squamicaudata</i> Alexander, 1918
<u>Subfamily Ailuropinae Flannery, Archer and Maynes, 1987 - ‘Cuscuses’</u>	
Genus <i>Ailurops</i> Wagler, 1830	<i>Ailurops ursinus</i> Temminck, 1824; <i>A. melanotis</i> Thomas, 1898; <i>A. furvus</i> Miller and Hollister, 1922
Genus <i>Strigocuscus</i> Gray, 1862	<i>Strigocuscus celebensis</i> Gray, 1858; <i>St. sangirensis</i> Meyer, 1896
<u>Subfamily Phalangerinae Thomas, 1888 - ‘Cuscuses’</u>	
Genus <i>Spilocuscus</i> Gray, 1862	<i>Spilocuscus maculatus</i> E. Geoffroy, 1803; <i>Sp. papuensis</i> Desmarest, 1822; <i>Sp. nudicaudatus</i> Gould, 1850; <i>Sp. kraemeri</i> Schwarz, 1910; <i>Sp. rufoniger</i> Zimara, 1937; <i>Sp. wilsoni</i> Helgen and Flannery, 2004
Genus <i>Phalanger</i> Storr, 1780	<i>Phalanger orientalis</i> Pallas, 1766; <i>P. ornatus</i> Gray, 1860; <i>P. gymnotis</i> Peters and Doria, 1875; <i>P. vestitus</i> Milne-Edwards, 1877; <i>P. intercastellanus</i> Thomas, 1895; <i>P. lullulae</i> Thomas, 1896; <i>P. rothschildi</i> Thomas, 1898; <i>P. carmelitae</i> Thomas, 1898; <i>P. sericeus</i>

Thomas, 1907; <i>P. mimicus</i> Thomas, 1922; <i>P. pelegensis</i> Tate, 1945; <i>P. matanim</i> Flannery, 1987; <i>P. alexandrae</i> Flannery and Boeadi, 1995; <i>P. breviceps</i> Thomas, 1888

2.2 DNA Extraction and Sequencing

A total of 20 surface/sub-surface cuscus samples collected from various localities in Timor-Leste, and 15 archaeological samples recovered from sites in North Maluku were processed for aDNA (see Supplementary Information Table SX). DNA extraction and sequencing techniques followed those used by Kealy et al. (in review) for their Timor samples, with sequences mapped to the complete mitochondrial genome (MITObim consensus 75pc 3r truncated) for the Timor *Phalanger orientalis* Australian Biological Tissue Collection sample number ABTC62229 (GenBank accession no: *forthcoming*) (see Supplementary Information S2 for the detailed methodology). Unfortunately, due to the tropical origin of these samples, DNA recovery was limited (Hofreiter et al., 2015). Following sorting and quality filtering (Supplementary Information S2), only five of the Timor samples and one North Maluku sample retained sufficient (>100 reads) DNA for analysis purposes.

All other molecular sequence data used in this study was obtained from the previous study by Kealy et al. (in review) and the online database GenBank. All available, appropriate, mitochondrial sequences were combined with sequences for the following 5 nuclear genes: Apolipoprotein B (ApoB), breast cancer type 1 susceptibility protein (BRCA1), Retinol-binding protein 3, interstitial (RBP3), Recombination activating gene 1 (RAG1), and von Willebrand Factor (vWF). See Supplementary Information S1 for the list of genes and corresponding accession numbers for individual species.

2.3 DNA Alignment and Partitioning

The complete and partial mitochondrial genome sequences as well as the singular gene sequences were aligned manually using BioEdit v.7.2.6.1 (Hall, 1999), resulting in a master alignment of 22027 bp for a total of 31 taxa, with genes and secondary structures annotated. For mitochondrial ribosomal genes (rRNA) the secondary structure (i.e. stems and loops) were identified based on published structure models (Springer and Douzery, 1996; Burk et al., 2002; Kealy and Beck, 2017), while secondary structures for the mitochondrial transfer RNA genes (tRNA) were identified based on the online tRNA database Mamit-tRNA (Pütz et al. 2007; <http://mamit-tRNA.u-strasbg.fr>). Mitochondrial protein-coding genes and the five nuclear genes were all aligned to account for codons in MEGA v.7.0.26 (Kumar et al., 2016) with the alignment algorithm MUSCLE (Edgar, 2004) for codons.

Following alignment, genes, secondary structures for rRNA and tRNA sequences, and codon positions for mt protein-coding and nuclear genes were designated so that an appropriate partitioning scheme and nucleotide substitution models for each partition could be identified with PartitionFinder v2.1.1 (Lanfear et al., 2016). For the PartitionFinder analysis, we restricted comparisons to models implemented by MrBayes, with the assumption of linked branch lengths, the “greedy” search algorithm, and with the Bayesian Information Criterion used for model selection, as suggested by Lanfear et al. (2012). The best-fitting partitioning scheme and

nucleotide substitution models identified by PartitionFinder were then implemented in the phylogenetic analysis (see Supplementary Information S3, Table S3).

2.4 Morphological data collection

Our morphological characters were modified from the craniodental phylogenetic matrix of Crosby (2002) with additions and modifications based on Menzies and Pernetta (1986), Flannery et al. (1987), George (1987), Horovitz and Sánchez-Villagra (2003), Crosby and Norris (2003), Crosby (2007), and Archer et al. (2016). We reviewed all 74 original characters defined by Crosby (2002) and excluded those that were not relevant to our study focus (i.e. appeared ambiguous or that we could not score consistently). Additional characters and modifications to the remaining characters and character states were added based on previously published morphological studies of phalangerids and marsupials more generally (Menzies and Pernetta, 1986; Flannery et al., 1987; George, 1987; Horovitz and Sánchez-Villagra, 2003; Crosby and Norris, 2003; Crosby, 2007; Archer et al., 2016), and our observations during analysis of specimens. This resulted in a final set of 58 craniodental characters. We ordered 10 multistate characters which we identified as representing apparent morphoclines. We then scored these characters for the additional terminals not present in the Flannery et al. (1987), George (1987), Crosby (2002), Horovitz and Sánchez-Villagra (2003), Crosby and Norris (2003), and Crosby (2007) matrices. We also reassessed the original scorings of the other terminals and revised some character scores as a result.

Where possible, multiple specimens for each species was examined, but with close attention paid to the collection localities of specimens identified as the same species in an effort to avoid miss-identification issues. In cases of intraspecific polymorphism without any clear geographic differentiation, the modal condition was scored if one character state clearly predominated, following Voss and Jansa (2003, 2009). If the different character states were approximately equally common, the character was scored as polymorphic. If a geographic differentiation was identified the locality closest to that of the corresponding molecular samples was selected and the other region excluded from the analysis, again with the goal of minimising miss-identification problems. A list of our revised morphological characters and specimens examined is given in Supplementary Information S5 & S6. The final morphological matrix (in Nexus format) is provided in Supplementary Information S7.

2.5 Phylogenetic Analysis

Four phylogenetic analyses were performed for this study.

2.5.1 Molecular Phylogeny

We conducted an undated, model-based Bayesian phylogenetic analysis on our combined molecular (mitochondrial+nuclear gene) dataset, implemented in MrBayes v.3.2.6 (Ronquist et al., 2012) and run on the CIPRES Science Gateway (Miller et al., 2010). The analysis comprised four runs of four chains (one cold, three heated) each, sampling trees every 5000 generations, and run for 10 million generations. The post-burn-in trees were summarized using 50% majority rule consensus, with mean percentage Bayesian posterior probabilities (BPPs) as support values (see Supplementary Information Figure S4 for the consensus molecular-only phylogenetic tree).

2.5.2 Morphological Phylogeny

We also carried out a similar undated, model-based Bayesian analysis using MrBayes v.3.2.6 (Ronquist et al., 2012) on our morphological matrix using a single Mk model applied to the morphological characters (Lewis, 2001; Ronquist et al., 2011), with the default assumption that only variable characters were scored, and with a gamma distribution to model rate heterogeneity across characters (i.e. the Mk + G model), see Supplementary Information Figure S8 for the morphological-only phylogenetic tree.

2.5.3 Total Evidence Phylogeny

We then carried out an undated, model-based Bayesian phylogenetic analysis on our total evidence (molecular+morphology) dataset, implemented in MrBayes v.3.2.6 (Ronquist et al., 2012) and run on the CIPRES Science Gateway (Miller et al., 2010). As with the molecular analysis, this analysis comprised four runs of four chains (one cold, three heated) each, sampling trees every 5000 generations, and run for 10 million generations. The post-burn-in trees were summarised using 50% majority rule consensus, with Bayesian posterior probabilities (BPP) as support values (Supplementary Information S9).

We then performed a dated analysis using node and tip dating as suggested by O'Reilly and Donoghue (2016) and supported by Kealy and Beck (2017), to find the most accurate estimates for divergence times within Phalangeridae. Also executed in MrBayes v.3.2.6 (Ronquist et al., 2012) and run on the CIPRES Science Gateway (Miller et al., 2010), using the same run settings as for the undated analysis. We used a single Independent Gamma Rates (IGR) clock model, implementing a fossilised birth-death tree branching prior that assumed “diversity” sampling (Zhang et al., 2016) and a sample probability of 0.45 for our non-fossil taxa. This sample value is slightly less than the proportion of known phalangerid species in our matrices (0.5), but allows for the likely existence of additional undescribed species. We used the MrBayes default values for the fossilisation, extinction and speciation priors (Ronquist et al., 2012).

Modern terminals were all assigned an age of 0 ka, whereas the two fossil, one archaeological, and three sub-recent taxa were assigned age ranges, specified as uniform distributions. For the sub-recent samples, a range from 0 to 0.5 ka was implemented to allow for slight temporal differences in the DNA sequences in relation to modern samples. The archaeological *Phalanger ornatus* sample from the site of Siti Nafisah, Halmahera was assigned the range 5.6 – 4.9 ka (calibrated date from ANU 7788: 4890 ± 70 ; Bellwood et al., 1998). This is not a direct date from the bone but an associated date from an estuarine shell recovered from the same spit. While work by O'Connor (2015) has demonstrated that there can be significant differences between a direct date and associated dates, in the case of Siti Nafisah, recent efforts in direct dating on *Dorcopsis* samples recovered from the same excavation have been largely congruent with the pre-existing dates from associated spits (Philip Piper pers. comm.). We therefore consider the spit date best associated with our sample to represent a suitable age estimate for our analysis. As the radiocarbon date was obtained from estuarine shell (Bellwood et al., 1998), we calibrated it twice against the marine curve, firstly assuming a 100 % marine environment and then only 50% marine. The results of these two alternative calibrations were combined to produce the broadened date range used here, to account for the unknown variability of the estuarine shell habitat.

The two fossil taxa incorporated in our analysis, *Trichosurus dicksoni* and *Onirotocus reidi*, are recognised as members of the Riversleigh Faunal Zone C (FZC) which is estimated to be middle Miocene in age (Flannery and Archer, 1987; Arena et al., 2016). Here, we used the entire date range, as indicated by Cohen et al. (2013; updated), adjusted to post-date the node calibration for Phalangeridae. This resulted in an age range of 15.97 – 11.6299 Ma for the two fossil taxa.

We employed three node calibrations (Phalangeroidea, Burramyidae, and Phalangeridae) in addition to a root calibration as defined and implemented by Kealy et al. (in review), with node contents defined by the results of the molecular and morphological phylogenies produced in this study (see Supplementary Information Figures S4 and S8). The total evidence tip and node dated analyses was run for 50 million generations, with MrBayes settings otherwise the same as for the undated analysis (above).

2.6 Biogeographic Analysis

The two Timor *Phalanger orientalis* clades (sub-recent and modern, respectively) in the dated total evidence phylogeny were collapsed to a single representative tip each for the biogeographic analysis. Six geographic regions (Australia, New Guinea, Melanesia, Moluccas, Sulawesi, and Nusa Tenggara Timur) were recognised in our analysis (Figure 1) and taxa distributions assigned based on Helgen and Jackson (2015). In assigning geographic distributions, we allowed for taxa to be present in multiple regions (see Supplementary Information Table S1). The simplified phylogeny; converted to newick format, and the geographic distribution data were implemented in the R package BioGeoBEARS (Matzke, 2013) to infer the biogeographic history of the Phalangeridae.

BioGeoBEARS allows for the implementation (within a likelihood framework) and statistical comparison between the three most widely used models for investigating historical biogeography: Dispersal-Extinction-Cladogenesis (DEC) (Ree and Smith, 2008), Dispersal-Vicariance Analysis (DIVA) (Ronquist, 1997) and Bayesian Analysis of Biogeography (BayArea) (Landis et al., 2013). The BioGeoBEARS program also allows the inclusion of an additional parameter to incorporate founder-event speciation (+J) into the model.

As a result, we ran our dataset through BioGeoBEARS under six different models; DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, and BAYAREALIKE+J (where 'LIKE' indicates likelihood implementations of the models with regards to cladogenesis assumptions; Matzke, 2013). The results were then compared statistically based on Log Likelihood (LnL) and Akaike Information Criterion (AIC) to assess the data-to-model fit. P-values were also calculated to assess whether the null models; without founder-event speciation (+J), could be rejected. These statistical analyses were used to select the model which best fitted our data. The final biogeographic model was then compared with the archaeological record and palaeogeography to infer the possibility of human translocations in addition to natural dispersal events.

3 RESULTS

3.1 Phylogenetic Analysis

As this study is focused on divergence times and dispersal patterns of the Phalangeridae we focus here on the results of our dated total evidence analysis. The results of the molecular-

only, morphology-only, and undated total evidence phylogenetic analyses are included in Supplementary Information S4, S8, and S9, respectively.

Our dated, total evidence phylogenetic analysis produced a consensus tree with high support values (BPP > 0.91) for the majority of clades (Figure 2). Phalangeridae and its three modern subfamilies, Trichosurinae, Ailuropinae, and Phalangerinae, were all recovered as monophyletic with strong support (BPP > 0.91). The fossil trichosurid *Trichosurus dicksoni* is recovered as a basal member of the Trichosurinae clade, with low support (BPP < 0.80) and in paraphyly with the modern *Trichosurus* genus. With this exception, all genera represented by more than one species are recovered as monophyletic with strong support (BPP > 0.91).

Within *Phalanger*, a moderately supported (BPP = 0.80 – 0.91) clade including *P. pelengensis* and *P. ornatus* is the first to branch off, followed by a poorly supported clade (BPP < 0.80) consisting of *P. lullulae* and *P. gymnotis*. The branching position of *P. vesitus* and *P. breviceps* is reversed in the total evidence tree, placing *P. breviceps* in a monophyletic clade with *P. orientalis* (although with low support; BPP < 0.80), contrary to the molecular phylogenies of both this study (Figure S4) and Kealy et al. (in review). *P. orientalis* is recovered as monophyletic (BPP > 0.91) with the Timor samples forming a monophyletic clade comprising two subclades separating the sub-recent samples from Timor-Leste and the modern samples from west Timor.

3.2 Divergence Estimates

All the divergence estimates recovered in our dated total evidence phylogeny are markedly younger than those recovered in previous mitochondrial phylogenies of Phalangeridae but congruent with those from nuclear analyses (Table 3). Our estimates show remarkable congruence with those of Meredith et al. (2009), while all our 95% HPD intervals overlap with the Raterman et al. (2006) estimates. All our 95% HPD ranges fall outside of those of Ruedas and Morales (2005), while some overlap with the Kealy et al. (in review) estimates is recovered for all clades except *Phalanger orientalis* and the *P. orientalis* Timor samples (Table 3).

Table 3: Divergence estimates (in millions of years, to 2 d.p.) for select nodes from the calibrated phylogenetic analysis, modified from Kealy et al. (in review: Table 3).^a

Clade	95% HPD ^b (Ma)	Median Age (Ma)	Kealy et al. (in review)	Ruedas and Morales (2005)	Raterman et al. (2006)*	Meredith et al. (2009)
Crown Phalangeridae	20.12	17.04	35.54 –	27.3 –	36.2 –	21.7 –
(Trichosurinae (<i>Trichosurus</i> + <i>Wyulda</i>) –	–	–	18.57	24.7	17.55	13.6
Ailuropinae+Phalangerinae split)	13.62	–	–	–	–	–
Ailuropinae (<i>Ailurops</i> + <i>Strigocuscus</i>) –	17.2	14.13	30.39 –	23.2 –	32.47 –	17.9 –
Phalangerinae (<i>Phalanger</i> + <i>Spilococus</i>) split	–	–	15.55	21.1	13.95	10.7
	10.88	–	–	–	–	–

Crown Phalangerinae	12.59 – 7.66	10.14	24.42 – 11.93	16.1 – 14.6	19.43 – 6.00	11.6 – 6.2
<i>Phalanger</i>	11.72 – 6.88	9.34	19.12 – 9.16	13.8 – 12.5	16.18 – 4.07	10.5 – 5.4
<i>Phalanger orientalis</i>	1.18 – 0.25	0.64	4.07 – 1.13	n/a	n/a	n/a
<i>Phalanger orientalis</i> Timor samples	0.49 – 0.07	0.24	1.5 – 0.35	n/a	n/a	n/a

^aCompared with most recent estimates from molecular phylogenies of Phalangeridae (Ruedas and Morales, 2005; Raterman et al., 2006; Meredith et al., 2009; Kealy et al., in review). ^bHPD = Highest posterior density. *Raterman et al., (2006) date ranges are the compound ranges of both their Multidivtime and BEAST estimates.

3.3 Biogeographic Analysis

Our BioGeoBEARS model comparisons show strong support for a statistical difference ($p << 0.05$) between models without founder-event speciation (+J) and those with +J (Table 4). Furthermore, the LnL and AIC values recovered for the six model variations show greater support for those models which include +J than those where it is excluded. This shows that the DEC, DIVALIKE, and BAYAREALIKE models with the +J founder-event speciation are favoured over the implementation of these models without +J. Of the three +J models, the DEC+J model is the best fit for our dataset, based on LnL and AIC (Table 4), and thus the most likely to infer the correct ancestral range for each node. We therefore focus here on the results of the DEC+J model, however all model results are included in the Supplementary Information Figures S10-12.

Our DEC+J biogeographic model for Phalangeridae (Figure 3) recovers good support for an Australian origin of the family with a likely founder event out of Australia to Sulawesi occurring in the middle Miocene. The genera *Ailurops* and *Strigocuscus* are suggested to be the result of in-situ diversification on Sulawesi, while the *Spilococus* supports extensive inter-island dispersals throughout Indonesia and Melanesia. The *Phalanger* results suggest at least three, possibly four likely founder-events throughout its biogeographic history (Figure 3). The first of these founder-events is less well supported than the latter three, but suggests possible back dispersal from a Sulawesi/Sulawesi+Molucca phalangerine ancestor to New Guinea in the middle – late Miocene. Also in the late Miocene, two separate founder-events occur; the first to the Moluccas with the diversification of the *P. ornatus* and *P. pelengensis* clade, and the second from New Guinea to the Woodlark island group (i.e. Melanesia) with the appearance of *P. lullulae* (Figure 3).

The later Miocene and early Pliocene evolutionary patterns in *Phalanger* appear to be largely the result of in-situ diversification on New Guinea with some later inter-island dispersals from New Guinea to Melanesia (and in the case of *P. orientalis*, the Moluccas). The final founder-event recovered here is for the Timor *P. orientalis* population (Figure 3). While not recognised as a separate species or distinct subspecies; the Timor population is consistently recovered as

a separate monophyletic clade to the New Guinea *P. orientalis* samples (Figure 2; Figures S4, S9; Kealy et al., in review), and for the purposes of our investigation the application of a founder-event model at the population level is considered appropriate. The divergence of *P. brecevi* is also a likely founder-event, however, the lack of data on this species and its possible source population in Oro, PNG (Kealy et al., in review), makes further inferences into this dispersal beyond the scope of our current dataset.

Table 4: Comparison of biogeographic models run in BioGeoBEARS on the dated total evidence Phalangeridae phylogeny. LnL = [natural] log Likelihood, d = rate of dispersal, e = rate of extinction, and j = relative probability of founder-event speciation at cladogenesis, AIC = Akaike Information Criterion. P-values are shown for each model test with and without founder-event speciation (+J).

Model	Parameter Estimates				Likelihood-ratio Test	
	LnL	d	e	j	AIC	P -value
DEC	-52.6	0.0076	1.0e-12	0	109.2	
DEC+J	-48.58	0.0054	1.0e-12	0.033	103.2	0.0046
DIVALIKE	-58.29	0.010	0.010	0	120.6	
DIVALIKE+J	-52.23	0.0062	1.0e-12	0.042	110.5	0.0005
BAYAREALIKE	-70.42	0.010	0.053	0	144.8	
BAYAREALIKE+J	-51.93	0.0049	1.0e-07	0.052	109.9	0.0000000012

4 DISCUSSION

4.1 Classifications within Phalangeridae

The total evidence, dated phylogeny produced by our analysis is largely congruent with previous molecular phylogenies (e.g. Ruedas and Morales, 2005; Meredith et al. 2009; Kealy et al., in review), as expected due to the re-use of many of the same sequences. While not the most taxonomically comprehensive (see Kealy et al., in review), this is the first total evidence (molecular + morphology) phylogeny to be produced for the Phalangeridae, incorporating fossil and aDNA data. The position of *T. dicksoni* and corresponding low support values (BPP > 0.80) supports Crosby's (2007) tentative suggestion that '*Trichosurus*' *dicksoni* could represent an, as yet, undescribed genus of Trichosurinae. Regarding the position of our aDNA taxa, *P. ornatus*, the genus classification is well supported and a close relationship to *P. pelengensis* is reasonable based on biogeography. The future sequencing of modern *P. ornatus* samples will be required for any further investigations into the relationships and evolutionary history of this archaeological sample.

The sister relationship between *P. gymnotis* and *P. lullulae* recovered in our molecular-only (Figure S4) and total evidence (Figure 2) phylogenies is not found by previous studies

incorporating the same molecular sequences (Hamilton and Springer, 1999; Osborne and Christidis, 2001; Raterman et al., 2006; Kealy et al., in review). In the earlier studies *P. lullulae* is recovered in closer relationship to *P. orientalis* (Hamilton and Springer, 1999; Osborne and Christidis, 2001; Raterman et al., 2006), however, as shown by Kealy et al. (in review) the *P. orientalis* identification in these analyses is unreliable and could potentially represent a species not included in our analysis. Kealy et al. (in review) recovers *P. gymnotis* and *P. lullulae* as two separate clades comprising additional species, a result of the significantly greater number of taxa incorporated in their analysis. Future clarification and sequencing efforts of the additional species recovered in the *P. gymnotis* and *P. lullulae* clades (i.e. *P. matanim*, *P. intercastellanus* and *P. mimicus*) will likely resolve this relationship.

The reversed branching order of *P. vestitus* and *P. breviceps* in our total evidence phylogeny (Figure 2), compared to our molecular analysis (Figure S4) and that of Kealy et al. (in review), appears to be the result of 'hidden' support provided by the morphological dataset (Gatesy et al., 1999). A morphological analysis of *P. breviceps*, in addition to the likely source population on Oro, PNG (Kealy et al., in review), and further molecular sequencing of both these groups would be particularly helpful for improving our understanding of *P. breviceps* and the branching order between *P. vestitus*, *P. breviceps*, and *P. orientalis*.

Similarly, an extensive investigation into the morphology and genetics of *P. orientalis* populations, not just on Timor, but also the Moluccan islands (e.g. Ambon) and West Papua, will be required to determine the details of this group's evolutionary history (Kealy et al., in review). Our analysis recovers the aDNA samples as sister to the modern Timor samples, however, this is likely a reflection of geography; the modern samples are from west Timor, the aDNA from the east, rather than a temporal or methodological separation.

4.2 Biogeographic History of the Phalangeridae

Our divergence estimates and biogeographic model for the Phalangeridae (Table 3, Figure 3), provides strong support for the origin of this family in Australia sometime in the Oligocene to early Miocene. Following on from this we see the split between the Australian trichosurines and the Asia-Pacific cuscuses, with a founder-effect speciation event upon arrival of the cuscus ancestor on Sulawesi. The dispersal to Sulawesi is estimated to have occurred during the early to middle Miocene. While some land was present on both Sulawesi and western New Guinea at the end of the Oligocene, it was not until the early Miocene that the first volcanic activity and emergence of land between Sulawesi and New Guinea occurred (Hall, 2009). These small volcanic and uplifted islands likely enabled the cuscus ancestor to 'island hop' from Australia+New Guinea across to Sulawesi. Palaeogeographic reconstructions of Sulawesi suggest the emergence of highland regions over 1000 m for the first time at ca. 20 Ma (Nugraha and Hall, 2018), increasing the likely presence of ecosystems suitable for cuscus colonisation from this time. The later expansions in the size of Sulawesi during the late Miocene (Nugraha and Hall, 2018) likely drove the diversification of the ailuropines.

At ca. 10 Ma (late Miocene), we see the dispersal of the Phalangerinae ancestor back east from Sulawesi. This is entirely congruent with the palaeogeography, as until this time, those islands between New Guinea and Sulawesi were still moving rapidly north and west to become part of the Sulawesi island complex (Hall, 2009). It is not until the late Miocene that non-Sulawesi islands emerge for the first time. Additionally, these non-Sulawesi islands are connected to an

enlarged Sulawesi, and westerly extending New Guinea by shallow seas and coral reefs (Hall, 2009), significantly increasing the likelihood of successful cuscus dispersals at this time. These non-Sulawesi islands are all early members of the present-day Moluccan islands (Hall, 2009), also supporting a likely founder-event for the *Phalanger ornatus*+*P. pelengensis* clade at this time (Figure 3).

The latter diversification of *Phalanger* on New Guinea during the late Miocene – Pliocene corresponds with the steady uplift and expansion of this region during this period (Hall, 2009). The later dispersals into Melanesia is also congruent with the later emergence of these islands (Hall, 2001, 2009). The Pleistocene dispersal of *P. orientalis* also corresponds to the complete formation and emergence of the Moluccan and Nusa Tenggara islands in their present-day positions (Hall, 2009).

4.3 Anthropogenic Translocation vs. Natural Dispersal

We focus here on the possible prehistoric cuscus translocations for which there is an archaeological record (Table 1). Based on current distribution and classification data (Helgen and Jackson, 2015; Kealy et al., in review), we consider the following five species as possible translocations: *Phalanger orientalis* (Timor Island), *P. ornatus* (Halmahera Islands), *P. breviceps* (New Ireland and the Solomon Islands), *Spilocuscus maculatus* (St Matthias Islands), and *Sp. kraemeri* (Admiralty Islands) (Table 1). Unfortunately, there is currently insufficient data on the Admiralty spotted cuscus (*Sp. kraemeri*) for its inclusion in our phylogenetic analysis. The archaeological record from Manus Island does not provide any clear evidence for human introductions (Table 1), while the distinct morphology of *Sp. kraemeri* and its absence outside of the Admiralty Islands also supports an earlier, ‘natural’ dispersal (Helgen and Jackson, 2015; Heinsohn, 2010). Future analysis and incorporation into the total evidence phylogeny will be required to clarify the evolutionary relationships of this species.

The other *Spilocuscus* species considered here, *Sp. maculatus*, is known to have been introduced to the New Ireland and New Britain Islands in historic times (20th and 21st centuries; Heinsohn, 2010). Regarding prehistoric translocations, the St Matthias island group population has been suggested to result from human translocation, however, the archaeological record provides no clear evidence to support or disprove this hypothesis, as cuscus remains are recovered from the earliest deposits (Kirch, 1988; Kirch et al., 1991). The future discovery of natural faunal deposits which pre-date the human arrival record and lack cuscus remains would be required to support human translocation. Alternatively, DNA sequencing of modern St Matthias Island *Sp. maculatus* populations and possible aDNA from archaeological samples would enable a much clearer understanding of the evolutionary and biogeographic history of this group. Similarly, molecular and morphological studies of populations in the Moluccas and on Selayar Island (Sulawesi island group), in addition to further archaeological efforts in these regions, will significantly improve our understanding of this species’ biogeographic history, and likely identify cryptic species and subspecies within this diverse group (Helgen and Jackson, 2015).

The recently re-defined species *Phalanger breviceps* (Kealy et al., in review) is currently distributed throughout the Bismark Archipelago and the Solomon Islands (Helgen and Jackson, 2015). As a result of its previous classification as a subspecies of *P. orientalis*, the archaeological records for the region which document ‘*P. orientalis*’ most likely refer to *P.*

breviceps or its ancestor. The identification of an ancestral source population in Oro Province, PNG, by Kealy et al. (in review), raises further interesting questions about the origin and dispersal of this species. Here we recover *P. breviceps* in a closer relationship with *P. orientalis* than Kealy et al. (in review), however, its Pliocene divergence estimate supports its species-level classification. The archaeological evidence suggests an anthropogenic translocation of *P. breviceps* or its ancestor to New Ireland at ca. 23.6 – 22.5 ka (Leavesley et al., 2002; Leavesley and Chappell, 2004), followed by later translocations to the Solomon Islands at ca. 9 – 8.5 ka (Wickler, 2001). Due to the limited number of taxa in our phylogeny, we cannot determine if the Pliocene divergence estimate for *P. breviceps* reflects the *in-situ* evolution of its Oro ancestor, or a natural founder-event into the Bismark Archipelago. The lack of cuscus remains in the earlier archaeological deposits on New Ireland supports the former of these two hypotheses, with a single introduction from Oro ca. 23.6 – 22.5 ka, followed by consecutive eastward introductions out from New Ireland. Future DNA sequencing efforts of the Oro population, modern day Bismark and Solomon populations and aDNA from the archaeological deposits will be required to determine the divergence and dispersal history of *P. breviceps* and its island and ‘mainland’ (New Guinean) ancestor.

An initial analysis of the Gebe Island archaeological record may suggest translocation for *P. ornatus* based on the apparent gap in the record between human arrival and earliest recorded cuscus remains (Table 1). However, a closer examination of the Golo and Wetef sites on Gebe show that no animal bone whatsoever is recorded for the lower levels of the archaeological deposits, raising the possibility that the absence of cuscus remains in earlier levels is likely an issue of preservation and not a true representation of absence on the island (e.g. Bellwood et al., 1998; Irwin et al., 1999; Pasveer and Bellwood, 2004; Louys et al., 2017). *P. ornatus* archaeological records on Halmahera and Morotai both correspond with the earliest deposits and so cannot be used to support a translocation event. As for *Spilocuscus maculatus* on the St Matthias islands, future discoveries of faunal deposits lacking cuscus remains and pre-dating the current archaeological records are also required to support translocation. The early divergence estimates recovered here along with the biogeographic model and suggested founder-event speciation in the Moluccas, provides strong indications for a natural dispersal origin of the Halmahera cuscus.

Good archaeological and fossil evidence supports an anthropogenic translocation of *P. orientalis* to the island of Timor (Table 1; O’Connor, 2015). Additionally, model support for a founder-event speciation origin of the Timor populations in our biogeographic analysis and a recent divergence estimate from our phylogeny provide further support for a human introduction. While our divergence estimate for the Timor *P. orientalis* (Table 3) pre-dates both the archaeological record for cuscus (O’Connor, 2015) and the earliest dates for human occupation of the region (Clarkson et al., 2017; Westaway et al., 2017), it is significantly younger than the estimate produced by the *ND2* analysis of Kealy et al. (in review). Mitochondrial data is notorious for overestimating divergence times (Ho et al., 2005), as indicated by the comparison between nuclear and mitochondrial results in Table 3. The incorporation of nuclear DNA, in addition to fossil and archaeological tip calibrations in our analysis, makes our divergence estimates here the most reliable for Phalangeridae. A split between the east and west Timor populations ca. 240 – 90 ka ago could potentially represent introductions from different source populations that separated at this time, or alternatively be the result of increased mutation rates upon arrival on Timor, pushing divergence estimates

back in time due to temporal dependency of the molecular clock (Ho et al., 2005). Regarding *P. orientalis* and the Timor population specifically, as in the case of *P. breviceps* and its Oro ancestor, the lack of data concerning the intervening populations between east New Guinea and Timor makes further inferences on the divergence times for the Timor *P. orientalis* not possible at this time.

4.4 Methodological Considerations

The application of phylogeographical methods to investigations of possible translocation events shows promise. While unfortunate limitations in data availability and the current issue of unreliable species identifications has hindered a more refined result, our results still provide insights into some translocation hypotheses. The combination of divergence estimates produced by the total evidence phylogeny with dispersal hypotheses produced by the biogeographic model adds a unique line of evidence to that already provided by the archaeological records. In particular, the incorporation of the +J parameter in the BioGeoBEARS program for founder-event speciation enables the detection of long-distance colonisation events which result in genetically isolated populations (Matzke, 2014). Founder-events are considered rare under natural circumstances, although slightly more common in island regions (Mayr, 1954). A modelled founder-event for the dispersal of the Timor *Phalanger orientalis*, however, provides strong support for an anthropogenic translocation event, as long-distance dispersal can also be the result of human agency. The founder-effect to speciation, whereby the new (small) population experiences strong and rapid genetic drift as a result of genetic bottlenecks in the colonising population (Mayr, 1954; Matzke, 2014), is also seen in our phylogeographic analysis as evidence for translocation. Individuals selected by humans for introductory purposes are likely to be from the same population (or even the same family group) and representative of just one or two generations, thus representing a very small subset of the genetic diversity of the species. Natural dispersals, while also susceptible to genetic bottlenecks, have greater potential for wider genetic diversity across time and space. The likely rapid rates of evolution in the Timor *P. orientalis* population due to the founder-effect is suggested in the over-estimates of divergence times recovered by our phylogeny due to temporal dependency of the molecular clock.

In contrast, the possible introductions of the *Phalanger ornatus* species group to the north Moluccas is not supported by our phylogeography. The analysis here, with its early divergence estimates and good correlation between the biogeographic model and palaeogeological reconstructions, provides strong support for natural dispersals. Thus, this study provides hope for future use of this methodology for testing translocation hypotheses. Importantly, using phylogeography to investigate questions of prehistoric human-environment interactions enables the application of a largely separate line of evidence for hypothesis testing and validation. This is particularly important for cases such as *P. ornatus* where there is a lack of pre-cuscus faunal deposits and so the archaeological record is insufficient evidence to support or refute a translocation hypothesis.

The most significant addition which biogeography can add to questions of translocations concerns directionality. Our study has produced two key results on this point. Firstly, determinations of directionality for dispersal/translocation events using phylogenetics and biogeographic models is demonstrated. Even with the limited dataset used here, we are able to determine that colonisation (probably due to translocation) of New Ireland likely occurred

from populations in Oro province, PNG, and that later translocations to the other Bismark islands and the Solomon Islands were sourced not from New Guinea, but the New Ireland or other island populations. Similarly, the *P. orientalis* population on Timor was introduced from the east from an evolutionary origin on New Guinea, although the exact source population, either New Guinea or various Moluccan islands, is still in question. The uncertainty regarding *P. orientalis* highlights the second key conclusion of directional investigations using this methodology: the current lack of data at a greater geographic and population-level resolution. Our study shows that determination of directionality in dispersals and translocations is possible with phylogeography, but that accurate and fine inter-island scale results require similarly extensive datasets. Excitingly, our study has very clearly indicated regions and species where brief, concerted efforts in data collection, followed by their implementation into our model, will provide unique insights into cuscus biogeography and their earliest human interactions.

5 CONCLUSION

This study has produced the first dated, total evidence phylogeny of the Phalangeridae and the first biogeographic model of the family's history. This is also the first attempt to apply phylogenetic and biogeographic analyses to questions of prehistoric translocations of animals by people. We recovered strong support for a Miocene origin for all three phalangerid subfamilies, and much geographic and temporal congruence between the biogeographic model and the palaeogeography of the region. In particular, the founder-effect speciation event to Sulawesi and later, back dispersals east to the Moluccas and New Guinea is well supported by our biogeographic model and the palaeogeological reconstructions of Hall (2009).

Concerning possible cuscus translocations in prehistory, we find good support for anthropogenic translocations of *Phalanger breviceps* from New Ireland to islands in the Bismarks and Solomon Islands, and likely from Oro, PNG to New Ireland. Good support for an anthropogenic translocation origin of the Timor *P. orientalis* populations is recovered by our phylogeny and biogeographic model, suggesting a New Guinea origin for the species although the exact source population location remains unknown. *Spiloglossus maculatus* likely also owes some of its present distribution to prehistoric dispersals but the current lack of data on this species group makes investigations of this not possible. We also found good evidence against translocation for *Phalanger ornatus* on the islands of the Halmahera island group, north Moluccas. Instead an early, pre-human arrival scenario of biogeographic dispersal and vicariance is suggested by our biogeographic model and palaeogeological comparisons.

The secondary consideration of this model for investigating directionality is less well tested by our study due to the limitations of our dataset. However, there are still a number of conclusions we are able to make. Firstly, the likely translocation of the *P. breviceps* ancestor to New Ireland was probably only a single event, originating from cuscus populations in Papua New Guinea's Oro province. Once populations became established on New Ireland, these would have been the source for translocations to the Solomon Islands, not additional translocations from New Guinea. This scenario supports a more localised focus on cuscus translocations within individual archipelagos. Some degree of directionality can also be inferred for the Timor *P. orientalis* based on its close relationship to the New Guinea populations. However, the lack of data for populations on the intervening islands makes it

currently impossible to determine if translocations occurred directly from New Guinea or via the islands of the Moluccas.

This study demonstrates the potential this method has for future investigations of prehistoric anthropogenic translocations of island species. In particular, detailed biogeographic histories at the subspecies and population level have the potential to determine the regularity and direction of human introductions between islands. Key areas for future study (as detected by our analysis) include the aDNA record of the Bismark and Solomon cuscus, the Oro *P. breviceps* ancestral population, *P. orientalis* populations from Indonesian Papua (west New Guinea) and the Moluccas, modern *P. ornatus* data, and population-level information on *Spiloglossus maculatus* from St Matthias, the Moluccas, and Selayar island. Detailed phylogeographic analysis into all of these areas, and their input into our model, will doubtlessly uncover a wealth of information regarding cuscus biogeographic history, dispersals and translocation events.

Acknowledgments

This research was partially funded by an Australian Archaeology Association Student Research Grant awarded to S.K., an ARC Laureate awarded to S.O. (FL120100156), an ARC Discovery grant (DP140103650) awarded to SCD, KA and PP, PhD student research funds provided to S.K. by the School of Culture, History and Language, College of Asia and the Pacific, ANU, and Archaeology and Natural History at ANU student research funding awarded to S.K. We thank Dr Alejandro Velasco Castrillon for performing the Sanger sequencing and everyone at the Australian Centre for Ancient DNA (University of Adelaide) for their assistance. We thank Dr Sandy Inglby at the Australian Museum and Dr Kenny Travouillon at the Western Australian Museum for providing assistance and access to specimens. We thank Dr Kirsten Crosby, Dr Anna Gillesby, Dr Robin Beck, and Prof. Mike Archer for advice and access to data and specimens for the morphological and fossil aspects of this study.

Supplementary Information

Additional information on genes and GenBank accession numbers (S1), methods of DNA extraction and sequencing (S2), sequence partitions, nucleotide substitution models, and node calibrations (S3), results of the molecular-only phylogeny (S4), characters scored for the morphological analysis (S5), museum specimen vouchers analysed in morphological analysis (S6), morphological matrix scores (S7), morphological-only phylogeny (S8), undated total evidence phylogeny (S9), BioGeoBEARS models (S10-12), range probabilities for nodes in biogeographic model (S13), and corresponding node numbers used by the biogeographic analysis (S14) are in the supplementary document. Nexus files for the molecular-only and total evidence analysis will be made available online following manuscript publication. All new molecular sequences will be made available on GenBank following manuscript publication; see <https://www.ncbi.nlm.nih.gov/genbank/>.

REFERENCES

Archer, M., Hand, S.J., Black, K.H., Beck, R.M.D., Arena, D.A. and Kealy, S., 2016. A new family of bizarre durophagous carnivorous marsupials from Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland. *Scientific Reports*, 6, 26911.

- Arena, D.A., Travouillon, K.J., Beck, R.M., Black, K.H., Gillespie, A.K., Myers, T.J., Archer, M. and Hand, S.J., 2016. Mammalian lineages and the biostratigraphy and biochronology of Cenozoic faunas from the Riversleigh World Heritage Area, Australia. *Lethaia*, 49(1), 43-60.
- Bellwood, P., Nitihaminoto, G., Irwin, G., Gunadi, A.W. and Tanudirjo, D., 1998. 35,000 years of prehistory in the northern Moluccas. In: Bartstra, G.J. (Ed.), *Bird's Head Approaches: Irian Jaya Studies, a Programme for Interdisciplinary Research. Modern Quaternary research in Southeast Asia Vol. 15*. A. A. Balkema Publishers, Rotterdam, Netherlands, pp.233-75.
- Burk, A., Douzery, E.J. and Springer, M.S., 2002. The secondary structure of mammalian mitochondrial 16S rRNA molecules: refinements based on a comparative phylogenetic approach. *Journal of Mammalian Evolution*, 9(3), 225-252.
- Calaby J. 1984. Forward. In: Smith, A.P. and Hume, I.D. (Eds.), *Possums and Gliders*. Surrey Beatty and Sons with Australian mammal Society, Sydney, pp. iii-iv.
- Cohen, K.M., Finney, S.C., Gibbard, P.L. and Fan, J.-X., 2013 (updated: 2018/08). The ICS International Chronostratigraphic Chart. *Episodes*, 36, 199-204.
- Colgan, D.J., Flannery, T.F., Trimble, J. and Aplin, K.P., 1993. Electrophoretic and Morphological Analysis of the Systematics of the Phalanger-Orientalis (Marsupialia) Species Complex in Papua-New-Guinea and the Solomon-Islands. *Australian Journal of Zoology*, 41(4), 355-378.
- Clarkson, C., Jacobs, Z., Marwick, B., Fullagar, R., Wallis, L., Smith, M., Roberts, R.G., Hayes, E., Lowe, K., Carah, X., Florin, S.A., et al., 2017. Human occupation of northern Australia by 65,000 years ago. *Nature*, 547(7663), 306-310.
- Crosby, K., 2002. Studies in the diversity and evolution of phalangeroid possums (Marsupialia; Phalangerida; Phalangeroidea). PhD Thesis, University of New South Wales, Sydney.
- Crosby, K., 2007. Rediagnosis of the fossil species assigned to *Strigocuscus* (Marsupialia, Phalangeridae), with description of a new genus and three new species. *Alcheringa*, 31(1), 33-58.
- Crosby, K., Bassarova, M., Archer, M. and Carbery, K., 2004. Fossil possums in Australasia: discovery, diversity and evolution. In: Goldingay, R.L. and Jackson, S.M. (Eds.), *The Biology of Australian Possums and Gliders*. Surrey Beatty and Sons Pty Ltd., Chipping Norton, NSW, pp.161-176.
- Crosby, K. and Norris, C.A., 2003. Periotic morphology in the trichosurin possums *Strigocuscus celebensis* and *Wyulda squamicaudata* (Diprotodontia, Phalangeridae) and a revised diagnosis of the tribe Trichosurini. *American Museum Novitates*, 3414, 1-14.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32(5), 1792-1797.
- Flannery, T., 1994. *Possums of the World: A Monograph of the Phalangeroidea*. Australian Museum/Geo Productions, Sydney.
- Flannery, T., 1995. *Mammals of the South-West Pacific and Moluccan Islands*. Australian Museum/Reed Books, Sydney.

Flannery, T. and Archer, M., 1987. *Strigocuscus reidi* and *Trichosurus dicksoni*, two new fossil phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. In: Archer, M. (Ed.), *Possums and Opossums: Studies in Evolution*. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney, pp. 527-536.

Flannery, T., Archer, M. and Maynes, G., 1987. The phylogenetic relationships of living phalangerids (Phalangerioidea: Marsupialia) with a suggested new taxonomy. In: Archer, M. (Ed.), *Possums and Opossums: Studies in Evolution*. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney, pp. 477-506.

Flannery, T.F and White, J.P. 1991. Animal translocations. *National Geographic Research and Exploration*, 7(1), 96-113.

Fredericksen, C., Spriggs, M. and Ambrose, W., 1993. Pamwak rockshelter: a Pleistocene site on Manus Island, Papua New Guinea. In: Smith, M.A., Spriggs, M. and Fankhauser, B.L. (Eds.), *Sahul in Review: Pleistocene Archaeology in Australia, New Guinea and Island Melanesia. Occasional Papers in Prehistory, No. 24*. Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra, pp.144-154.

Gatesy, J., O'Grady, P. and Baker, R.H., 1999. Corroboration among data sets in simultaneous analysis: hidden support for phylogenetic relationships among higher level artiodactyl taxa. *Cladistics*, 15(3), 271-313.

George, G.C., 1987. Characterisation of the living species of cuscus (Marsupialia: Phalangeridae). In: Archer, M. (Ed.), *Possums and Opossums: Studies in Evolution*. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney, pp. 507-526.

Glover, I., 1986. *Archaeology in Eastern Timor, 1966-67. Terra Australis* 11. Australian National University, Canberra.

Groves, C.P., 1976. The origin of the mammalian fauna of Sulawesi (Celebes). *Zeitschrift für Säugetierkunde*, 41, 201-216.

Groves, C.P., 2005. Order Diprotodontia. In: Wilson, D.E. and Reeder, D.M. (Eds.), *Mammal species of the world: A taxonomic and geographic reference, 3rd edition*. The Johns Hopkins University Press, Baltimore, MD, pp. 43-70.

Hall, R., 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall, R. and Holloway, J.D. (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, The Netherlands, pp. 99-131.

Hall, R., 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. In: Metcalfe I., Smith J.M.B., Morwood M. and Davidson I.D. (Eds.), *Faunal and Floral Migrations and Evolution in SE Asia–Australasia*. Balkema (Swets, Zeitlinger Publishers), Lisse, pp.35-56.

Hall, R., 2009. Southeast Asia's changing palaeogeography. *Blumea-Biodiversity, Evolution and Biogeography of Plants*, 54(1-2), 148-161.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95-98.

Hamilton, A.T., and Springer, M.S., 1999. DNA sequence evidence for placement of the ground cuscus, *Phalanger gymnotis*, in the tribe Phalangerini (Marsupialia: Phalangeridae). *Journal of Mammalian Evolution*, 6, 1-17.

Hawkins, S., O'Connor, S., Maloney, T.R., Litster, M., Kealy, S., Fenner, J.N., Aplin, K., Boulanger, C., Brockwell, S., Willan, R. and Pidot, E., 2017. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. *Quaternary Science Reviews*, 171, 58-72.

Heinsohn, T., 1997. Phantoms in the foliage: human influences on the rainforests of the New Guinea Archipelago. In: Dargavel, J. (Ed.), *Australia's Ever-changing Forests III*. Australian Forest History Society/Centre for Resource and Environmental Studies, Australian National University, Canberra, pp. 278-295.

Heinsohn T.E., 1998. *The Realm of the Cuscus: Animal Translocation and Biological Invasions East of Wallace's Line*. Masters Thesis, Australian National University, Canberra.

Heinsohn, T.E., 2001. Human influences on vertebrate zoogeography: animal translocation and biological invasions across and to the east of Wallace's Line. In: Metcalfe, I., Smith, J.M.B., Morwood, M. and Davidson, I. (Eds.), *Faunal and Floral Migrations and Evolution in SE Asia-Australasia*. A.A. Balkema, Lisse, pp. 153-170.

Heinsohn T.E., 2004. Phalangeroids as ethnotramps: A brief history of possums and gliders as introduced species. In: Goldingay, R.L. and Jackson, S.M. (Eds.), *The Biology of Australian Possums and Gliders*. Surrey Beatty and Sons Pty Ltd., Chipping Norton, NSW, pp. 506-526.

Heinsohn, T.E., 2010. Marsupials as introduced species: Long-term anthropogenic expansion of the marsupial frontier and its implications for zoogeographic interpretation. In: Haberle, S., Stevenson, J. and Prebble, M. (Eds.), *Altered Ecologies: Fire, climate and human influence on terrestrial landscapes. Terra Australis Vol. 32*. ANU E Press, Canberra, pp.133-176.

Helgen, K. M., and Jackson, S. M. (2015). Family Phalangeridae (Cuscuses, Brush-tailed Possums and Scaly-tailed Possum). In: Wilson, D.E. and Mittermeier, R.A. (Eds.), *Handbook of The Mammals of the World, Vol. 5: Monotremes and Marsupials*. Lynx Edicions, Barcelona, pp. 456-497.

Ho, S.Y., Phillips, M.J., Cooper, A. and Drummond, A.J., 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Molecular Biology and Evolution*, 22(7), 1561-1568.

Hofreiter, M., Paijmans, J.L., Goodchild, H., Speller, C.F., Barlow, A., Fortes, G.G., Thomas, J.A., Ludwig, A. and Collins, M.J., 2015. The future of ancient DNA: Technical advances and conceptual shifts. *BioEssays*, 37(3), 284-293.

Horovitz, I. and Sánchez-Villagra, M.R., 2003. A morphological analysis of marsupial mammal higher-level phylogenetic relationships. *Cladistics*, 19(3), 181-212.

Irwin, G., Bellwood, P., Nitihaminoto, G., Tanudirjo, D. and Siswanto, L., 1999. Prehistoric relations between Island Southeast Asia and Oceania: recent archaeological investigations in the Northern Moluccas. In: Galipaud, J.-C. and Lilley, I. (Eds.), *Le Pacifique de 5000 à 2000*

avant le present: Supplements a l'histoire d'une colonisation. Editions de IRD, Paris, pp. 363-374.

Kealy, S. and Beck, R., 2017. Total evidence phylogeny and evolutionary timescale for Australian faunivorous marsupials (Dasyuromorphia). *BMC Evolutionary Biology*, 17(1), 240.

Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S. and Louys, J., (*in review*). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial *ND2* gene. *Australian Mammalogy*.

Kirch, P.V., 1988. The Talepakemalai Lapita site and oceanic prehistory. *National Geographic Research*, 4(3), 328-342.

Kirch, P.V., Hunt, T.L., Weisler, M., Butler, V. and Allen, M.S., 1991. Mussau Islands prehistory: Results of the 1985-86 excavations. In: Allen, J. and Gosden, C. (Eds.), *Report of the Lapita Homeland Project. Occasional Papers in Prehistory, No. 20*. Highland Press, Canberra, pp.144-163.

Kirsch, J.A. and Wolman, M.A., 2001. Molecular relationships of the bear cuscus, *Ailurops ursinus* (Marsupialia: Phalangeridae). *Australian Mammalogy*, 23(1), 23-30.

Kumar, S., Stecher, G. and Tamura, K., 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33(7), 1870-1874.

Landis, M.J., Matzke, N.J., Moore, B.R. and Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, 62(6), 789-804.

Lanfear, R., Calcott, B., Ho, S.Y. and Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29(6), 1695-1701.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. and Calcott, B., 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34(3), 772-773.

Leavesley, M.G., 2005. Prehistoric hunting strategies in New Ireland, Papua New Guinea: The evidence of the cuscus (*Phalanger orientalis*) remains from Buang Merabak cave. *Asian Perspectives*, 44, 207-218.

Leavesley, M.G., Bird, M.I., Fifield, L.K., Hausladen, P.A., Santos, G.M. and Di Tada, M.L., 2002. Buang Merabak: early evidence for human occupation in the Bismarck Archipelago, Papua New Guinea. *Australian Archaeology*, 54(1), 55-57.

Leavesley, M.G. and Chappell, J., 2004. Buang Merabak: additional early radiocarbon evidence of the colonisation of the Bismarck Archipelago, Papua New Guinea. *Antiquity*, 78(301), <http://antiquity.ac.uk/ProjGall/leavesley/index.html>

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6), 913-925.

- Louys, J., Kealy, S., O'Connor, S., Price, G.J., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Tanudirjo, D.A., Santoso, W.D. and Hidayah, A.R., 2017. Differential preservation of vertebrates in Southeast Asian caves. *International Journal of Speleology*, 46(3), 379-408.
- Matzke, N., 2013. *BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts. R Package Version 1.1*. University of California, Berkeley, CA.
<http://CRAN.R-project.org/package=BioGeoBEARS>
- Matzke, N.J., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, 63(6), 951-970.
- Mayr, E., 1954. Change of genetic environment and evolution. In: Huxley, J., Hardy, A.C. and Ford, E.B. (Eds.), *Evolution as a Process*. George Allen and Unwin, London, pp. 157-180.
- Mayr, E. and Diamond, J., 2001. *The Birds of Northern Melanesia: Speciation, Ecology and Biogeography*. Oxford University Press, Oxford.
- Meijer, H.J., Louys, J. and O'Connor, S., 2019. First record of avian extinctions from the Late Pleistocene and Holocene of Timor Leste. *Quaternary Science Reviews*, 203, 170-184.
- Menzies, J.I. and Pernetta, J.C., 1986. A taxonomic revision of cuscuses allied to *Phalanger orientalis* (Marsupialia: Phalangeridae). *Journal of Zoology*, 1(3), 551-618.
- Meredith, R.W., Westerman, M., and Springer, M.S., 2009. A phylogeny of Diprotodontia (Marsupialia) based on sequences for five nuclear genes. *Molecular Phylogenetics and Evolution*, 51, 554-571.
- Miller, M.A., Pfeiffer, W. and Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE), November 2010*. New Orleans, LA, pp. 1-8.
- Mitchell, K.J., Pratt, R.C., Watson, L.N., Gibb, G.C., Llamas, B., Kasper, M., Edson, J., Hopwood, B., Male, D., Armstrong, K.N., Meyer, M., et al., 2014. Molecular phylogeny, biogeography, and habitat preference evolution of marsupials. *Molecular Biology and Evolution*, 31(9), 2322-2330.
- Norris, C.A., 1994. The periotic bones of possums and cuscuses: cuscus polyphyly and the division of the marsupial family Phalangeridae. *Zoological Journal of the Linnean Society*, 111, 73-98.
- Norris, C.A., and Musser, G.G., 2001. Systematic revision within *Phalanger orientalis* complex (Diprotodontia, Phalangeridae): a third species of lowland gray cuscus from New Guinea and Australia. *American Museum Novitates*, 3356, 1-20.
- Nugraha, A.M.S. and Hall, R., 2018. Late Cenozoic palaeogeography of Sulawesi, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 490, 191-209.
- O'Connor, S., 2006. Unpacking the Island Southeast Asian Neolithic Cultural Package, and finding local complexity. In: Bacus, E.A., Glover, I.C. and Pigott, V.C. (Eds.), *Uncovering Southeast Asia's Past: Selected Papers from the 10th International Conference of the European Association of Southeast Asian Archaeologists*. NUS Press, Singapore, pp. 74-87.

- O'Connor, S., 2007. New evidence from East Timor contributes to our understanding of earliest modern human colonisation east of the Sunda Shelf. *Antiquity*, 81(313), 523-535.
- 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. and Aplin, K., 2007. A matter of balance: An overview of Pleistocene occupation history and the impact of the Last Glacial Phase in East Timor and the Aru Islands, eastern Indonesia. *Archaeology in Oceania*, 42(3), 82-90.
- O'Connor, S., Robertson, G. and 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. and 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'Reilly, J.E. and Donoghue, P.C., 2016. Tips and nodes are complementary not competing approaches to the calibration of molecular clocks. *Biology Letters*, 12(4), 20150975.
- Osborne, M.J., and Christidis L., 2002. Molecular relationships of the cuscuses, brushtail and scaly-tailed possums (Phalangerinae). *Australian Journal of Zoology*, 50, 135-149.
- Pasveer, J.M. and Bellwood, P., 2004. Prehistoric bone artefacts from the northern Moluccas, Indonesia. In: Keates, S.G. and Pasveer, J.M. (Eds.), *Quaternary Research in Indonesia. Modern Quaternary Research in Southeast Asia, Vol. 18*. A. A. Balkema Publishers, Netherlands, pp.301-360.
- Pigram, C.J. and Symonds, P.A., 1991. A review of the timing of the major tectonic events in the New Guinea Orogen. *Journal of Southeast Asian Earth Sciences*, 6(3-4), 307-318.
- Pütz, J., Dupuis, B., Sissler, M. and Florentz, C., 2007. Mamit-tRNA, a database of mammalian mitochondrial tRNA primary and secondary structures. *RNA*, 13(8), 1184-1190.
- Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, 51(1), 337-360.
- Raterman, D., Meredith, R.W., Ruedas, L.A., and Springer, M.S., 2006. Phylogenetic relationships of the cuscuses and brushtail possums (Marsupialia: Phalangeridae) using the nuclear gene BRCA1. *Australian Journal of Zoology*, 54, 353-361.
- Ree, R.H. and Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57(1), 4-14.
- 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., et al., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, 55(4), 1869-1887.
- Ronquist, F., 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, 46(1), 195-203.

- Ronquist, F., Huelsenbeck, J. and Teslenko, M., 2011. Draft MrBayes version 3.2 manual: tutorials and model summaries. Distributed with the software from <http://brahms.biology.rochester.edu/software.html>.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. and Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539-542.
- Ruedas, L.A., and Morales, J.C., 2005. Evolutionary relationships among genera of Phalangeridae (Metatheria: Diprotodontia) inferred from mitochondrial DNA. *Journal of Mammalogy*, 86, 353-365.
- Shipton, C., O'Connor, S., Jankowski, N., O'Connor-Veth, J., Maloney, T., Kealy, S. and Boulanger, C. (*in review*). Conditions for continuity in human behaviour: A new sequence spanning 44,000 years from Asitau Kuru (Jerimalai), Timor-Leste, Wallacea. *Archaeological and Anthropological Sciences*.
- Spriggs, M., 1997. *The Island Melanesians*. Blackwell, Oxford.
- Springer, M.S. and Douzery, E., 1996. Secondary structure and patterns of evolution among mammalian mitochondrial 12S rRNA molecules. *Journal of Molecular Evolution*, 43(4), 357-373.
- Summerhayes, G.R., 2007. Island Melanesian pasts: a view from archaeology. In: Friedlaender, J. (Ed.), *Genes, language, and culture history in the Southwest Pacific*. Oxford University Press, New York, pp.10-35.
- Voss, R.S. and Jansa, S.A., 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. *Bulletin of the American Museum of Natural History*, 276, 1-82.
- Voss, R.S. and Jansa, S.A., 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. *Bulletin of the American Museum of Natural History*, 322, 1-177.
- 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., et al., 2017. An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature*, 548(7667), 322-325.
- Wickler, S., 2001. *The Prehistory of Buka: A Stepping Stone Island in the Northern Solomons*. *Terra Australis*, Vol. 16. University Printing and Duplicating Service, The Australian National University, Canberra.
- Williams, C., 1999. Faunal composition of Pamwak site, Manus Island, PNG. In: Galipaud, J. -C. and Lilley I. (Eds.), *Le Pacifique de 5000 à 2000 avant le présent: suppléments à l'histoire d'une colonisation*. Institut de Recherche pour le Développement, Paris, pp. 241-249
- Zhang, C., Stadler, T., Klopstein, S., Heath, T.A. and Ronquist, F., 2016. Total-evidence dating under the fossilized birth–death process. *Systematic Biology*, 65(2), 228-249.

FIGURE CAPTIONS

Figure 1: Map showing distribution of the Phalangeridae (dark shading), with geographic regions used for the biogeographic analysis shaded in colours corresponding to Figure 3.

Figure 2: Time-calibrated total evidence phylogeny of the Phalangeridae. Nodes coloured according to mean Bayesian posterior probabilities (BPP), black = >0.91, orange = 0.80-0.91, red = <0.80. Branch lengths are proportional to time and correspond to the scale at the base, in millions of years before present. Bars at nodes represent 95% Highest Posterior Densities (HPD).

Figure 3: Dispersal-Extinction-Cladogenesis with founder-event speciation (DEC+J) biogeographic model for Phalangeridae based on the calibrated total evidence analysis (Figure 2). Pie charts indicate relative probabilities of the most likely ancestral ranges for each node corresponding to geographic ranges in Figure 1. Colours of widespread ranges are shown as mixtures of the colours used for the single areas, e.g. *Phalanger pelengensis* = Sulawesi (red) + Moluccas (yellow) = orange. Percentage probability of the modelled ancestral range (see Supplementary Information Table S13) is shown in corresponding colour at each node. J indicates a likely “jump-dispersal” or founder-event. Blue = Australia, Green = Melanesia, Yellow = Moluccas, Teal = New Guinea, Pink = Nusa Tenggara Timur, Red = Sulawesi.

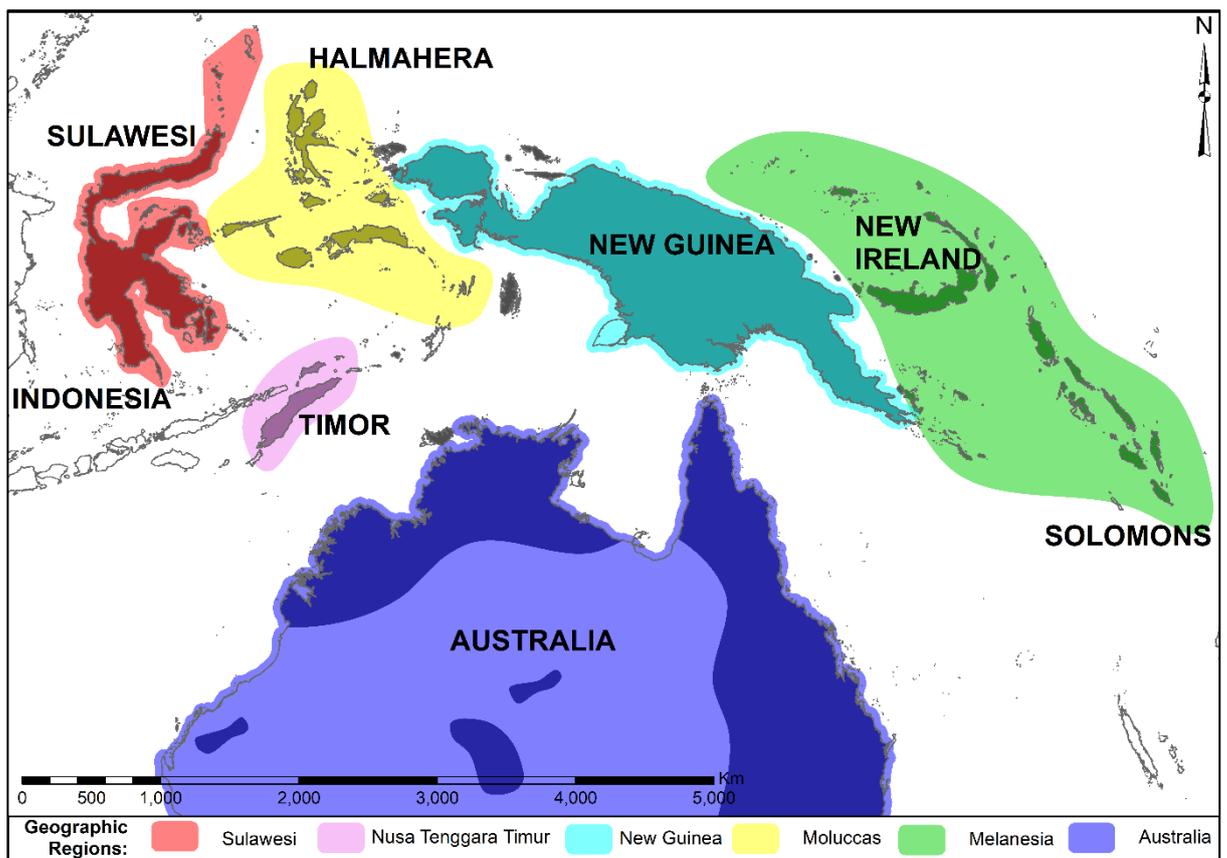


Figure 1: Map showing distribution of the Phalangeridae (dark shading), with geographic regions used for the biogeographic analysis shaded in colours corresponding to Figure 3.

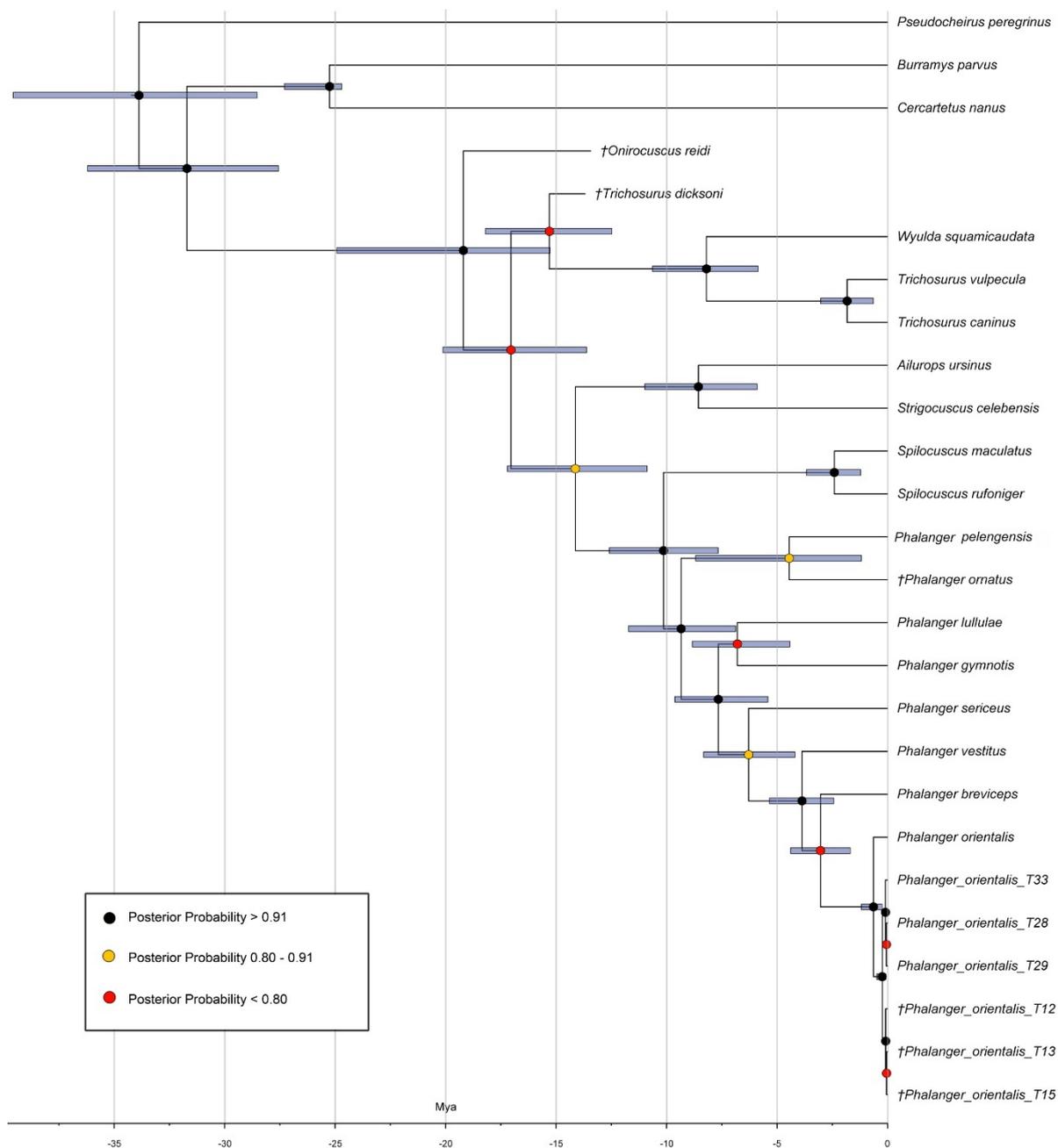


Figure 2: Time-calibrated total evidence phylogeny of the Phalangeridae. Nodes coloured according to mean Bayesian posterior probabilities (BPP), black = >0.91, orange = 0.80-0.91, red = <0.80. Branch lengths are proportional to time and correspond to the scale at the base, in millions of years before present. Bars at nodes represent 95% Highest Posterior Densities (HPD).

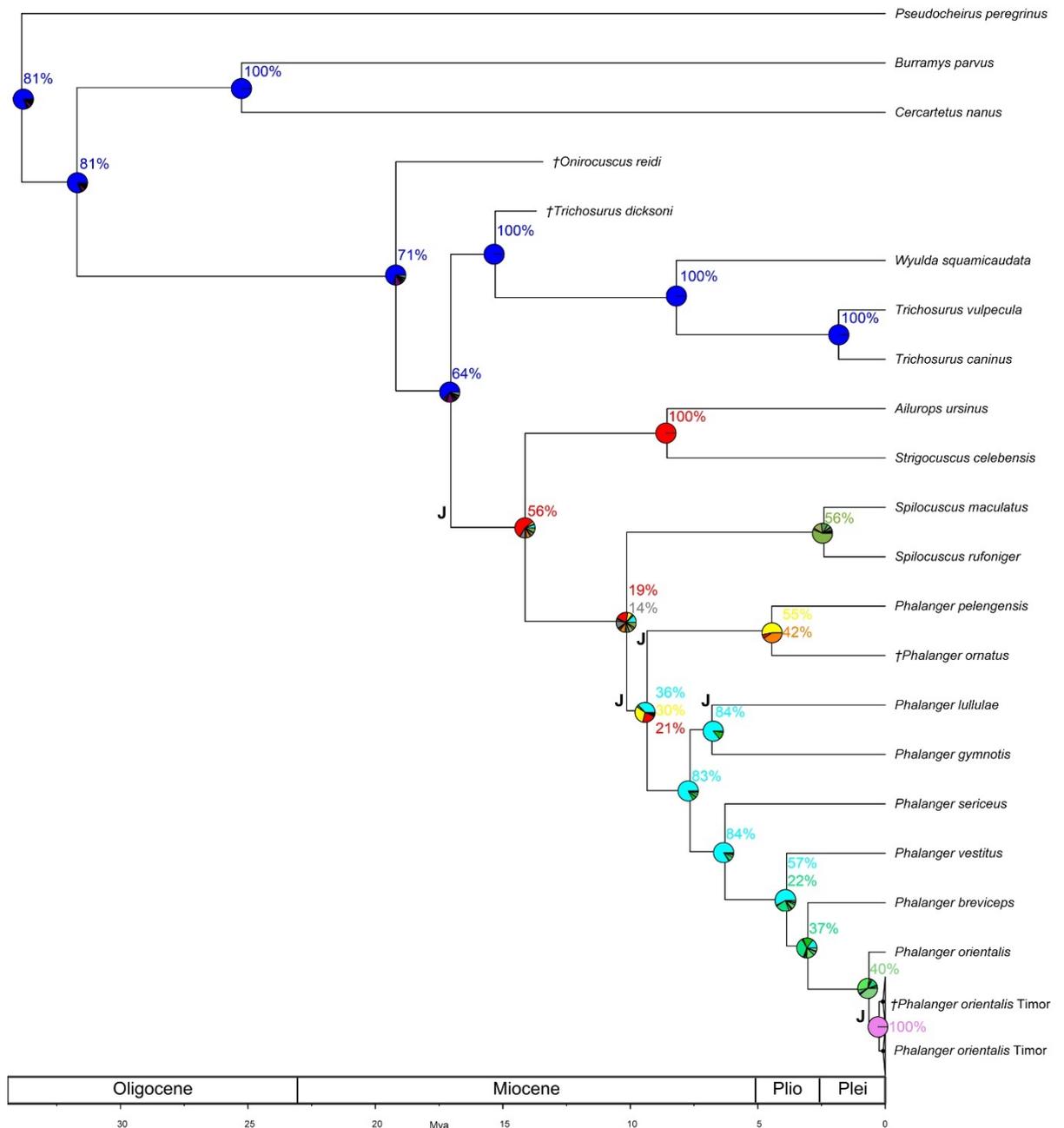


Figure 3: Dispersal-Extinction-Cladogenesis with founder-event speciation (DEC+J) biogeographic model for Phalangeridae based on the calibrated total evidence analysis (Figure 2). Pie charts indicate relative probabilities of the most likely ancestral ranges for each node corresponding to geographic ranges in Figure 1. Colours of widespread ranges are shown as mixtures of the colours used for the single areas, e.g. *Phalanger pelengensis* = Sulawesi (red) + Moluccas (yellow) = orange. Percentage probability of the modelled ancestral range (see Supplementary Information Table S13) is shown in corresponding colour at each node. J indicates a likely "jump-dispersal" or founder-event. Blue = Australia, Green = Melanesia, Yellow = Moluccas, Teal = New Guinea, Pink = Nusa Tenggara Timur, Red = Sulawesi.

Chapter 9. Conclusion

Sometime after 70,000 years ago, early modern humans (EMH) first made the crossing from continental Sunda (Southeast Asia) into the island archipelago of Wallacea (Indonesia and Timor-Leste): the earliest sea voyages of our species. Comprising the final stage of an epic journey, with its beginnings on the African continent tens of thousands of kilometres away, EMH then traversed the Wallacean seascape to land in Sahul between ca. 65 – 50 ka ago. The most likely route taken has been much debated, with two primary routes proposed, a northern and a southern one. Researchers have argued for one route over the other based on parsimony; depending on the distance between islands and various factors of visibility which are predicated to some extent by relative sea level models (Birdsell, 1977; Irwin, 1992; Oppenheimer, 2009). To date no resolution has been forthcoming from archaeological sites along either route (Kealy et al., 2016, 2018a). The capabilities required to make the maritime crossings and to what degree various factors such as distance of water crossing, intervisibility between islands, steepness of topography, and access to necessary resources would have facilitated or hindered the passage to Sahul has also been extensively discussed without much resolution. The Wallacean archipelago consists of thousands of potentially habitable islands and archaeological excavations have been undertaken on only a small percentage of these, with just nine islands with evidence for Pleistocene occupation. One method of addressing these issues in the absence archaeological evidence is modelling and the examination of proxies for human movement. Predictive modelling and remote survey analyses of the landscape can focus future research by improving the chances of successful recovery of evidence for initial EMH occupation. In this PhD dissertation I set out to investigate the initial movements of EMH into and throughout the Wallacean Archipelago using modelling techniques in combination with archaeological and proxy datasets. In the process I reconstructed and explored the palaeo-Wallacean seascape during initial EMH dispersal. The models produced by this project have determined the most likely initial route taken by EMH from Sunda to Sahul: a northern route from Sulawesi with a landing on the New Guinea Bird's Head peninsula.

This PhD dissertation had five key aims:

1. To reconstruct the palaeogeography of Wallacea and the neighbouring coastlines of Sunda and Sahul for the periods of possible EMH arrival and dispersal (Chapters 3, 5, & 6).
2. To model the intervisibility of islands within the Wallacean palaeo-archipelago, as they might have been viewed by EMHs (Chapters 5 & 6).
3. To construct and run a least-cost surface model for human movement from Sunda to Sahul, based on the palaeogeographic reconstructions and intervisibility (Chapter 6).
4. To develop a proxy model of EMH movement between islands based on the biogeography and possible human translocations of the Cuscus (*Phalanger*) (Chapters 7 & 8).
5. To compare the least-cost model results with proxies for movement and the latest archaeological data from the region to test model validity and identify key regions for future archaeological focus (Chapter 6, 8 and below).

Below I summarise how each of these aims has been addressed and could be expanded on in the future.

8.1. The Palaeogeography of Wallacea

Palaeogeographic reconstructions are essential for determining island connectivity and thus, the development of models of human movement through the Wallacean archipelago. There is an unfortunate trend in our use of sea levels and time, whereby only specific sea levels are examined due to a time of interest, or a time is selected based on lowest sea levels. Both these scenarios suffer a blinker problem, with the substantial variability in sea levels on either side of these narrow foci largely ignored.

Despite repeated suggestions that rising seas likely had a positive effect on Wallacean dispersal (Clark, 1991; Chappell, 1993; O'Connor and Chappell, 2003; O'Connell et al., 2010), the trend of selecting the period of lowest sea level for predicting the likely time of Wallacean dispersal (Birdsell, 1977; Oppenheimer, 2009) is still used by modellers of palaeogeography and dispersal today (e.g. Norman et al., 2018). Similarly, the selection of a single sea level based on estimates of likely human dispersal are still applied in current models (e.g. Bird et al., 2018), despite the lack of resolution in archaeological dates (Clarkson et al., 2017; O'Connell et al., 2018) and significant variation in sea levels over very short periods of time (Lambeck and Chappell, 2001).

For this dissertation I attempted a broader focus, with the reconstruction of Wallacean palaeogeography for multiple temporal intervals and differing sea levels. In particular, for the least-cost models (Kealy et al., 2018a), the time slices of 65 ka and 70 ka were selected primarily for the extremes in sea level they represent. This selection, in addition to the initial intervisibility models (Kealy et al., 2017), enabled the consideration of all sea level variations found between the periods of ca. 70 – 45 ka (Aim 1).

The palaeogeographic reconstructions produced by this study indicate that the Wallacean Archipelago was significantly connected visually during the likely period of initial EMH colonisation. Continuous relative intervisibility at select intervals is recovered for both northern and southern routes, although this is absent for the Timor – Australia (southern route) option between the period of ca. 62 – 47 ka (Kealy et al., 2017). Furthermore, the reconstructions show substantial increases in physical connectivity throughout palaeo-Wallacea, with lowered sea levels revealing numerous enlarged and emergent islands (Kealy et al., 2016). These palaeogeographic reconstructions, and the substantial inter-island connectivity which they promote, are particularly important for our understandings of how the first Wallacean peoples would have viewed their world and interacted with it.

Importantly, the application of geographic information system (GIS) software and digital bathymetric (and topographic) datasets enabled the development of multiple, extensive, and detailed palaeogeographic reconstructions across a broad temporal and spatial scale. For Wallacea, the best available dataset for these reconstructions is still the General Bathymetric Chart of the Oceans (GEBCO) dataset. Used in all the latest palaeogeographic reconstruction and modelling (Kealy et al., 2016, 2017, 2018a; Bird et al., 2018; Norman et al., 2018), the GEBCO dataset, however, is known to contain some errors that might significantly affect palaeogeographic reconstructions of Wallacea (Bird et al., 2018; Kealy et al., 2018a). These

errors are the result of GEBCO's only moderate resolution, and interpolation and averaging of the data between known points.

Bathymetric data at finer resolutions do exist for much of Wallacea as a result of early oceanographic survey efforts by 19th century Dutch ships (Department of Hydrography, Netherlands, 1902). Specifically, the various channel soundings recorded by Dutch captains along the many trade routes of the [then] Dutch East Indies (Indonesia). These measurements are currently only available in the form of physical charts, such as those of the map collection at the National Library of Australia, with the first efforts to produce digital scans of these charts having just begun (Martin Woods pers. comm.). Such digital scans hold great potential for future incorporation into the current GEBCO dataset to improve the accuracy and resolution of the Wallacean digital bathymetry.

Such an improved bathymetry could have significant implications to the palaeogeographic reconstructions and corresponding intervisibility calculations, and thus our interpretations of connectivity in Wallacea. The major island configurations in Wallacea are unlikely to change as a result of a revised bathymetry, and the northern route to Sahul favoured by the models here would remain the most likely path. Slight variations in specific islands crossed along the way, however, may result from these bathymetric updates. This will affect the prospection of islands for future archaeological efforts. An improved bathymetry also has implications for other modelling efforts such as palaeocurrents, as well as interpretations of inter-island connections and biogeography.

8.2. Early Human Movement through Wallacea

In this PhD I compiled a series of spatial variables in order to develop a least-cost pathway model of early modern human (EMH) movement through Wallacea, and initial colonisation of Sahul. I then assessed the validity of the model results based on current archaeological evidence.

8.2.1. The Model Results

Modelling efforts enable the investigation of the different possible routes through Wallacea to Sahul in the absence of currently available archaeological data. Recent model efforts have relied on various forms of visibility between islands, palaeogeographic reconstructions and the effects of palaeo-currents and winds (Bird et al., 2018, in review; Kealy et al., 2018a, Norman et al., 2018). The reconstructions of visibility used in the models here (Aim 2) concern two variables: relative intervisibility and an estimate of absolute intervisibility (Kealy et al., 2017, 2018a). While Norman et al. (2018) also consider relative intervisibility (their visibility buffers) in their model, they focus on island-to-island visibility ("visual connectivity") from the highest available vantage points on the 'home' island. Bird et al. (2018) used a visibility estimate somewhat between that of Norman et al. (2018) and the absolute intervisibility (shore-to-shore) variable employed here. They used the same calculation as Norman et al (2018) but limited their vantage points to only those within 10 km of the coast. Recently, Bird et al. (in review) used two alternative methods of visibility, one, an accurate measure of absolute intervisibility (their 'outer' visibility), and the other based on similar methodologies of the previous study (Bird et al., 2018) but with vantage points limited to those located within just 1 km of the shore.

The measures of island-to-island visibility used by Norman et al. (2018) and Bird et al. (2018, in review) may be more accurate than the absolute intervisibility values used here, which represent basic estimates with few assumptions. The Norman et al. (2018) and Bird et al. (2018) visibility estimates, however, requires the viewer to travel some distance inland and uphill, presumably away from their settlement. Additionally, while viewing from a high vantage point significantly extends visibility distance, once a distant island is identified, navigation of the initial portion of the voyage must be undertaken based on memory if relative intervisibility is absent (Kealy et al., 2017, 2018a). With relative intervisibility, however, it is possible to measure all the regions where the voyager can travel without ever going out of sight of land. Furthermore, as all models assume some maritime capabilities (Bird et al., 2018, in review; Kealy et al., 2018a; Norman et al., 2018), and the archaeological record supports deep sea fishing activities (O'Connor, 2007), it is probably the people out fishing in these zones of relative intervisibility that likely first saw distant island(s). This means that while islands with absolute [shore-to-shore] intervisibility (e.g. Bird et al., in review) were likely easily identified and more likely to be colonised, the identification of relative intervisible islands would also have been a common occurrence (based on assumptions of a maritime focus; O'Connor, 2007; Samper Carro et al., 2016, 2017). Early fishermen in the relative intervisibility zones would have also more likely possessed the skills and equipment required to undertake a voyage beyond their home island. While the use of look-out points could have provided these early voyagers with additional and supportive knowledge about neighbouring islands, for the purposes of modelling the earliest inter-island movements, relative intervisibility appears to be the more realistic variable.

The latest studies to model the EMH colonisation of Sahul, which considered the whole of the Wallacean Archipelago (Kealy et al., 2018a; Norman et al., 2018; Bird et al., in review), have found strong support for a northern route into Sahul. The least-cost model here finds overwhelming support for a northern route from Sulawesi, through the central Maluku islands with a Sahul landing point on the present-day island of Misool (Aim 3). Regardless of time (between 70 – 45 ka), sea level (between 85 – 25 m below present), or maritime favourability (high, medium, or low), every iteration of the least-cost model recovered this northern path as the most likely initial route taken by EMH from Sunda to Sahul (Kealy et al., 2018a).

8.2.2. The Archaeological Evidence

The archaeological records from Sunda and Sahul suggest EMH likely entered Wallacea sometime between 70 ka and 50 ka ago. Dates for EMH occupation from archaeological sites in Wallacea, however, remain elusive for this time period (Kealy et al., 2016; Chapter 1). Survey work during the course of this PhD (and as part of the larger Laureate Project) was successful in identifying and excavating a number of prehistoric archaeological sites in Nusa Tenggara Timur and Maluku Barat Daya (O'Connor et al., 2015, 2017b,c, 2018a,b,c,d; Samper Carro et al., 2016, 2017; Hawkins et al., 2017; Louys et al., 2017, 2018; Kealy et al., 2018b; Shipton et al., in review). Unfortunately, none of these sites have yet revealed evidence for EMH occupation which pre-dates the earliest known sites for Wallacea (Sutikna et al., 2018; Shipton et al., in review), let alone those for Sahul (Clarkson et al., 2017; O'Connell et al., 2018).

Recent publications on new or revised dates from Sulawesi, Borneo, Flores, and Timor (Aubert et al. 2014; 2018; Brumm et al. 2018; Sutikna et al., 2018; Shipton et al., in review), have all contributed to greater expansions of the Wallacean dataset, and in some cases have pushed

back known occupation dates, although they have yet to fall within our expected range of Wallacean occupation. Furthermore, the archaeological surveys and excavations conducted as part of this project, the wider Laureate Project, and other research endeavours have yet to provide any definitive data to support either a northern or southern route through Wallacea (Kealy et al., 2016, 2018a,b).

8.2.3. Validation by Proxy

The goal of any model is to conduct some form of validation process upon the results, through comparisons with other points of evidence. For the least-cost model of initial human dispersal through Wallacea to Sahul, the first obvious validation attempt comes from comparisons with the archaeological dataset. While Sulawesi has an impressive archaeological record with some of the oldest dates for EMH occupation for the region (Aubert et al., 2014; Brumm et al., 2018); the islands of central Maluku to the east are significantly lacking in early records of EMH occupation (Kealy et al., 2018a,b). Furthermore, none of the dates for Wallacean EMH occupation yet fall within the predicted range based on the bracketing Sunda and Sahul dated (see Chapter 1). Thus, validation of this modelled path using archaeological dates is currently unavailable.

The alternative is to validate via proxy. Here preliminary efforts to investigate the prehistoric translocation of the cuscus in Wallacea have been conducted with the goal of identifying proxies for early human movements. The phylogeographic studies of the cuscus (Kealy et al., in review, in prep) recovered strong support for cuscus translocations eastwards from New Guinea in the late Pleistocene-early Holocene, and westwards to the island of Timor in the late Holocene. This evidence for translocation provides good support for the existence of relatively advanced maritime technologies and forward-planning in island occupation by this time (Aim 4). This study did not, however, recover any evidence for translocations during the period of initial EMH arrival in Wallacea (Kealy et al., in prep), although future expansions on this dataset hold potential.

Recent studies on ancient DNA of black rats from the Talaud Islands has been used to support directional movements from Sulawesi rather than previous hypotheses of a Philippine origin (Louys et al., 2018). However, this study is very restricted both temporally and spatially, and so of limited assistance for validation of the model presented here. The earliest proxy evidence for inter-island movements of EMH comes from obsidian sourcing methods (Reepmeyer et al., 2011, 2016). These studies provide excellent support for the presence of an early trade network between the islands of Timor, Alor, Kisar, and a currently unknown source island at ca. 15 ka (Reepmeyer et al., 2016; Christian Reepmeyer pers. comm). The existence of such a network that enabled the movement of substantial material between islands (Reepmeyer et al., 2016; Maloney et al., 2018a; pers. obs.) by this time provides strong support for advanced maritime technologies and inter-connected island communities. The lack of an identified source island makes determinations of directionality and explicit links between the islands of Timor, Alor, Kisar, difficult. However, the obsidian evidence does provide very strong support for the high degree of inter-island connectivity suggested by the palaeogeographic reconstructions and intervisibility models (Kealy et al., 2016, 2017). As the least-cost pathway model is based upon the results of the palaeogeographic reconstructions and intervisibility calculations, support for these variables provides some indirect support for the modelled

pathway results themselves (Aim 5). Unfortunately, evidence from the earlier period of initial EMH arrival, and from the modelled northern path, remains elusive.

The least-cost pathway model produced by this PhD demonstrates the most likely initial route taken by EMH from Sunda to Sahul based on the currently available data. This route is tentatively supported by proxy records but also works to highlight the substantial gaps in our knowledge of archaeology and biogeography for this time period, and particularly for the north eastern Indonesian region.

8.3. Future Research Directions

Future refinements to modelling early modern human (EMH) dispersal from Sunda to Sahul will require the development of a more accurate bathymetry for Wallacea, more extensive uplift records throughout the region, and a fine-scale paleocurrent model of Wallacea. Greater model validation capabilities will also be achieved through collection of more modern and archaeological data, and future archaeological survey and excavations in the central Maluku region.

8.3.1. A New Bathymetry for Wallacea

The current efforts in digital scanning at the National Library of Australia of the Dutch sounding charts provides a unique opportunity to improve the currently available bathymetric data for Wallacea. Once these digital scans are finalised they could be rectified in a GIS program and their sounding points converted into a digital bathymetric dataset. While the sounding charts do not record the entirety of the Wallacean sea floor equally, they are particularly detailed for the channels between the various island which is the region of poorest resolution in the GEBCO dataset, and also the most significant for palaeo-island reconstructions.

The digitised sounding data could be combined with currently available digital elevation model (DEM) data from NASA's Space Shuttle Radar Topography Mission (SRTM) which produced a DEM for the entire globe, above sea level, at a resolution of just 30 m. For the regions of Wallacea below present sea level for which data would still be missing following this combination, estimates could be obtained through GIS interpolation techniques or alternative data sources sought. One such source is the US National Oceanic and Atmospheric Administration (NOAA) National Center for Environmental Information (NCEI)'s Marine Trackline Geophysical database. The NCEI's Marine Trackline includes single-beam bathymetry data collected during marine cruises of the Wallacean region from the 1960s to the present. Data sources include US and non-US oceanographic institutions, universities, and government agencies with worldwide data coverage. A brief review of both the 19th century Dutch sounding charts and the NCEI's Marine Trackline's data coverage suggests these two datasets are complimentary, with the Dutch surveys providing essential near-shore and narrow channel information and the Trackline's covering much of the deeper, more open sea regions and major channels. Once digital data points from all three sources have been obtained, a much more accurate interpolation analysis could produce a more reliable bathymetry of Wallacea. Any significant gaps in the data coverage that might remain could be filled in with the GEBCO measurements until more accurate records become available.

Potential collaboration with the GEBCO team itself to integrate these different datasets into a more refined bathymetry of Wallacea is also possible. GEBCO, and in particular Pauline

Weatherall (the GEBCO Digital Atlas Manager), encourages the sharing of bathymetric data within the international community, and are grateful for contributions of data to help update their gridded data sets. There exist a variety of options for data contribution and collaboration with GEBCO, any of which could be carried out in the future following the digitisation of the Dutch soundings.

8.3.2. *Calculating Island Uplift Rates for Wallacea*

Currently, only eight islands in Wallacea have an uplift rate calculated. Due to this small sample size, the palaeogeographic reconstructions used here had to rely on an averaged rate in order to account for uplift (Kealy et al., 2017, 2018a). The incredibly complex geological nature of Wallacea, however, means that uplift rates throughout the region are likely to be highly variable. As uplift plays an important role in our understandings of palaeogeography, working to fill in the gaps in Wallacea's uplift record should be one of the key priorities for future research in the region. Specifically, we should aim to at least have an uplift record from every region of Wallacea, making Maluku a top priority as it lacks any uplift records whatsoever (Kealy et al., 2017). Ultimately, calculations of island uplift rates for every Wallacean island greater than ca. 50 km² (about 100 islands) would enable a truly detailed and precise reconstruction of the palaeogeography.

8.3.3. *A Palaeocurrent Model for Wallacea*

An improved palaeogeography could then be applied to model efforts concerning palaeocurrents in Wallacea for the period of likely EMH arrival. Unfortunately, the complex nature of ocean currents means their modelling in Wallacea was outside the scope of this study. This is not to say that they played an insignificant role in determining the likely route taken by EMH from Sunda to Sahul. While model studies such as Norman et al. (2018), Bird et al. (2018), and Bird et al. (in review) rely on modern current patterns to predict likelihood and directionality of crossings, the use of modern currents fails to take into consideration the multitude of effects the palaeogeography would have had on current strength and direction between islands. To resolve this, palaeo-oceanographic modelling of Wallacea and its surrounding connected systems during the late Pleistocene is strongly recommended for future research. The improved palaeogeographic reconstruction mentioned above could even be used to construct a physical model of the region for implementation in a flume or hydraulic scale model (Roelvink, 2011; Potter and Pettijohn, 2012).

8.3.4. *Cuscus Phylogenetics and Tracing Translocations*

Further research efforts are also required to improve our understanding of prehistoric inter-island connections and movements in Wallacea. The translocation of the cuscus has shown significant potential and the studies conducted here have provided clear indications of areas for future research focus (Kealy et al., in review, in prep). Specifically, attempts to extract ancient DNA for cuscus remains known from pre-existing archaeological collections from the Solomon islands, New Ireland, St Matthias, and New Guinea would significantly improve our understanding of prehistoric species and population distributions in the region. Modern DNA and morphological analyses of the Oro cuscus, *Phalanger orientalis* from Ambon and west New Guinea, *P. ornatus* from the Halmahera island group, and *Spiloglossus maculatus* from Maluku and Selayar island, would all contribute substantially to improved understandings of the cuscuses biogeographic history. The model and method constructed here (Kealy et al., in prep)

provides the framework to allow these future findings to be entered and phylogeographic results recovered with relative ease. Similar phylogeographic analyses can also be applied to other possible translocations such as the *Dorcopsis* wallaby on Halmahera and Gebe, and the rufous spiny bandicoot and dusky pademelon on the Kai islands (Heinsohn, 2010).

8.3.6. An Integrated Survey Effort

An improved understanding of EMH inter-island connections based on animal translocation records would also be aided by an improved archaeological record for the region. The large number of unexplored islands in Wallacea and their remote locations makes the development of remote techniques for island selection, prior to physical surveys, a vital component of future research efforts. The least-cost pathway models produced by this project can be applied as a predictive model to identify islands more likely to have early records of EMH occupation. Once identified, remote survey efforts involving surface geology data, topographic maps, and satellite images can be employed to select the islands with the greatest potential for archaeological survey, and the regions of these islands with the best probability of preserving pre-50 ka records of EMH occupation (Kealy et al., 2018b).

The expanded uplift-rate dataset for Wallacea (8.4.2.), combined with the sea level models, and applied to these islands of interest will also enable the identification of regions that were above sea level during the period of likely EMH arrival. GIS programs can be used to compile a dataset of the geological, topographic, and relative uplift/sea level data for future predictive models of areas with the greatest chance of preserving early occupation sites, and thus the points of focus for intensive, physical surveys. As demonstrated for the island of Babar, remote survey significantly helps to narrow the focus of these time and cost intensive reconnaissance efforts, while the physical survey itself is still essential for the successful identification of sites (Kealy et al., 2018b).

Once surveys have successfully identified sites with excavation potential, future archaeological efforts should also aim to increase the sample size not only at the inter-island level but on individual islands as well. Furthermore, cave excavations should also aim to recover a comprehensive sample of the deposit to best account for non-uniform cave stratigraphies (e.g. excavations larger than a 1 x 1 m test pit; O'Connor et al., 2010, 2017). Any culturally sterile deposits recovered underlying the earlier occupations layers of a site should also be dated as best as possible to establish when occupation is absent.

Attempts to address some of the association concerns raised by O'Connell et al. (2018) regarding dates and evidence for EMH occupation on Sunda and Sahul would also be of value for refining the window of likely Wallacean arrival. For example, at Lida Ajer (Westaway et al., 2017), if direct dating of the human teeth proves unsuccessful, a possible method which could be applied to test the association between the teeth and the dated context is fluorine absorption analysis. This technique has been successfully applied elsewhere for intra-site sample comparison (e.g. Theden-Ringl et al., 2018). In Arnhem Land, new surveys, augering, excavation and OSL dating are underway to attempt to duplicate the early occupation dates obtained from Madjedbebe (Clarkson et al., 2017; Chris Clarkson pers. comm.). It should be noted, however, that the 65 ka date for Madjedbebe is the mean of an age estimate for when sediment accumulation began in the zone of first occupation (Clarkson et al., 2017). This estimate is precise to +3.7 ka and -5.7 ka, which as Wood et al. (2016) show, can hinder

interpretations of the chronology. Until more precise estimates can be obtained, these age estimates provide an envelope of time during which colonisation could have occurred with equal probability.

8.3.7. Testing the Northern Pathway

As the least-cost pathway model results have so clearly demonstrated, there is a remarkable lack of early archaeological sites currently known for northeastern Indonesia (Kealy et al., 2018a,b). This highlights the Wallacean region most in need of future research focus, first with surveys for possible habitation sites, and secondly with follow-up excavations and dating of the sites. Recent excavations on Misool Island hint at a revival of interest in Maluku and Papuan archaeology, although radiocarbon dates are still pending and the excavation is still in its earliest stages (Adhi Agus Octaviana pers. comm.). To adequately test the validity of a northern (as the model suggests) vs southern (the next likely alternative) route through Wallacea, future surveys, both remote and physical (Kealy et al., 2018b), of the islands of Obi, Seram, Buru, Sula, and Peleng are all required. In addition, continued efforts in the south, such as the recent re-excavation of Asitau Kuru (previously Jerimalai) on Timor (Shipton et al., in review), aid in the compilation of the necessary comparative dataset.

In response to the key gap in our archaeological records for north eastern Indonesia, the Northern Gateway Flagship project was recently ratified at the annual symposium for the Australian Research Council's Centre of Excellence for Australian Biodiversity and Heritage. This flagship will focus on filling the archaeological and biological knowledge for this important region, with an eye for testing its likelihood as the 'gateway' into Sahul. Hopefully, this project will provide ample scope to address some of these future research opportunities.

Exegesis References (Chapters 1, 2 & 9)

Agustiyanto, D.A., Suparman, M., Partoyo, E., Sukarna, D., 1994. *Peta Geologi Lembar Moa, Damar dan Bandanaira, Maluku*. Bandung, Indonesia: Pusat Penelitian dan Pengembangan Geologi.

Allen, J. and O'Connell, J.F., 2008. Getting from Sunda to Sahul. In Clark, G.R., O'Connor, S., Leach, B.F. (Eds.), *Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes. Terra Australis 29*. Canberra, Australia: ANU E Press, pp.31-46.

Athreya, S., 2015. Modern human emergence in South Asia: a review of the fossil and genetic evidence. In Kaifu, Y., Izuho, M., Goebel, T., Sato, H., Ono, A. (Eds.), *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*. Texas, USA: Texas A&M University Press, pp. 61-79.

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

Aubert, M., Setiawan, P., Oktaviana, A.A., Brumm, A., Sulistyarto, P.H., Saptomo, E.W., Istiawan, B., Ma'rifat, T.A., Wahyuono, V.N., Atmoko, F.T., Zhao, J.X. 2018. Palaeolithic cave art in Borneo. *Nature*. <https://doi.org/10.1038/s41586-018-0679-9>

Ayliffe, L.K., Gagan, M.K., Zhao, J.X., Drysdale, R.N., Hellstrom, J.C., Hantoro, W.S., Griffiths, M.L., Scott-Gagan, H., St Pierre, E., Cowley, J.A., Suwargadi, B.W. 2013. Rapid interhemispheric climate links via the Australasian monsoon during the last deglaciation. *Nature Communications*, 4, 2908.

Bae, C.J., Douka, K., Petraglia, M.D. 2017a. On the origin of modern humans: Asian perspectives. *Science*, 358(6368), eaai9067.

Bae, C.J., Douka, K., Petraglia, M.D. 2017b. Human colonization of Asia in the Late Pleistocene: An introduction to supplement 17. *Current Anthropology*, 58(S17), S373-S382.

Barker, N.P., Weston, P.H., Rutschmann, F., Sauquet, H. 2007. Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *Journal of Biogeography*, 34(12), 2012-2027.

Bednarik, R.G. 2001. Replicating the first known sea travel by humans: the Lower Pleistocene crossing of Lombok Strait. *Human Evolution*, 16(3-4), 229-242.

Besenbacher, S., Hvilsom, C., Marques-Bonet, T., Mailund, T., Schierup, M.H. 2018. Direct estimation of mutations in great apes reveals significant recent human slowdown in the yearly mutation rate. *bioRxiv: The Preprint Server for Biology*. <https://doi.org/10.1101/287821>

Bird, M.I., Beaman, R.J., Condie, S.A., Cooper, A., Ulm, S., Veth, P. 2018. Palaeogeography and voyage modeling indicates early human colonization of Australia was likely from Timor- Roti. *Quaternary Science Reviews*, 191, 431-439.

- Bird, M.I., Condie, S.A., O'Connor, S., O'Grady, D., Reepmeyer, C., Ulm, S., Zega, M., Saltré, F., Bradshaw, C.J.A. *in review*. Early human settlement of Sahul was not an accident. *Nature Ecology & Evolution*
- Bird, M.I., O'Grady, D., Ulm, S. 2016. Humans, water, and the colonization of Australia. *Proceedings of the National Academy of Sciences*, 113(41), 11477-11482.
- 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(20-21), 2228-2242.
- Bird, M.I., Turney, C.S.M., Fifield, L.K., Jones, R., Ayliffe, L.K., Palmer, A., Cresswell, R., Robertson, S. 2002. Radiocarbon analysis of the early archaeological site of Nauwalabila I, Arnhem Land, Australia: implications for sample suitability and stratigraphic integrity. *Quaternary Science Reviews*, 21(8-9), 1061-1075.
- Blinkhorn, J., 2018. Buddha Pushkar revisited: Technological variability in Late Palaeolithic stone tools at the Thar Desert margin, India. *Journal of Archaeological Science: Reports*, 20, 168-182.
- Blinkhorn, J., Ajithprasad, P., Mukherjee, A. 2017. Did modern human dispersal take a coastal route into India? New evidence from palaeolithic surveys of Kachchh, Gujarat. *Journal of Field Archaeology*, 42(3), 198-213.
- Böhm, E., Lippold, J., Gutjahr, M., Frank, M., Blaser, P., Antz, B., Fohlmeister, J., Frank, N., Andersen, M.B., Deininger, M., 2015. Strong and deep Atlantic meridional overturning circulation during the last glacial cycle. *Nature*, 517(7532), 73-76.
- Bohren, C.F., Fraser, A.B. 1986. At what altitude does the horizon cease to be visible? *American Journal of Physics*, 54(3), 222-227.
- 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.
- Börner, K., Boyack, K.W., Milojević, S., Morris, S. 2012. An introduction to modeling science: Basic model types, key definitions, and a general framework for the comparison of process models. In Scharnhorst, A., Börner, K., van den Besselaar, P. (Eds.), *Models of science dynamics: Encounters between complexity theory and information sciences*. Berlin, Heidelberg: Springer-Verlag, pp. 3-22.
- Bouteaux, A., Moigne, A.M., Sémah, F., Jacob, T. 2007. Les assemblages fauniques associés aux sites à *Homo erectus* du dôme de Sangiran (Pléistocène moyen, Java, Indonésie). *Comptes Rendus Palevol*, 6(3), 169-179.
- Bowler, J.M., Johnston, H., Olley, J.M., Prescott, J.R., Roberts, R.G., Shawcross, W., Spooner, N.A. 2003. New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature*, 421(6925), 837-840.

- Breeze, P.S., Groucutt, H.S., Drake, N.A., White, T.S., Jennings, R.P., Petraglia, M.D. 2016. Palaeohydrological corridors for hominin dispersals in the Middle East~ 250–70,000 years ago. *Quaternary Science Reviews*, 144, 155-185.
- 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. 2013. Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 44, 411-435.
- Brumm, A., Hakim, B., Ramli, M., Aubert, M., van den Bergh, G.D., Li, B., Burhan, B., Saiful, A.M., Siagian, L., Sardi, R., Jusdi, A., et al. 2018. A reassessment of the early archaeological record at Leang Burung 2, a Late Pleistocene rock-shelter site on the Indonesian island of Sulawesi. *PloS One*, 13(4), e0193025.
- 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.
- Bulbeck, D. 2007. Where river meets sea: a parsimonious model for *Homo sapiens* colonization of the Indian Ocean rim and Sahul. *Current Anthropology*, 48(2), 315-321.
- Cai, Y., Qiang, X., Wang, X., Jin, C., Wang, Y., Zhang, Y., Trinkaus, E., An, Z. 2017. The age of human remains and associated fauna from Zhiren Cave in Guangxi, southern China. *Quaternary International*, 434, 84-91.
- Chappell, J. 1993. Late Pleistocene coasts and Human migrations in the Austral Region. In Spriggs, M., Yen, D., Ambrose, W., Jones, R., Thorne, A. and Andrews, A. (Eds.), *A Community of Culture: The People and Prehistory of the Pacific*. Canberra: Department of Prehistory, Research School of Pacific and Asian Studies, Australian National University, pp. 43-48.
- Chappell, J., Veeh, H.H. 1978. Late Quaternary tectonic movements and sea-level changes at Timor and Atauro Island. *Geological Society of America Bulletin*, 89(3), 356-368.
- Clark, J.T. 1991. Early settlement in the Indo-Pacific. *Journal of Anthropological Archaeology*, 10(1), 27-53.
- Clarkson, C., Jacobs, Z., Marwick, B., Fullagar, R., Wallis, L., Smith, M., Roberts, R.G., Hayes, E., Lowe, K., Carah, X., Florin, S.A., McNeil, J., Cox, D., Arnold, L.J., Hua, Q., Huntley, J., Brand, H.E.A., Manne, T., Fairbairn, A., Shulmeister, J., Lyle, L., Salinas, M., Page, M., Connell, K., Park, G., Norman, K., Murphy, T., Pardoe, C. 2017. Human occupation of northern Australia by 65,000 years ago. *Nature*, 547(7663), 306.
- Clarkson, C., Jones, S., Harris, C. 2012. Continuity and change in the lithic industries of the Jurreru Valley, India, before and after the Toba eruption. *Quaternary International*, 258, 165-179.
- Clarkson, C., Petraglia, M., Harris, C., Shipton, C., Norman, K. 2018. The South Asian Microlithic: *Homo sapiens* Dispersal or Adaptive Response? In Robinson, E., Sellet, F. (Eds.), *Lithic technological organization and Paleoenvironmental change: global and diachronic perspectives*. *Studies in Human Ecology and Adaptation, Series Vol.9*. New York: Springer, pp. 37-61.

- Cox, N.L. 2009. *Variable Uplift from Quaternary Folding Along the Northern Coast of East Timor, Based on U-series Age Determinations of Coral Terraces*. PhD Thesis. Provo, UT: Brigham Young University.
- Davidson, I., Noble, W. 1992. Why the first colonisation of the Australian region is the earliest evidence of modern human behaviour. *Archaeology in Oceania*, 27(3), 135-142.
- Davies, B., Bickler, S.H. 2015. Sailing the simulated seas: A new simulation for evaluating prehistoric seafaring. In Traviglia, A. (Ed.), *Across Space and Time: Papers from the 41st Conference on Computer Applications and Quantitative Methods in Archaeology, Perth, 25–28 March 2013*. Amsterdam: Amsterdam University Press, pp. 215-223.
- Delannoy, J.-J., David, B., Geneste, J.-M., Katherine, M., Sadier, B. and Gunn, R., 2017. Engineers of the Arnhem Land plateau: Evidence for the origins and transformation of sheltered spaces at Nawarla Gabarnmang. In David, B., Taçon, P.S.C., Delannoy, J.-J., Geneste, J.-M., (Eds.), *The Archaeology of Rock Art in Western Arnhem Land, Australia, Terra Australis Vol. 47*, p.197-244.
- Dennell, R., 2014. Smoke and mirrors: the fossil record for *Homo sapiens* between Arabia and Australia. In Dennell, R., Porr, M. (Eds.), *Southern Asia, Australia and the Search for Human Origins*. New York: Cambridge University Press, pp. 33-50.
- Dennell, R., Petraglia, M.D. 2012. The dispersal of *Homo sapiens* across southern Asia: how early, how often, how complex? *Quaternary Science Reviews*, 47, 15-22.
- Dennell, R.W., Louys, J., O'Regan, H.J., Wilkinson, D.M. 2014. The origins and persistence of *Homo floresiensis* on Flores: biogeographical and ecological perspectives. *Quaternary Science Reviews*, 96, 98-107.
- Department of Hydrography Netherlands, 1902. *Hydrographic Charts of the Netherlands*. Ministerie van Marine, Afdeeling Hydrographie, The Hage.
- Deshpande, O., Batzoglou, S., Feldman, M.W., Cavalli-Sforza, L.L. 2009. A serial founder effect model for human settlement out of Africa. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1655), 291-300.
- Dickson, J.A.D. 1966. Carbonate identification and genesis as revealed by staining. *Journal of Sedimentary Research*, 36(2), 491-505.
- Douka, K., Higham, T.F., Hedges, R.E. 2010. Radiocarbon dating of shell carbonates: old problems and new solutions. *Munibe Suplemento*, 31, 18-27.
- Emerson, B.C., Cicconardi, F., Fanciulli, P.P., Shaw, P.J. 2011. Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1576), 2391-2402.
- Endicott, P., Metspalu, M., Kivisild, T. 2007. Genetic evidence on modern human dispersals in South Asia: Y chromosome and mitochondrial DNA perspectives: The world through the eyes of two haploid genomes. In Petraglia, M.D., Allchin, B. (Eds.), *The Evolution and History of Human Populations in South Asia*. Dordrecht: Springer, pp. 229-244.

- Erlanson, J.M., Braje, T.J. 2015. Coasting out of Africa: The potential of mangrove forests and marine habitats to facilitate human coastal expansion via the Southern Dispersal Route. *Quaternary International*, 382, 31-41.
- Field, J.S., Lahr, M.M. 2005. Assessment of the southern dispersal: GIS-based analyses of potential routes at Oxygen Isotopic Stage 4. *Journal of World Prehistory*, 19(1), 1-45.
- Field, J.S., Petraglia, M.D., Lahr, M.M. 2007. The southern dispersal hypothesis and the South Asian archaeological record: examination of dispersal routes through GIS analysis. *Journal of Anthropological Archaeology*, 26(1), 88-108.
- Fregel, R., Cabrera, V., Larruga, J.M., Abu-Amero, K.K., González, A.M. 2015. Carriers of mitochondrial DNA Macrohaplogroup N lineages reached Australia around 50,000 years ago following a northern Asian route. *PloS ONE*, 10(6), e0129839.
- French, A.P. 1982. How far away is the horizon? *American Journal of Physics*, 50(9), 795-799.
- Gagan, M.K., Ayliffe, L.K., Smith, G.K., Hellstrom, J.C., Scott-Gagan, H., Drysdale, R.N., Anderson, N., Suwargadi, B.W., Aplin, K.P., Zhao, J.X., Groves, C.W., Hantorod, W.S., Djubiantono, T. 2015. Geoarchaeological finds below Liang Bua (Flores, Indonesia): A split-level cave system for *Homo floresiensis*? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 440, 533-550.
- Gingele, F.X., De Deckker, P., Girault, A., Guichard, F. 2002. History of the South Java Current over the past 80 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183(3-4), 247-260.
- Grant, K.M., Rohling, E.J., Ramsey, C.B., Cheng, H., Edwards, R.L., Florindo, F., Heslop, D., Marra, F., Roberts, A.P., Tamisiea, M.E., Williams, F. 2014. Sea-level variability over five glacial cycles. *Nature Communications*, 5, 5076.
- Green, R.C., Jones, M., Sheppard, P. 2008. The reconstructed environment and absolute dating of SE-SZ-8 Lapita site on Nendö, Santa Cruz, Solomon Islands. *Archaeology in Oceania*, 43(2), 49-61.
- Greig, K., Gosling, A., Collins, C.J., Boocock, J., McDonald, K., Addison, D.J., Allen, M.S., David, B., Gibbs, M., Higham, C.F.W., Liu, F., McNiven, I.J., O'Connor, S., Tsang, C.H., Walter, R., Matisoo-Smith, E. 2018. Complex history of dog (*Canis familiaris*) origins and translocations in the Pacific revealed by ancient mitogenomes. *Scientific Reports*, 8(1), 9130.
- Groucutt, H.S., Grün, R., Zalmout, I.A., Drake, N.A., Armitage, S.J., Candy, I., Clark-Wilson, R., Louys, J., Breeze, P.S., Duval, M., Buck, L.T., et al. 2018. *Homo sapiens* in Arabia by 85,000 years ago. *Nature Ecology & Evolution*, 2(5), 800-809.
- Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M., Parton, A., Clark-Balzan, L., Jennings, R.P., Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S. 2015. Rethinking the dispersal of *Homo sapiens* out of Africa. *Evolutionary Anthropology: Issues, News, and Reviews*, 24(4), 149-164.
- Hall, R. 2009. Southeast Asia's changing palaeogeography. *Blumea-Biodiversity, Evolution and Biogeography of Plants*, 54(1-2), 148-161.

- Hamm, G., Mitchell, P., Arnold, L.J., Prideaux, G.J., Questiaux, D., Spooner, N.A., Levchenko, V.A., Foley, E.C., Worthy, T.H., Stephenson, B., Coulthard, V., Coulthard, C., Wilton, S., Johnston, D. 2016. Cultural innovation and megafauna interaction in the early settlement of arid Australia. *Nature*, 539(7628), 280-283.
- Hantoro, W.S., Pirazzoli, P.A., Jouannic, C., Faure, H., Hoang, C.T., Radtke, U., Causse, C., Best, M.B., Lafont, R., Bieda, S., Lambeck, K. 1994. Quaternary uplifted coral reef terraces on Alor Island, East Indonesia. *Coral reefs*, 13(4), 215-223.
- Haslam, M., Clarkson, C., Petraglia, M., Korisettar, R., Jones, S., Shipton, C., Ditchfield, P., Ambrose, S.H. 2010. The 74 ka Toba super-eruption and southern Indian hominins: archaeology, lithic technology and environments at Jwalapuram Locality 3. *Journal of Archaeological Science*, 37(12), 3370-3384.
- Hawkins, S., O'Connor, S., Kealy, S. 2016. Late Quaternary hominin-bat (Chiroptera) interactions in the Asia-Pacific. *Archaeology in Oceania*, 51, 7-17. [see Appendix F].
- Hawkins, S., O'Connor, S., Maloney, T. M., Lister, M., Kealy, S., Fenner, J. N., Aplin, K., Boulanger, C., Brockwell, S., Willan, R., Piotto, E., Louys, J. 2017. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. *Quaternary Science Reviews*, 171, 58-72. [see Appendix I].
- Heinsohn, T.E., 2010. Marsupials as introduced species: Long-term anthropogenic expansion of the marsupial frontier and its implications for zoogeographic interpretation. In Haberle, S., Stevenson, J., Prebble, M. (Eds.), *Altered ecologies: Fire, climate and human influence on terrestrial landscapes, Vol. 32*, ANU E Press, Canberra, pp.133-176.
- Hershkovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A., Bar-Matthews, M., Valladas, H., Mercier, N., Arsuaga, J.L., et al. 2018. The earliest modern humans outside Africa. *Science*, 359(6374), 456-459.
- Higham, T.F., Barton, H.U.W., Turney, C.S., Barker, G., Ramsey, C.B., Brock, F. 2009. Radiocarbon dating of charcoal from tropical sequences: results from the Niah Great Cave, Sarawak, and their broader implications. *Journal of Quaternary Science: Published for the Quaternary Research Association*, 24(2), 189-197.
- Hill, C., Soares, P., Mormina, M., Macaulay, V., Clarke, D., Blumbach, P.B., Vizuete-Forster, M., Forster, P., Bulbeck, D., Oppenheimer, S., Richards, M. 2007. A mitochondrial stratigraphy for island southeast Asia. *The American Journal of Human Genetics*, 80(1), 29-43.
- Ho, S.Y., Lanfear, R., Bromham, L., Phillips, M.J., Soubrier, J., Rodrigo, A.G., Cooper, A. 2011. Time-dependent rates of molecular evolution. *Molecular Ecology*, 20(15), 3087-3101.
- Hofreiter, M., Paijmans, J.L., Goodchild, H., Speller, C.F., Barlow, A., Fortes, G.G., Thomas, J.A., Ludwig, A., Collins, M.J. 2015. The future of ancient DNA: Technical advances and conceptual shifts. *BioEssays*, 37(3), 284-293.
- Hope, G., Kershaw, A.P., Kaars, S.V.D., Xiangjun, S., Liew, P.M., Heusser, L.E., Takahara, H., McGlone, M., Miyoshi, N., Moss, P.T. 2004. History of vegetation and habitat change in the Austral-Asian region. *Quaternary International*, 118, 103-126.

- Hublin, J.J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P. 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. *Nature*, 546(7657), 289-292.
- Hudjashov, G., Karafet, T.M., Lawson, D.J., Downey, S., Savina, O., Sudoyo, H., Lansing, J.S., Hammer, M.F., Cox, M.P. 2017. Complex patterns of admixture across the Indonesian archipelago. *Molecular Biology and Evolution*, 34(10), 2439-2452.
- Hudjashov, G., Kivisild, T., Underhill, P.A., Endicott, P., Sanchez, J.J., Lin, A.A., Shen, P., Oefner, P., Renfrew, C., Villems, R., Forster, P. 2007. Revealing the prehistoric settlement of Australia by Y chromosome and mtDNA analysis. *Proceedings of the National Academy of Sciences*, 104(21), 8726-8730.
- Huxley, T.H. 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London*, 1868, 294–319.
- Ingicco, T., Bergh, G.D., Jago-On, C., Bahain, J.J., Chacón, M.G., Amano, N., Forestier, H., King, C., Manalo, K., Nomade, S., Pereira, A., et al. 2018. Earliest known hominin activity in the Philippines by 709 thousand years ago. *Nature*, 557(7704), 233-237.
- Irwin, G. 1989. Against, across and down the wind: a case for the systematic exploration of the remote Pacific Islands. *The Journal of the Polynesian Society*, 98(2), 167-206.
- Irwin, G. 1992. *The prehistoric exploration and colonisation of the Pacific*. Cambridge: Cambridge University Press.
- Irwin, G., Bickler, S., Quirke, P. 1990. Voyaging by canoe and computer: experiments in the settlement of the Pacific Ocean. *Antiquity*, 64(242), 34-50.
- Jouannic, C., Hoang, C.T., Hantoro, W.S., Delinom, R.M. 1988. Uplift rate of coral reef terraces in the area of Kupang, West Timor: Preliminary results. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 68(2-4), 259-272.
- Kawamura, H., Holbourn, A., Kuhnt, W. 2006. Climate variability and land–ocean interactions in the Indo Pacific Warm Pool: a 460-ka palynological and organic geochemical record from the Timor Sea. *Marine Micropaleontology*, 59(1), 1-14.
- Kealy, S., Beck, R. 2017. Total evidence phylogeny and evolutionary timescale for Australian faunivorous marsupials (Dasyuromorphia). *BMC Evolutionary Biology*, 17(1), 240.
- Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S., Louys, J. (*in review*). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial *ND2* gene. *Australian Mammalogy*. [see Chapter 7].
- Kealy, S., Herrera, M., Aplin, K., Mitchell, K., Donnellan, S., Louys, J., O'Connor, S. (*in prep*). The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae). [see Chapter 8]

Kealy, S., Louys, J., O'Connor, S. 2016. Islands under the sea: a review of early modern human dispersal routes and migration hypotheses through Wallacea. *The Journal of Island and Coastal Archaeology*, 11(3), 364-384. [see Chapter 3].

Kealy, S., Louys, J., O'Connor, S. 2017. Reconstructing palaeogeography and inter-island visibility in the Wallacean archipelago during the likely period of Sahul colonization, 65–45 000 years ago. *Archaeological Prospection*, 24(3), 259-272. [see Chapter 5].

Kealy, S., Louys, J., O'Connor, S. 2018a. Least-cost pathway models indicate northern human dispersal from Sunda to Sahul. *Journal of Human Evolution*. [see Chapter 6].

Kealy, S., Wattimena, L., O'Connor, S. 2018b. A Geological and Spatial Approach to Prehistoric Archaeological Surveys on Small Islands: Case Studies from Maluku Barat Daya, Indonesia. *Kapata Arkeologi*, 14(1), 1-14. [see Chapter 4].

Kennett, D.J., Ingram, B.L., Southon, J.R., Wise, K. 2002. Differences in ¹⁴C age between stratigraphically associated charcoal and marine shell from the archaic period site of Kilometer 4, Southern Peru: old wood or old water? *Radiocarbon*, 44(1), 53-58.

Kirch, P.V. 2010. Peopling of the Pacific: a holistic anthropological perspective. *Annual Review of Anthropology*, 39, 131-148.

Koesoemadinata, S., Noya, N. 1989. *Peta Geologi Lembar Lombok, Nusatenggara Timur*. Bandung, Indonesia: Pusat Penelitian dan Pengembangan Geologi.

Kopp, R.E., Simons, F.J., Mitrovica, J.X., Maloof, A.C., Oppenheimer, M. 2009. Probabilistic assessment of sea level during the last interglacial stage. *Nature*, 462(7275), 863-867.

Korisettar, R. 2007. Toward developing a basin model for Paleolithic settlement of the Indian subcontinent: geodynamics, monsoon dynamics, habitat diversity and dispersal routes. In Petraglia, M.D., Allchin, B. (Eds.), *The Evolution and History of Human Populations in South Asia*. Springer: Dordrecht, pp. 69-96.

Lambeck, K., Chappell, J. 2001. Sea level change through the last glacial cycle. *Science*, 292(5517), 679-686.

Lewis, D. 1971. 'Expanding' the target in Indigenous navigation. *The Journal of Pacific History*, 6, 83-95.

Li, B., Roberts, R.G., Brumm, A., Guo, Y.G., Hakim, B., Ramli, M., Aubert, M., Grün, R., Zhao, J.X., Saptomo, E.W. 2016. IRSL dating of fast-fading sanidine feldspars from Sulawesi, Indonesia. *Ancient TL*, 34(2), 1-13.

Lipson, M., Cheronet, O., Mallick, S., Rohland, N., Oxenham, M., Pietruszewsky, M., Pryce, T.O., Willis, A., Matsumura, H., Buckley, H., Domett, K., et al. 2018. Ancient genomes document multiple waves of migration in Southeast Asian prehistory. *Science*, 361, 92-95.

Lisiecki, L.E., Raymo, M.E. 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography*, 20(1), PA1003.

Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K., Shih, H.T., Carvalho, G.R. von Rintelen, T. 2011. Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 42, 205-226.

Louys, J., Herrera, M., Hawkins, S., Aplin, K., Reepmeyer, C., Hopf, F., Donnellan, S.C., O'Connor, S., Tanudirjo, D.A. 2018. Neolithic dispersal implications of murids from late Holocene archaeological and modern natural deposits in the Talaud Islands, northern Sulawesi. In O'Connor, S., Bulbeck, D., Meyer, J. (Eds.), *The Archaeology of Sulawesi: Recent Research on the Pleistocene to the Historic Period*. ANU Press: Acton, Australian, pp. 223-242.

Louys, J., Kealy, S., O'Connor, S., Price, G. J., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Mahirta, Tanudirjo, D. A., Santoso, W. D., Hidayah, A. R., Trihascaryo, A., Wood, R., Bevitt, J., & Clark, T. 2017. Differential preservation of vertebrates in Southeast Asian caves. *International Journal of Speleology*, 46(3), 379-408. [see Appendix H].

Lydekker, R. 1896. *A Geographical History of Mammals*. New York: Cambridge University Press.

Major, J., Harris, R., Chiang, H.W., Cox, N., Shen, C.C., Nelson, S.T., Prasetyadi, C., Rianto, A. 2013. Quaternary hinterland evolution of the active Banda Arc: Surface uplift and neotectonic deformation recorded by coral terraces at Kisar, Indonesia. *Journal of Asian Earth Sciences*, 73, 149-161.

Malaspinas, A.S., Westaway, M.C., Muller, C., Sousa, V.C., Lao, O., Alves, I., Bergström, A., Athanasiadis, G., Cheng, J.Y., Crawford, J.E., Heupink, T.H., et al. 2016. A genomic history of Aboriginal Australia. *Nature*, 538(7624), 207.

Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P. 2016. The Simons genome diversity project: 300 genomes from 142 diverse populations. *Nature*, 538(7624), 201.

Maloney, T.R., O'Connor, S., Reepmeyer, C. 2018a. Specialised lithic technology of terminal Pleistocene maritime peoples of Wallacea. *Archaeological Research in Asia*, 16, 78-87.

Maloney, T., O'Connor, S., Wood, R., Aplin, K., Balme, J. 2018b. Carpenters Gap 1: A 47,000 year old record of indigenous adaption and innovation. *Quaternary Science Reviews*, 191, 204-228.

Maria, A. 1997. Introduction to modeling and simulation. In Andradóttir, S., Healy, K.J., Withers, D.H., Nelson, B.C. (Eds.), *Proceedings of the 1997 Winter Simulation Conference*, 7-10 December, Atlanta, Winter Simulation Conference Board of Directors, Atlanta, Georgia, pp. 7-13.

Mark, D.F., Renne, P.R., Dymock, R.C., Smith, V.C., Simon, J.I., Morgan, L.E., Staff, R.A., Ellis, B.S. Pearce, N.J. 2017. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Pleistocene tuffs and temporal anchoring of the Matuyama-Brunhes boundary. *Quaternary Geochronology*, 39, 1-23.

McColl, H., Racimo, F., Vinner, L., Demeter, F., Gakuhari, T., Moreno-Mayar, J.V., Van Driem, G., Wilken, U.G., Seguin-Orlando, A., De la Fuente Castro, C., Wasef, S., et al. 2018. The prehistoric peopling of Southeast Asia. *Science*, 361(6397), 88-92.

- McDonald, J., Reynen, W., Petchey, F., Ditchfield, K., Byrne, C., Vannieuwenhuysse, D., Leopold, M., Veth, P. 2018. Karnatukul (Serpent's Glen): A new chronology for the oldest site in Australia's Western Desert. *PLoS One*, 13(9), e0202511.
- Mercier, N., Valladas, H., Bar-Yosef, O., Vandermeersch, B., Stringer, C., Joron, J.L. 1993. Thermoluminescence date for the Mousterian burial site of Es-Skhul, Mt. Carmel. *Journal of Archaeological Science*, 20(2), 169-174.
- Merrill, E.D. 1923. The Correlation of Biological Distribution with the Geological History of Malaysia. *Proceedings of the Pan-Pacific Science Congress, Australia*, 2, 1148-1155.
- Michaux, B. 2010. Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biological Journal of the Linnean Society*, 101(1), 193-212.
- Mijares, A.S., Détroit, F., Piper, P., 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.
- Mithen, S., Reed, M. 2002. Stepping out: a computer simulation of hominid dispersal from Africa. *Journal of Human Evolution*, 43(4), 433-462.
- Moorjani, P., Gao, Z., Przeworski, M. 2016. Human germline mutation and the erratic evolutionary clock. *PLoS Biology*, 14(10), e2000744.
- Morley, M.W. 2017. The geoarchaeology of hominin dispersals to and from tropical Southeast Asia: A review and prognosis. *Journal of Archaeological Science*, 77, 78-93.
- Morwood, M., van Oosterzee, P. 2007. *A New Human: The Startling Discovery and Strange Story of the "Hobbits" of Flores, Indonesia*. New York: Smithsonian Books.
- Nagle, N., Ballantyne, K.N., Van Oven, M., Tyler-Smith, C., Xue, Y., Wilcox, S., Wilcox, L., Turkalov, R., Van Oorschot, R.A., van Holst Pellekaan, S., Schurr, T.G., et al. 2017. Mitochondrial DNA diversity of present-day Aboriginal Australians and implications for human evolution in Oceania. *Journal of Human Genetics*, 62(3), 343-353.
- Nexer, M., Authemayou, C., Schildgen, T., Hantoro, W.S., Molliex, S., Delcaillau, B., Pedroja, K., Husson, L., Regard, V. 2015. Evaluation of morphometric proxies for uplift on sequences of coral reef terraces: A case study from Sumba Island (Indonesia). *Geomorphology*, 241, 145-159.
- Nielsen, R., Akey, J.M., Jakobsson, M., Pritchard, J.K., Tishkoff, S., Willerslev, E. 2017. Tracing the peopling of the world through genomics. *Nature*, 541(7637), 302.
- Norman, K., Inglis, J., Clarkson, C., Faith, J.T., Shulmeister, J., Harris, D. 2018. An early colonisation pathway into northwest Australia 70-60,000 years ago. *Quaternary Science Reviews*, 180, 229-239.
- Noya, Y., Burhan, G., Koesoemadinata, S., Mangga, S.A. 1997. *Peta Geologi Lembar Alor Dan Wetar Barat, Nusa Tenggara*. Bandung, Indonesia: Pusat Penelitian dan Pengembangan Geologi.

- Nugraha, A.M.S., Hall, R. 2018. Late Cenozoic palaeogeography of Sulawesi, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 490, 191-209.
- O'Connell, J.F., Allen, J., Hawkes, K. 2010. Pleistocene Sahul and the origins of seafaring. In Anderson, A., Barret, J.H., Boyle, K.V. (Eds.), *The Global Origins and Development of Seafaring*. Cambridge, UK: McDonald Institute for Archaeology Research, pp.57-68.
- O'Connell, J.F., Allen, J., Williams, M.A., Williams, A.N., Turney, C.S., Spooner, N.A., Kamminga, J., Brown, G., Cooper, A. 2018. When did Homo sapiens first reach Southeast Asia and Sahul? *Proceedings of the National Academy of Sciences*, 115(34), 8482-8490.
- O'Connor, S. 2007. New evidence from East Timor contributes to our understanding of earliest modern human colonisation east of the Sunda Shelf. *Antiquity*, 81(313), 523-535.
- O'Connor, S. 2015. Rethinking the Neolithic in Island Southeast Asia, with particular reference to the archaeology of Timor-Leste and Sulawesi. *Archipel. Études interdisciplinaires sur le monde insulindien*, 90, 15-47.
- O'Connor, S., Barham, A., Aplin, K., Maloney, T. 2017a. Cave stratigraphies and cave breccias: Implications for sediment accumulation and removal models and interpreting the record of human occupation. *Journal of Archaeological Science*, 77, 143-159.
- O'Connor, S., Barham, A., Spriggs, M., Veth, P., Aplin, K., St Pierre, E. 2010. Cave archaeology and sampling issues in the tropics: a case study from Lene Hara Cave, a 42,000 year old occupation site in East Timor, Island Southeast Asia. *Australian Archaeology*, 71(1), 29-40.
- O'Connor, S., Chappell, J. 2003. Colonisation and coastal subsistence in Australia and Papua New Guinea: Different timing, different modes. In Sand, C. (Ed.), *Pacific Archaeology: Assessments and Prospects. Proceedings of the International Conference for the 50th anniversary of the First Lapita Excavation (July 1952), Koné-Nouméa 2002*. Nouméa: Le Cahiers de l'Archéologie en Nouvelle-Calédonie, pp. 17-32.
- O'Connor, S., Louys, J., Kealy, S., Mahirta. 2015. First record of painted rock art near Kupang, West Timor, Indonesia, and the origins and distribution of the Austronesian painting tradition. *Rock Art Research*, 32(2), 193-201. [see Appendix E].
- O'Connor, S., Louys, J., Kealy, S., Samper Carro, S. 2017b. Hominin dispersal and settlement east of Huxley's Line: The role of sea-level changes, island size, and subsistence behavior. *Current Anthropology*, 58(17), 567-582. [see Appendix J].
- O'Connor, S., Mahirta, Kealy, S., Boulanger, C., Maloney, T., Hawkins, S., Langley, M., Kaharudin, H. A. F., Suniarti, Y., Husni, M., Ririmasse, M., Tanudirjo, D. A., Wattimena, L., Handoko, W., Alifah, Louys, J. 2018a. Kisar and the archaeology of small island in the Wallacean Archipelago. *Journal of Island and Coastal Archaeology*. [see Appendix O].
- O'Connor, S., Mahirta, Kealy, S., Louys, J., Kaharudin, H. A. F., Lebuan, A., Hawkins, S. 2018b. Unusual painted anthropomorph in Lembata island extends our understanding of rock art diversity in Indonesia. *Rock Art Research*, 35(1), 79-84. [see Appendix M].

O'Connor, S., Mahirta, Louys, J., Kealy, S., Brockwell, S. 2018c. New engraving finds in Alor Island, Indonesia extend known distribution of engravings in Oceania. *Archaeological Research in Asia*, 15, 116-128. [see Appendix N].

O'Connor, S., Mahirta, Samper Carro, S., Hawkins, S., Kealy, S., Louys, J., Wood, R. 2017c. Fishing in life and death: Oldest evidence of Pleistocene fish-hooks from a burial context. *Antiquity*, 91(360), 1451-1468. [see Appendix K].

O'Connor, S., Mahirta, Tanudirjo, D., Ririmasse, M., Husni, M., Kealy, S., Hawkins, S., Alifah. 2018d. Ideology, ritual performance and its manifestations in the rock art of Timor-Leste and Kisar Island, Island South East Asia. *Cambridge Archaeological Journal*, 28(2), 225-241. [see Appendix L].

O'Connor, S., Mahirta., Louys, J., Hawkins, S., Nayati, W., Tandjiro, D., Brockwell, S., Samper Carro, S.C., Kealy, S., et al. 2018e. *The Archaeology of Island use in the Wallacean Archipelago*. Unpublished final report for the Ministry of Research, Technology and Higher Education of the Republic of Indonesia (RISTEK).

Oppenheimer, S. 2009. The great arc of dispersal of modern humans: Africa to Australia. *Quaternary International*, 202(1-2), 2-13.

Oppenheimer, S. 2012a. A single southern exit of modern humans from Africa: before or after Toba?. *Quaternary International*, 258, 88-99.

Oppenheimer, S. 2012b. Out-of-Africa, the peopling of continents and islands: tracing uniparental gene trees across the map. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1590), 770-784.

Pagani, L., Lawson, D.J., Jagoda, E., Mörseburg, A., Eriksson, A., Mitt, M., Clemente, F., Hudjashov, G., DeGiorgio, M., Saag, L., Wall, J.D. 2016. Genomic analyses inform on migration events during the peopling of Eurasia. *Nature*, 538(7624), 238.

Petraglia, M.D., Ditchfield, P., Jones, S., Korisettar, R., Pal, J.N. 2012. The Toba volcanic super-eruption, environmental change, and hominin occupation history in India over the last 140,000 years. *Quaternary International*, 258, 119-134.

Pirazzoli, P.A., Radtke, U., Hantoro, W.S., Jouannic, C., Hoang, C.T., Causse, C., Best, M.B. 1993. A one million-year-long sequence of marine terraces on Sumba Island, Indonesia. *Marine Geology*, 109(3-4), 221-236.

Posth, C., Wißing, C., Kitagawa, K., Pagani, L., van Holstein, L., Racimo, F., Wehrberger, K., Conard, N.J., Kind, C.J., Bocherens, H., Krause, J. 2017. Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. *Nature Communications*, 8, 16046.

Potter, P.E., Pettijohn, F.J. 2012. *Paleocurrents and Basin Analysis, 2nd Edition*. New York: Springer Science & Business Media.

Prell, W.L., Hutson, W.H., Williams, D.F., Bé, A.W., Geitzenauer, K., Molino, B. 1980. Surface circulation of the Indian Ocean during the last glacial maximum, approximately 18,000 yr BP. *Quaternary Research*, 14(3), 309-336.

- Premathilake, R., Hunt, C.O. 2018. Late Pleistocene humans in Sri Lanka used plant resources: A phytolith record from Fahien rock shelter. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 505, 1-17.
- Ramsey, C.B. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon*, 51(1), 337-360.
- Raup, D.M. 1986. Biological extinction in earth history. *Science*, 231(4745), 1528-1533.
- Reepmeyer, C., O'Connor, S., Mahirta, Maloney, T., Kealy, S. 2016. Late Pleistocene/early Holocene maritime interaction in Southeastern Indonesia – Timor Leste. *Journal of Archaeological Science*, 76, 21-30. [see Appendix G].
- Reepmeyer, C., Spriggs, M., Lape, P., Neri, L., Ronquillo, W.P., Simanjuntak, T., Summerhayes, G., Tanudirjo, D., Tiauzon, A. 2011. Obsidian sources and distribution systems in Island Southeast Asia: new results and implications from geochemical research using LA-ICPMS. *Journal of Archaeological Science*, 38(11), 2995-3005.
- Reich, D., Patterson, N., Kircher, M., Delfin, F., Nandineni, M.R., Pugach, I., Ko, A.M.S., Ko, Y.C., Jinam, T.A., Phipps, M.E., Saitou, N., et al. 2011. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *The American Journal of Human Genetics*, 89(4), 516-528.
- 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., et al. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, 55(4), 1869-1887.
- 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., Perera, N., Wedage, O., Deraniyagala, S., Perera, J., Eregama, S., Petraglia, M.D., Lee-Thorp, J.A. 2017. Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. *Journal of Human Evolution*, 106, 102-118.
- Roberts, P., Stewart, B.A. 2018. Defining the 'generalist specialist' niche for Pleistocene *Homo sapiens*. *Nature Human Behaviour*, 2, 542–550.
- Roelvink, D., 2011. *Advances in Coastal and Ocean Engineering – Vol. 12. A Guide to Modeling Coastal Morphology*. Danvers, MA: World Scientific Publishing Co. Pte. Ltd.
- Roosmawati, N., Harris, R. 2009. Surface uplift history of the incipient Banda arc-continent collision: Geology and synorogenic foraminifera of Rote and Savu Islands, Indonesia. *Tectonophysics*, 479(1-2), 95-110.
- Samper Carro, S.C., Louys, J., O'Connor, S. 2017. Methodological considerations for ichthyoarchaeology from the Tron Bon Lei sequence, Alor, Indonesia. *Archaeological Research in Asia*, 12, 11-22.

- Samper Carro, S.C., O'Connor, S., Louys, J., Hawkins, S., Mahirta, M. 2016. Human maritime subsistence strategies in the Lesser Sunda Islands during the terminal Pleistocene–early Holocene: New evidence from Alor, Indonesia. *Quaternary International*, 416, 64-79.
- Scally, A. 2016. The mutation rate in human evolution and demographic inference. *Current Opinion in Genetics & Development*, 41, 36-43.
- Schlebusch, C.M., Jakobsson, M. 2018. Tales of human migration, admixture, and selection in Africa. *Annual Review of Genomics and Human Genetics*, 19, 405-428.
- Schwarcz, H.P., Grün, R., Vandermeersch, B., Bar-Yosef, O., Valladas, H., Tchernov, E. 1988. ESR dates for the hominid burial site of Qafzeh in Israel. *Journal of Human Evolution*, 17(8), 733-737.
- Sémah, F., Saleki, H., Falguères, C., Féraud, G., Djubiantono, T. 2000. Did early man reach Java during the Late Pliocene? *Journal of Archaeological Science*, 27(9), 763-769.
- Shackelford, L., Demeter, F., Westaway, K., Durringer, P., Ponche, J.L., Sayavongkhamdy, T., Zhao, J.X., Barnes, L., Boyon, M., Sichanthongtip, P., Sénégas, F., Patole-Edoumba, E., Coppens, Y., Dumoncel, J., Bacon, A.-M. 2018. Additional evidence for early modern human morphological diversity in Southeast Asia at Tam Pa Ling, Laos. *Quaternary International*, 466, 93-106.
- Shipton, C., O'Connor, S., Jankowski, N., O'Connor-Veth, J., Maloney, T., Kealy, S., Boulanger, C. (*in review*). Conditions for continuity in human behaviour: A new sequence spanning 44,000 years from Asitau Kuru (Jerimalai), Timor-Leste, Wallacea. *Journal of Archaeological Method and Theory*. [see Appendix P].
- Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, C., Meischner, D., Schmelzer, I., Smeed, D.A. 2003. Sea-level fluctuations during the last glacial cycle. *Nature*, 423(6942), 853-858.
- Signor, P.W., Lipps, J.H. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. In Silver, L.T. and Schultz, P.H. (Eds.), *Geological implications of impacts of large asteroids and comets on the Earth, Special Paper 190*, The Geological Society of America Inc., Colorado, U.S.A., pp.291-296.
- Sikora, M. 2017. A genomic view of the Pleistocene population history of Asia. *Current Anthropology*, 58(S17), S397-S405.
- Simpson, G.G. 1977. Too many lines; the limits of the Oriental and Australian zoogeographic regions. *Proceedings of the American Philosophical Society*, 121(2), 107–120.
- Smith, W.H., Sandwell, D.T. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. *Science*, 277(5334), 1956-1962.
- Soares, P., Trejaut, J.A., Loo, J.H., Hill, C., Mormina, M., Lee, C.L., Chen, Y.M., Hudjashov, G., Forster, P., Macaulay, V., Bulbeck, D., Oppenheimer, S., Martin, M.L., Richards, B. 2008. Climate change and postglacial human dispersals in Southeast Asia. *Molecular Biology and Evolution*, 25(6), 1209-1218.

- Sondaar, P.Y. 1989. Did man reach Australia via the giant rat and dingo route? *Publication of the Geological Research and Development Center, Paleontology Series*, 5, 76-83.
- Stelbrink, B., Albrecht, C., Hall, R., von Rintelen, T. 2012. The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"? *Evolution: International Journal of Organic Evolution*, 66(7), 2252-2271.
- Storey, A.A., Clarke, A.C., Ladefoged, T., Robins, J., Matisoo-Smith, E. 2013. DNA and Pacific commensal models: Applications, construction, limitations, and future prospects. *The Journal of Island and Coastal Archaeology*, 8(1), 37-65.
- Stringer, C. 2002. Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 357(1420), 563-579.
- Stringer, C., Galway-Witham, J. 2017. Palaeoanthropology: On the origin of our species. *Nature*, 546(7657), 212-214.
- Stringer, C.B., Grün, R., Schwarcz, H.P., Goldberg, P. 1989. ESR dates for the hominid burial site of Es Skhul in Israel. *Nature*, 338(6218), 756-758.
- Sudana, D., Yasin, A., Sutisna, K., 1994. *Peta Geologi Lembar Obi, Maluku*. Bandung, Indonesia: Pusat Penelitian dan Pengembangan Geologi.
- Sumosusastro, P.A. 1989. Quaternary Reef Record of Differential Uplift at Luwuk, Sulawesi East Arm, Indonesia. *Netherlands Journal of Sea Research*, 24(2-3), 277-285.
- Sutikna, T., Tocheri, M.W., Faith, J.T., Awe, R.D., Meijer, H.J., Saptomo, E.W., Roberts, R.G. 2018. The spatio-temporal distribution of archaeological and faunal finds at Liang Bua (Flores, Indonesia) in light of the revised chronology for *Homo floresiensis*. *Journal of Human Evolution*, 124, 52-74.
- Sutikna, T., Tocheri, M.W., Morwood, M.J., Saptomo, E.W., Awe, R.D., Wasisto, S., Westaway, K.E., Aubert, M., Li, B., Zhao, J.X., Storey, M., Alloway, B.V., Morley, M.W., Meijer, H.J.M., van den Bergh, G.D., Grün, R., Dosseto, A., Brumm, A., Jungers, W.L., Roberts, R.G. 2016. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. *Nature*, 532(7599), 366.
- Theden-Ringl, F., Hislop, K.P., Aplin, K., Grün, R., Schurr, M.R. 2018. The chronology and environmental context of a cave deposit and associated faunal assemblage including megafauna teeth near Wee Jasper, southeastern Australia. *The Holocene*, 28(9) 1467–1482.
- Tobler, R., Rohrlach, A., Soubrier, J., Bover, P., Llamas, B., Tuke, J., Bean, N., Abdullah-Highfold, A., Agius, S., O'Donoghue, A., O'Loughlin, I., Sutton, P., Zilio, F., Walshe, K., Williams, A.N., Turney, C.S.M., Williams, M., Richards, S.M., Mitchell, R.J., Kowal, E., Stephen, J.R., Williams, L., Haak, W., Cooper, A. 2017. Aboriginal mitogenomes reveal 50,000 years of regionalism in Australia. *Nature*, 544(7649), 180-184.
- Turney, C.S., Bird, M.I., Fifield, L.K., Roberts, R.G., Smith, M., Dortch, C.E., Grün, R., Lawson, E., Ayliffe, L.K., Miller, G.H., Dortch, J., Cresswell, R.G. 2001. Early human occupation at Devil's Lair, southwestern Australia 50,000 years ago. *Quaternary Research*, 55(1), 3-13.

- Underhill, P.A., Passarino, G., Lin, A.A., Shen, P., Mirazon Lahr, M., Foley, R.A., Oefner, P.J., Cavalli-Sforza, L.L. 2001. The phylogeography of Y chromosome binary haplotypes and the origins of modern human populations. *Annals of Human Genetics*, 65(1), 43-62.
- 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., Storey, M., Setiabudi, E., Morwood, M.J. 2016. Earliest hominin occupation of Sulawesi, Indonesia. *Nature*, 529(7585), 208-211.
- Veth, P., Ward, I., Manne, T., Ulm, S., Ditchfield, K., Dortch, J., Hook, F., Petchey, F., Hogg, A., Questiaux, D., Demuro, M., Arnold, L., Spooner, N., Levchenko, V., Skippington, J., Byrne, C., Basgall, M., Zeanah, D., Belton, D., Helmholz, P., Bajkan, S., Bailey, R., Placzek, C., Kendrick, P. 2017. Early human occupation of a maritime desert, Barrow Island, North-West Australia. *Quaternary Science Reviews*, 168, 19-29.
- Vyas, D.N., Al-Meerri, A., Mulligan, C.J. 2017. Testing support for the northern and southern dispersal routes out of Africa: an analysis of Levantine and southern Arabian populations. *American Journal of Physical Anthropology*, 164(4), 736-749.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E., Labracherie, M. 2002. Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews*, 21(1-3), 295-305.
- Wallace, A.R. 1860. On the zoological geography of the Malay Archipelago. *Zoological Journal of the Linnean Society*, 4(16), 172-184.
- Wallace, A.R. 1876. *The Geographical Distribution of Animals: With a study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface, Vol. 1*. Franklin Square, NY: Harper & Brothers, Publishers.
- Weatherall, P., Marks, K.M., Jakobsson, M., Schmitt, T., Tani, S., Arndt, J.E., Rovere, M., Chayes, D., Ferrini, V., Wigley, R. 2015. A new digital bathymetric model of the world's oceans. *Earth and Space Science*, 2(8), 331-345.
- Weaver, A.J., Eby, M., Wiebe, E.C., Bitz, C.M., Duffy, P.B., Ewen, T.L., Fanning, A.F., Holland, M.M., MacFadyen, A., Matthews, H.D., Meissner, K.J., Saenko, O., Schmittner, A., Wang, H., Yoshimori, M. 2001. The UVic Earth System Climate Model: Model description, climatology, and applications to past, present and future climates. *Atmosphere-Ocean*, 39(4), 361-428.
- 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., Demeter, F., Bacon, A.-M., Durringer, P. 2018. An old map, a lost cave and a missing link: Evidence for an early modern human arrival in Southeast Asia. Paper presented at the 21st Congress of the Indo-Pacific Prehistory Association, 23-28 September, 2018, Hue, Vietnam.
- 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., Trihasaryo, A., Kinsley, L., Sulistyanto, B. 2017. An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature*, 548(7667), 322-325.

White, C.M.N., Bruce, M.D. 1986. *The birds of Wallacea: an annotated check-list*. B.O.U Check-list No. 7. London: British Ornithologists' Union.

Wiens, J.J. 2009. Paleontology, genomics, and combined-data phylogenetics: can molecular data improve phylogeny estimation for fossil taxa? *Systematic Biology*, 58(1), 87-99.

Wild, S. 1986. Voyaging to Australia: 30,000 years ago. *Computers & graphics*, 10(3), 207-212.

Wiley, E.O., Lieberman, B.S. 2011. *Phylogenetics: the theory of phylogenetic systematics* (2nd edition). Hoboken, New Jersey: John Wiley and Sons Inc.

Wood, R., Jacobs, Z., Vannieuwenhuysse, D., Balme, J., O'Connor, S., Whitau, R. 2016. Towards an accurate and precise chronology for the colonization of Australia: The example of Riwi, Kimberley, Western Australia. *PLoS One*, 11(9), e0160123.

Appendix A

Procedure: Higher degree by research - thesis by compilation and thesis by creative works

Procedure: Higher degree by research – thesis by compilation and thesis by creative works

Purpose

This document outlines the content, format, and approval process for an HDR Thesis by Compilation or Thesis by Creative Works submission.

Procedure

1. This document is to be read in conjunction with the [Research Awards Rules](#).
2. This procedure supplements the information provided in the Submission and Examination of Higher Degree by Research Theses Procedure. Where information is not varied or detailed in this procedure the Submission and Examination of Higher Degree by Research Theses Procedure prevails.

Thesis by compilation

Content

3. A thesis by compilation includes papers (e.g. articles, chapters) where the student is the sole or joint author that are in the process of being prepared or approved for publication, have been accepted for publication, or have been published.
4. A thesis by compilation contains
 - a. An introduction to the field of study and the hypothesis or research questions, how these are addressed through the ensuing chapters, and a general account of the theory and methodological components of the research where these components may be distributed across separate papers/chapters.
 - b. Linking text to establish the relationship between one chapter and the next, such as through a foreword to each chapter.
 - c. A conclusion drawing together the published papers or works in a cohesive manner, and addresses how the individual publications link to the theory and methodology adopted and evaluate the contribution that the research in the submitted publications makes to the advancement of the research area.

5. Papers evidenced as in the following categories may be included with each presented as an individual chapter in the thesis:
 - a. Published papers
 - b. Manuscripts accepted for publication
 - c. Manuscripts submitted and under review by referees;
 - d. Manuscripts under revision following referees reports; and
 - e. Manuscripts in preparation for submission.
6. Unless otherwise approved by the Delegated Authority, a thesis by compilation consists primarily of published papers and manuscripts accepted for publication, and not primarily of manuscripts submitted and under review by referees or manuscripts under revision following referees reports.
7. A thesis by compilation may also include video recordings, film or other works of visual or sonic arts, computer software, digital material or other non-written material for which approval has been given for submission in alternative format.
8. The papers must have been researched and written during the course of the candidature, except in the case of students admitted to a PhD program as a staff member under the Research Awards Rules.
9. The scope and quality of a thesis by compilation is commensurate with the contribution to knowledge expected of a candidate for the relevant degree. The numbers of papers that constitute this requirement may vary between a single long monograph in disciplines such as mathematics to four to five peer-reviewed papers in other disciplines.

Format

10. A thesis by compilation includes a signed declaration that specifies:
 - a. Title, authorship and publication outlet of each paper.
 - b. The current status of each paper (In press, Accepted, Under Review, In preparation).
 - c. The extent of the contribution of the candidate to the research and the authorship of each paper.
11. For each paper where the candidate is not the sole author, either:
 - a. The collaborating authors sign the declaration; or
 - b. A senior author signs the declaration on behalf of the collaborating authors

12. The thesis may also include relevant appendices containing additional papers that are not related to the main thrust of the thesis, raw data, programs, questionnaires and other material as deemed appropriate for each discipline.

13. The thesis is otherwise formatted as per the Thesis in Standard Format Section in the *Submission and Examination of HDR Theses Procedure*, although journal formatting can be preserved for appropriate sections.

Process

14. Students submitting by compilation will normally obtain endorsement from their supervisory panel about the format of their thesis more than 12 months prior to submission, and no later than 6 months prior to submission.

15. In considering the request the supervisory panel provides the student with discipline*specific guidance on the appropriate quantity and quality of papers for submission as a thesis, as well as practical guidance about realistic peer*review and publication timeframes in their discipline.

16. Subsequent to endorsement by the supervisory panel, submission of a thesis by compilation requires approval by the Delegated Authority.

17. The Delegated Authority may permit the approval of a thesis by compilation and the composition of that thesis later than 6 months prior to submission in exceptional circumstances.

18. Following submission of the thesis the standard ANU examination procedures will apply.

Other

19. Students who are undertaking a thesis by compilation ensure publisher's agreements do not preclude the inclusion of the published work in their thesis.

20. Only in exceptional circumstances will approval be given to a candidate for a Master of Philosophy or Professional Doctorate to submit a thesis by compilation.

Thesis by creative works

Content

21. A thesis by creative works is an original work which includes one or more of the following: a multimedia or digital work, a film, an exhibition, a performance, a musical composition, a novel, a play, a series of poems, creative art work or other works considered acceptable by the Delegated Authority.

22. The written thesis accompanying the creative work may be a dissertation or

an exegesis or a combination of both as approved by the Delegated Authority.

23. The exegesis details the development of the creative work over the duration of the course of study, and provides the broad context for the ideas and precedents which inform the development of the research program. The exegesis enables the candidate to present an account of the research, demonstrating how the work addresses the objectives of the approved research project, and how the topic(s) of the dissertation or coursework have informed the creative work-based research.

24. For the dissertation, candidates present a substantial academic essay on a topic of relevance to the objectives of the creative work-based research project. The candidate presents a standalone paper or one that supports a lecture recital that is framed within appropriate academic methods through research, documentation and theoretical and conceptual discourse in a form that is relevant to the topic in question.

Length of thesis

25. In the case of a combined body of a Thesis by Creative Works PhD, the written work for a PhD must be a substantial work of 30,000 to 60,000 words that complements the other work submitted.

26. In the case of the combined body of a Thesis By Creative Works MPhil, the written work for an MPhil must be a substantial work of 15,000 to 30,000 words that complements the other work submitted.

27. The additional material submitted or presented in the form of a public recital must be:

- a. A substantial and genuine contribution to research; and
- b. A work of equivalent quality to a written thesis using criteria appropriate to the particular medium in which it is submitted.

28. The submission as a whole must be a coherent contribution to the advancement of knowledge and a pass standard must be achieved in all components.

29. In the case of resubmission being required only that component that has failed to meet the appropriate standard is required to be revised.

Examination of creative work other than a printed thesis

30. The final outcome of the creative work component of the thesis is presented for examination in the form of an exhibition, or audio-visual presentation, recital, lecture recital or in such other form as had been approved by the Delegated

Authority in the candidate's research program.

31. The Delegated Authority approves whether artistic practice is examined by a theoretical dissertation or by creative work and written thesis. If a creative work and written thesis is approved, they are be examined as an integrated whole.

32. In cases where the creative work is presented in the form of an exhibition, audio-visual presentation, recital, lecture recital etc, the written thesis is made available to the examiners at least one month before the presentation of the creative work so that the examiners are fully aware of the context of research which has led to the work in the final presentation. Any additional items such as video of the performance, visual presentation of artwork, recording, are either:

- a. supplied to the examiners with the written thesis; or
- b. supplied to examiners as soon as the documentation is available.

Document information

Title	Higher degree by research - thesis by compilation and thesis by creative works
Document Type	Procedure
Document Number	ANUP_003405
Version	11
Purpose	This document outlines the content, format, and approval process for an HDR Thesis by Compilation or Thesis by Creative Works submission.
Audience	Staff- Academic- Research, Students- Graduate- Research
Category	Academic
Topic	Students
Subtopic	Higher Research Degrees
Effective Date	1 Jan 2016
Review Date	1 Jan 2019
Responsible Officer	Dean, Higher Degree Research (dean.hdr@anu.edu.au)
Approved By	Deputy Vice- Chancellor (Research and Innovation) (dvc.research@anu.edu.au)
Contact Area	Office of the Dean, Higher Degree Research (dean.hdr@anu.edu.au)
Authority	Research Awards Rule 2017
Printed On	7 Oct 2018

Please ensure you have the latest version of this document from the Policy Library website before referencing this.

Appendix B

Supplimentary Information

Kealy, S., Donnellan, S., Mitchell, K., Herrera, M., Aplin, K., O'Connor, S., Louys, J. (in review). Phylogenetic relationships of the Cuscuses (Diprotodontia: Phalangeridae) of Island Southeast Asia and Melanesia based on the mitochondrial *ND2* gene. *Australian Mammalogy*.

Appendix C

Supplimentary Information

Kealy, S., Herrera, M., Aplin, K., Mitchell, K., Donnellan, S., Louys, J., & O'Connor, S. (in prep).
The application of phylogeography to investigate possible anthropogenic translocations: A preliminary analysis of the cuscus (Phalangeridae).

Appendix D

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Julien Louys, Shimona Kealy, & Mahirta

Publication: Rock Art Research

Current Status: Published

Citation: O'Connor, S., Louys, J., Kealy, S., Mahirta. 2015. First record of painted rock art near Kupang, West Timor, Indonesia, and the origins and distribution of the Austronesian painting tradition. *Rock Art Research*, 32(2), 193-201.

Link to Paper: <https://search.proquest.com/docview/1883505327?accountid=8330>

Appendix E

Co-authored publication produced during thesis tenure

Authors: Stuart Hawkins, Sue O'Connor, & Shimona Kealy

Publication: *Archaeology in Oceania*

Current Status: Published

Citation: Hawkins, S., O'Connor, S., Kealy, S. 2016. Late Quaternary hominin-bat (Chiroptera) interactions in the Asia-Pacific. *Archaeology in Oceania*, 51, 7-17.

Link to Paper: <https://doi.org/10.1002/arco.5084>

Appendix F

Co-authored publication produced during thesis tenure

Authors: Christian Reepmeyer, Sue O'Connor, Mahirta, Tim Maloney, & Shimona Kealy

Publication: Archaeological Science

Current Status: Published

Citation: Reepmeyer, C., O'Connor, S., Mahirta, Maloney, T., Kealy, S. 2016. Late Pleistocene/early Holocene maritime interaction in Southeastern Indonesia – Timor Leste. *Archaeological Science*, 76, 21-30.

Link to Paper: <https://doi.org/10.1016/j.jas.2016.10.007>

Appendix G

Co-authored publication produced during thesis tenure

Authors: Julien Louys, Shimona Kealy, Sue O'Connor, Gilbert J. Price, Stuart Hawkins, Ken Aplin, Yan Rizal, Jahdi Zaim, Mahirta, Daud A. Tanudirjo, Wahyu D. Santoso, Ati R. Hidayah, Agus Trihascaryo, Rachel Wood, Joseph Bevitt, & Tara Clark

Publication: International Journal of Speleology

Current Status: Published

Citation: Louys, J., Kealy, S., O'Connor, S., Price, G. J., Hawkins, S., Aplin, K., Rizal, Y., Zaim, J., Mahirta, Tanudirjo, D. A., Santoso, W. D., Hidayah, A. R., Trihascaryo, A., Wood, R., Bevitt, J., Clark, T. 2017. Differential preservation of vertebrates in Southeast Asian caves. *International Journal of Speleology*, 46(3), 379-408.

Link to Paper: <https://doi.org/10.5038/1827-806X.46.3.2131>

Appendix H

Co-authored publication produced during thesis tenure

Authors: Stuart Hawkins, Sue O'Connor, Tim R. Maloney, Mirani Lister, Shimona Kealy, Jack N. Fenner, Ken Aplin, Clara Boulanger, Sally Brockwell, Richard Willan, Elena Piotto, & Julien Louys

Publication: Quaternary Science Reviews

Current Status: Published

Citation: Hawkins, S., O'Connor, S., Maloney, T. R., Lister, M., Kealy, S., Fenner, J. N., Aplin, K., Boulanger, C., Brockwell, S., Willan, R., Piotto, E., Louys, J. 2017. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. *Quaternary Science Reviews*, 171, 58-72.

Link to Paper: <https://doi.org/10.1016/j.quascirev.2017.07.008>

Appendix I

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Julien Louys, Shimona Kealy, & Sofia Samper Carro

Publication: Current Anthropology

Current Status: Published

Citation: O'Connor, S., Louys, J., Kealy, S., Samper Carro, S. 2017. Hominin dispersal and settlement east of Huxley's Line: The role of sea-level changes, island size, and subsistence behavior. *Current Anthropology*, 58(17), 567-582.

Link to Paper: <https://doi.org/10.1086/694252>

Appendix J

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Mahirta, Sofia Samper Carro, Stuart Hawkins, Shimona Kealy, Julien Louys, & Rachel Wood

Publication: *Antiquity*

Current Status: Published

Citation: O'Connor, S., Mahirta, Samper Carro, S., Hawkins, S., Kealy, S., Louys, J., Wood, R. 2017. Fishing in life and death: Oldest evidence of Pleistocene fish-hooks from a burial context. *Antiquity*, 91(360), 1451-1468.

Link to Paper: <https://doi.org/10.15184/aqy.2017.186>

Appendix K

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Mahirta, Daud Tanudirjo, Marlon Ririmasse, Muhammad Husni, Shimona Kealy, Stuart Hawkins, & Alifah

Publication: Cambridge Archaeological Journal

Current Status: Published

Citation: O'Connor, S., Mahirta, Tanudirjo, D., Ririmasse, M., Husni, M., Kealy, S., Hawkins, S., Alifah. 2018. Ideology, ritual performance and its manifestations in the rock art of Timor-Leste and Kisar Island, Island South East Asia. *Cambridge Archaeological Journal*, 28(2), 225-241.

Link to Paper: <https://doi.org/10.1017/S0959774317000816>

Appendix L

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Mahirta, Shimona Kealy, Julien Louys, Hendri A. F. Kaharudin, Antony Lebuan, Stuart Hawkins

Publication: Rock Art Research

Current Status: Published

Citation: O'Connor, S., Mahirta, Kealy, S., Louys, J., Kaharudin, H. A. F., Lebuan, A., Hawkins, S. 2018. Unusual painted anthropomorph in Lembata island extends our understanding of rock art diversity in Indonesia. *Rock Art Research*, 35(1), 79-84.

Link to Paper:

<https://search.informit.com.au/documentSummary;dn=602378085841810;res=IELAPA>

Appendix M

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Mahirta, Julien Louys, Shimona Kealy, & Sally Brockwell

Publication: *Archaeological Research in Asia*

Current Status: Published

Citation: O'Connor, S., Mahirta, Louys, J., Kealy, S., Brockwell, S. 2018. New engraving finds in Alor Island, Indonesia extend known distribution of engravings in Oceania. *Archaeological Research in Asia*, 15, 116-128.

Link to Paper: <https://doi.org/10.1016/j.ara.2017.12.004>

Appendix N

Co-authored publication produced during thesis tenure

Authors: Sue O'Connor, Mahirta, Shimona Kealy, Clara Boulanger, Tim Maloney, Stuart Hawkins, Michelle Langley, Hendri A. F. Kaharudin, Yuni Suniarti, Muhammad Husni, Marlon Ririmasse, Daud A. Tanudirjo, Lucas Wattimena, Wuri Handoko, Alifah & Julien Louys,

Publication: Journal of Island and Coastal Archaeology

Current Status: In Press (Published Online)

Citation: O'Connor, S., Mahirta, Kealy, S., Boulanger, C., Maloney, T., Hawkins, S., Langley, M., Kaharudin, H. A. F., Suniarti, Y., Husni, M., Ririmasse, M., Tanudirjo, D. A., Wattimena, L., Handoko, W., Alifah, Louys, J. 2018. Kisar and the archaeology of small island in the Wallacean Archipelago. *Journal of Island and Coastal Archaeology*.

Link to Paper: <https://doi.org/10.1080/15564894.2018.1443171>

Appendix O

Co-authored publication produced during thesis tenure

Authors: Ceri Shipton, Sue O'Connor, Nathan Jankowski, Jack O'Connor-Veth, Tim Maloney, Shimona Kealy, & Clara Boulanger

Publication: Archaeological and Anthropological Sciences

Current Status: In Review

Citation: Shipton, C., O'Connor, S., Jankowski, N., O'Connor-Veth, J., Maloney, T., Kealy, S., Boulanger, C. (*in review*). Conditions for continuity in human behaviour: A new sequence spanning 44,000 years from Asitau Kuru (Jerimalai), Timor-Leste, Wallacea. *Archaeological and Anthropological Sciences*.

[Access restricted]