

Synchronous diversification of Sulawesi's iconic artiodactyls driven by recent geological events

Authors

Laurent A. F. Frantz^{1,2,a,*}, Anna Rudzinski^{3,*}, Abang Mansyursyah Surya Nugraha^{4,c,*}, Allowen Evin^{5,6,*}, James Burton^{7,8,*}, Ardern Hulme-Beaman^{2,6}, Anna Linderholm^{2,9}, Ross Barnett^{2,10}, Rodrigo Vega¹¹ Evan K. Irving-Pease², James Haile^{2,10}, Richard Allen², Kristin Leus^{12,13}, Jill Shephard^{14,15}, Mia Hillyer^{14,16}, Sarah Gillemot¹⁴, Jeroen van den Hurk¹⁴, Sharron Ogle¹⁷, Cristina Atofanei¹¹, Mark G. Thomas³, Friederike Johansson¹⁸, Abdul Haris Mustari¹⁹, John Williams²⁰, Kusdiantoro Mohamad²¹, Chandramaya Siska Damayanti²¹, Ita Djuwita Wiryadi^{21†}, Dagmar Obbles²², Stephano Mona^{23,24}, Hally Day²⁵, Muhammad Yasin²⁵, Stefan Meker²⁶, Jimmy A. McGuire²⁷, Ben J. Evans²⁸, Thomas von Rintelen²⁹, Simon Y. W. Ho³⁰, Jeremy B. Searle³¹, Andrew C. Kitchener^{32,33}, Alastair A. Macdonald^{7b}, Darren J. Shaw^{7b}, Robert Hall^{4,b}, Peter Galbusera^{14,b} and Greger Larson^{2,a,b}

¹ School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK

² The Palaeogenomics & Bio-Archaeology Research Network, Research Laboratory for Archaeology and History of Art, University of Oxford, Oxford OX1 3QY, UK

³ Research Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK

⁴ SE Asia Research Group, Department of Earth Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK

⁵ Institut des Sciences de l'Evolution, Université de Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

⁶ Department of Archaeology, Classics and Egyptology, University of Liverpool, 12-14 Abercromby Square, Liverpool, L69 7WZ, UK

⁷ Royal (Dick) School of Veterinary Studies & The Roslin Institute, University of Edinburgh, Easter Bush Campus, Roslin, Edinburgh EH25 9RG, UK

⁸ IUCN SSC Asian Wild Cattle Specialist Group and Chester Zoo, Cedar House, Caughall Road, Upton by Chester, Chester CH2 1LH, UK

⁹ Department of Anthropology, Texas A&M University, College Station, TX 77843-4352, USA.

¹⁰ Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, 1350 Copenhagen K, Denmark

¹¹ Ecology Research Group, Section of Life Sciences, School of Human and Life Sciences, Canterbury Christ Church University, North Holmes Road, Canterbury, CT1 1QU, Kent, UK

¹² Copenhagen Zoo, IUCN SSC Conservation Breeding Specialist Group - Europe, Roskildevej 38, Postboks 7, DK-2000 Frederiksberg, Denmark

¹³ European Association of Zoos and Aquaria, PO Box 20164, 1000 HD Amsterdam, The Netherlands

¹⁴ Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp, Koningin Astridplein 20-26, 2018 Antwerp, Belgium.

¹⁵ Environment and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Perth, WA 6150, Australia.

¹⁶ Molecular Systematics Unit / Terrestrial Zoology, Western Australian Museum, Welshpool, WA, Australia

¹⁷ Edinburgh Medical School: BMT0, University of Edinburgh, Teviot Place, Edinburgh, EH8 9AG, UK.

¹⁸ Gothenburg Natural History Museum, Box 7283, S 402 35 Gothenburg, Sweden

¹⁹ Department of Forest Resources Conservation and Ecotourism, Faculty of Forestry, Bogor Agricultural University, PO Box 168, Bogor 16001, Indonesia

²⁰ Davies Research Centre, School of Animal and Veterinary Sciences, Faculty of Sciences, University of Adelaide, Roseworthy, SA 5371, Australia

²¹ Faculty of Veterinary Medicine, Bogor Agricultural University, Jalan Agatis, IPB Campus Darmaga Bogor 16680, Indonesia

²² Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Ch. Deberiotstraat 32, 3000 Leuven, Belgium

²³ Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 - CNRS, MNHN, UPMC, EPHE, Ecole Pratique des Hautes Etudes, 16 rue Buffon, CP39, 75005, Paris, France

²⁴ EPHE, PSL Research University, Paris, France

²⁵ No affiliation

²⁶ Department of Zoology, State Museum of Natural History Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

²⁷ Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

²⁸ Department of Biology, McMaster University, Hamilton, Ontario, Ontario, Canada

²⁹ Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany

³⁰ School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia

³¹ Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

³² Department of Natural Sciences, Chambers Street, National Museums Scotland, Edinburgh EH1 1JF, UK.

³³ Institute of Geography, School of Geosciences, Drummond Street, University of Edinburgh, Edinburgh EH8 9XP, UK.

† deceased

*: contributed equally

^b: co-supervised the study

^a corresponding authors: laurent.frantz@qmul.ac.uk and greger.larson@arch.ox.ac.uk

^c Present address: Pertamina University, Jl. Teuku Nyak Arief, Kawasan Simprug, Kebayoran Lama, Jakarta Selatan 12220, Indonesia

Keywords: biogeography, evolution, geology, Wallacea.

Abstract

The high degree of endemism on Sulawesi has previously been suggested to have vicariant origins, dating back 40 Myr ago. Recent studies, however, suggest that much of Sulawesi's fauna assembled over the last 15 Myr. Here, we test the hypothesis that recent uplift of previously submerged portions of land on Sulawesi promoted diversification, and that much of the its faunal assemblage is much younger than the island itself. To do so, we combined palaeogeographical reconstructions with genetic and morphometric data sets derived from Sulawesi's three largest mammals: the Babirusa, Anoa, and Sulawesi warty pig. Our results indicate that although these species most likely colonized the area that is now Sulawesi at different times (14 Myr ago to 2-3 Myr ago), they experienced an almost synchronous expansion from the central part of the island. Geological reconstructions indicate that this area was above sea level for most of the last 4 Myr, unlike most parts of the island. We conclude that recent emergence of land on Sulawesi (~1–2 Myr) may have allowed species to expand synchronously. Altogether, our results indicates that the establishment of the highly endemic faunal assemblage on Sulawesi was driven by geological events over the last few million years.

Introduction

Alfred Russel Wallace was the first to document the 'anomalous' biogeographic region in Island Southeast Asia now known as Wallacea [1,2]. This biodiversity hotspot [3] is bounded by Wallace's Line in the west and Lydekker's Line in the east [4]. It consists of numerous islands in the Indonesian archipelago, all of which boast a high degree of endemism. For example, on Sulawesi, the largest island in the region, at least 61 non-volant mammalian species are endemic [5] and this figure is likely to be an underestimate.

The geological origins of Wallacea are as complex as its biogeography. Until recently, Sulawesi had been regarded as the product of multiple collisions of continental fragments from the Late Cretaceous [6–9]. This assumption has been challenged and a recent reinterpretation suggests instead that the island began

to form as the result of continental collisions during the Cretaceous, which were then followed by Eocene rifting of the Makassar Strait. This process led to the isolation of small land areas in western Sulawesi from Sundaland. In the early Miocene, a collision with the Australian crust of the Sula Spur led to uplift and emergence of land [10–12]. Later extension, uplift and subsidence from the middle Miocene to the present day led to the modern uneven distribution of micro-continental fragments, and the emergence of islands (separated by deep seas) between Borneo and Australia [13,14].

Previous geological interpretation involving the assembly of multiple terranes by collision was used to suggest that Sulawesi's peculiar species richness resulted from vicariance and amalgamation over long geological time periods [10,15,16]. However, recent molecular-clock analyses suggest that a dispersal, starting in the middle Miocene (~15 Myr ago) from both Sunda and Sahul is a more plausible explanation [17,18] [17,19][17,18]. These conclusions suggest a limited potential for animal dispersal to Sulawesi prior to ~15 Myr ago. Rapid tectonic changes, coupled with the dramatic sea-level fluctuations over the past 5 Myr [20], might also have affected land availability and influenced patterns of species dispersal to Sulawesi, intra-island species expansion and speciation.

The hypothesis of a recent increase in land area [19] can be tested by comparing the population histories of multiple species on the island. Analyses of genetic and morphometric variability can be used to infer the timing and trajectories of dispersal, and the geographical and temporal origins of expansion. For example, if land area had increased, from a single smaller island, extant species now living on Sulawesi, would all have expanded from the same area. In addition, under this assumption, within the same geographical region their respective diversifications would be expected to have been roughly simultaneous.

Here, we focus on three large mammals endemic to Sulawesi: the Babirusa (*Babyrousa* spp.), the Sulawesi warty pig (SWP, *Sus celebensis*) and the Anoa, a dwarf buffalo, (*Bubalus* spp.). The Babirusa (*Babyrousa* spp.) is a suid

characterized by wrinkled skin and four extraordinary curved canine tusks displayed by males [21–23]. It represents a “ghost lineage” since there are no closely related extant species outside Sulawesi (e.g. African suids are more closely related to the Babirusa than Asian suids) and the Babirusa is unknown in the fossil record outside Sulawesi [24]. Three extant species of Babirusa (distributed primarily in the interior of Sulawesi and on surrounding islands [21–23] have been described: *Babyrousa babyrousa* (Buru and Sulu islands), *Babyrousa celebensis* (mainland Sulawesi) and *Babyrousa togeanensis* (Togian Island) [25].

The Anoa is an endemic “miniature buffalo” related to indigenous bovids in the Philippines and East Asia [26]. It stands approximately one metre tall, weighs 150–200 kg, and mostly inhabits pristine rainforest [27]. Although the subgenus *Anoa* has been divided into two species, the lowland Anoa (*Bubalus depressicornis*) and the highland Anoa (*Bubalus quarlesi*) [28], this classification is still contentious [29]. In contrast with Anoa and Babirusa, the Sulawesi warty pig (SWP; *Sus celebensis*) occupies a wide range of habitats, ranging from swamps to rainforests. This species is closely related to the Eurasian wild pig (*Sus scrofa*), from which it diverged during the early Pleistocene (~2 Myr ago) [24,30]. The SWP has been found on numerous islands throughout Island Southeast Asia (ISEA), probably as the result of human-mediated dispersal [31]. As its name implies, male SWPs develop facial warts. These three cultural icons (represented by some of the oldest prehistoric cave paintings [32,33]) have undergone recent and significant population reduction and range contraction due to overhunting and conversion of natural habitat for agricultural use.

Here, we establish when Sulawesi gained its modern shape and size, including connectivity between its constituent peninsulae, and assessed the impact of island formation on the evolution of Sulawesi’s biodiversity. To do so, we used new reconstructions of the island’s palaeogeography that allowed us to interpret the distribution of land and sea over the last 8 Myr at 1 Myr intervals. To determine the timings of diversification of the three largest endemic mammals

on the island, we generated and analysed genetic and morphometric data from a total of 1,289 samples of the SWP, Anoa, and Babirusa obtained from museums, zoos and wild populations (456, 520 and 313 samples respectively; Table S1). Although these taxa have been divided into multiple species (see taxonomic notes in the Supplementary Material), for the purpose of this study we treated SWP, Anoa and Babirusa as single taxonomic units.

Results and Discussion

Contemporaneous divergence

We generated mitochondrial DNA (mtDNA) sequences and/or microsatellite data from 230 SWPs, 155 Anoa and 213 Babirusas sampled across Sulawesi and the neighbouring islands (Supplementary Material Figure S1; Table S1). Using a molecular-clock analysis, we inferred the time to the most recent common ancestor (TMRCA) of each species. The estimates from this method represent coalescence times, which provide a reflection of the crown age of each taxon. The closer relationship between Babirusa and SWP (~13 Myr ago) [34], compared with the divergence of either species from the Anoa (~58 Myr ago)[35] allowed us to align sequences from Babirusa and SWP alongside one another and jointly infer their relative TMRCAs. Separate analyses were performed for the Anoa. The inferred TMRCA of SWP was 2.19 Myr (95% credibility interval [CI] 1.19–3.41 Myr; Supplementary Material Figure S2) and Babirusa was 2.49 Myr (95% CI 1.33–3.61 Myr) (Figure 1a; Supplementary Material Figure S2). The inferred TMRCA of Anoa was younger (1.06 Myr; Figure 1a; Supplementary Material Figure S3), though its 95% CI (0.81–1.96 Myr) overlapped substantially with the TMRCAs of the other two species.

The relatively recent divergence between Babirusa and SWP also allowed us compare their TMRCAs using identical microsatellite loci. To do so, we computed the average square distance (ASD)[36,37] between every pair of individuals within each species at the same 13 microsatellite loci. Although such an analysis might be affected by population structure (see below), we found that the distributions of ASD values were not significantly different between these two

species (Wilcoxon signed-rank test, $p=0.492$; Figure 1b). This is consistent with the mitochondrial evidence for the nearly identical TMRCAs in the two species.

Recent molecular analyses have indicated that Babirusa may have colonized Wallacea as early as 13 Myr ago, whereas SWP and Anoa appear to have only colonized Sulawesi within the last 2–4 Myr [17,30,32,34]. An early dispersal of Babirusa to Sulawesi (late Palaeogene) has also been suggested on the basis of palaeontological evidence [19]. In addition, our data corroborate previous studies in indicating that both SWP and Babirusa are monophyletic with respect to their most closely related taxa on neighbouring islands (*e.g.* Borneo), which is consistent with only one colonization of Sulawesi (Supplementary Material; Figure S4-6)[30].

We then examined whether patterns of morphological diversity in these taxa are consistent with the molecular date estimates. To do so, we obtained measurements of 356 second and third lower molar (M2 and M3) from 95 Babirusas and 132 SWPs. SWP and Babirusa do not overlap morphologically (Figure 2a) and we were thus able to assign each specimen to its correct species with success rates of 94.3% (CI: 92.7%–95.5%, distribution of leave-one-out cross validation of a discriminant analysis based on a balanced sample design) [38] and 94.7% (CI: 93.8%–96.7%) based on their M2 and M3, respectively. Our results also indicate that Babirusa did not accumulate more tooth shape variation within Sulawesi (Fligner-Killeen test $X^2=1.04$, $p=0.3$ for M2, $X^2=3.45$, $p=0.06$ for M3). The data instead suggests that SWP has greater variance in the size of its M3 ($X^2=4.52$, $p=0.03$, but not in the size of the M2, $X^2=3.44$, $p=0.06$), and that the population from West Central Sulawesi has an overall smaller tooth size than the two populations from North West and North East Sulawesi (Figure 2b, Table S2). While these results may result from different selective constraints, they indicate that Babirusa did not accumulate greater morphological variation in tooth shape than did the SWP, despite arriving on Sulawesi up to 10 Myr earlier.

Altogether our analyses suggest that although the three species are believed to have colonized the island at different times, their similar degrees of morphological diversity and their nearly synchronous TMRCA's raise the possibility that they (and possibly other species) responded to a common mechanism that triggered their contemporaneous diversification.

Past land availability correlates with the expansion origins

Increasing land area may have promoted a simultaneous diversification and range expansion in Babirusas, SWPs, and Anoa's. To test this hypothesis, we used a new reconstruction that depicts land area in the Sulawesi region through time using information from the geological record. The reconstructions in 1 Myr increments (Figure 3a; Figure S7; [39]) support a scenario in which most of Sulawesi was submerged until the late Pliocene to early Pleistocene (2–3 Myr ago). Large-scale uplifts over the last 2–3 Myr would have rapidly and significantly increased land area, making it possible for non-volant species to expand their ranges.

To further assess whether these Plio-Pleistocene uplifts were responsible for a synchronous expansion, we inferred the most likely geographical origin of expansion using microsatellite data under a model of spatial loss-of-diversity with distance from expansion origin (Supplementary Material). These estimates were obtained independently of, and uninformed by, either the geological reconstructions or modern phylogeographical boundaries inferred from other species. We deduced that the most likely origin for both SWP and Babirusa was in the East Central region of Sulawesi (Figure 3c and 3d), and the most likely origin of Anoa was in the West Central region (Figure 3b).

The origins of the population expansions of both SWP and Babirusa occurred in an area of Sulawesi that only emerged during the late Pliocene to early Pleistocene (Figure 3a; Supplementary Material Figure S7). On the other hand, the Anoa most likely origin of diversification lies in a region that was submerged until the Pleistocene, consistent with paleontological evidence [32] and with the

slightly more recent TMRCA inferred for this species (Figure 1a). Thus, for all three species, the inferred geographical origins of their range expansions match the land availability derived from our geological reconstruction of Sulawesi.

Geological history of past land isolation correlates with zones of endemism

Previous studies have identified endemic zones that are common to macaques, toads [18,40], tarsiers [41–44] and lizards [45]. We tested whether the same area of endemism are linked to the population structure in our three species by generating a phylogenetic tree for each species using mtDNA and defined 5–6 haplogroups per species based on well-supported clades (Figure 4a-c; *Supplementary Material* Figure S4-6). We found that haplogroup proportions were significantly different between previously defined areas of endemism in all three species (Pearson's chi-squared test; $p < 0.001$), suggesting population substructure.

We also used STRUCTURE [46] to infer population structure from microsatellite data. The optimum numbers of populations (K) were 5, 6 and 5 for Anoa, Babirusa and SWP, respectively (*Supplementary Material* Figure S8; Figure 4d-f). Plotting the proportion of membership of each sample onto a map revealed a strong correspondence with the previously described zones of endemism (Figure 4d-f). Using an analysis of molecular variance (AMOVA), we found that these areas of endemism explained approximately 17%, 27%, and 5% of the variance in allele frequencies in Anoa, Babirusa and SWP, respectively (Table S5). Populations of Babirusa and SWP in these zones of endemism were also strongly morphologically differentiated (Figure 2).

Altogether, these data and analyses indicate that, despite some differences, the zones of endemism identified in tarsiers, macaques, toads and lizards [18,40–45,47] are largely consistent with the population structure and morphological differentiation in the three species studied here. This is particularly striking for the north arm of Sulawesi (NW, NC, and NE in Figure 4), where we identify two highly differentiated populations (reflected in both mtDNA and nuclear data

sets) in all three taxa. This pattern could result from either adaptation to local environments or from isolation due to the particular geological history associated with the northern arm. Geological reconstructions (Figure 3a) indicate that although land was present in this region during the past 4 Myr, it was often isolated from the rest of Sulawesi until the mid-Pleistocene. Thus, the combined geological and biological evidence presented here indicate that the high degree of divergence observed in the northern-arm populations in a multitude of species (*e.g.* three ungulates, macaques, and tarsiers) might have been shaped by isolation from the rest of the island until until the last 1My (Figure 3a) .

Recent and contemporary land isolation also affected morphological evolution including dwarfism

Similar isolation is likely to have influenced the populations inhabiting the smaller islands adjacent to Sulawesi, including the Banggai archipelago, Buru, the Togian and Sula Islands. Interestingly, our geometric morphometric analyses demonstrated that these island populations of SWP and Babirusa are the most morphologically divergent (Figure 2a). For example, the insular populations from the Togian Islands (Babirusa) and the Banggai archipelago (SWP) were found to have much smaller tooth sizes than their counterparts on the mainland (Figure 2b).

The significant morphometric divergences between populations on various islands are consistent with the genetic differentiation between Babirusa/SWP on Togian, Sula, and Buru (Figure 4; *Supplementary Material* Figure S9; *Supplementary Material* Figure S10) and between island populations of SWP on Banggai archipelago, Buton, and Buru (Figure 4; *Supplementary Material* Figure S9; *Supplementary Material* Figure S10).

Together, these results show that while suture zones between tectonic fragments are consistent with genetic and morphometric differentiation within Sulawesi, isolation on remote islands is likely to have had a much greater effect on

morphological distinctiveness. Rapid evolution, on islands, has been described in many species (e.g [48]). Dwarfism on small islands has previously been suggested to be the result of environmental constraints, including in pigs [49] where island populations are known to have smaller tooth sizes than their mainland counterparts [50,51].

Demographic history

Isolation of subpopulations across Sulawesi might also be linked to recent anthropogenic disturbances, especially for Anoa and Babirusa, that occupy pristine forest or swamps [21,27]. In order to assess the impact of recent anthropogenic changes on the three species, we inferred their demographic history using approximate Bayesian computation (ABC). We fitted various demographic models to the genetic data (combining both mtDNA and microsatellite data; *Supplementary Material*; Figure S11). The best-supported demographic model involved a long-term expansion followed by a recent bottleneck in all three species (Table S3), corroborating the results of recent analyses of the SWP genome [30].

While our ABC analysis had insufficient power to retrieve the time of expansion (Table S4), it provided relatively narrow estimates of the current effective population sizes (Figure 5; Table S4). We inferred a larger effective population size in SWP (83,021; 95% CI 46,287–161,457) than in Babirusa (30,895; 95% CI 17,522–54,954) or Anoa (27,504; 95% CI 13,680–54,056). *Sus celebensis* occupies a wide range of habitats, including agricultural areas [52]. Thus, this species is likely to be less affected by continuing deforestation than Babirusa or Anoa, which are typically restricted to less disturbed forest and swamps [21,26]. Phylogenetic analyses of microsatellite data indicate more geographical structuring in Babirusa and Anoa than in SWP (*Supplementary Material* Figure S12; Table S5). Overall, our results are consistent with habitat loss and fragmentation coupled with species-specific differences in habitat tolerance have affected population size and structure.

Conclusions

Our results indicate that, while the different geological component of Sulawesi were assembled at about 23 Myr ago, the island only acquired its distinctive modern form in the last few million years. By 3 Myr ago there was a large single island at its modern centre, but the complete connection between the arms was established more recently. The increasing land area associated with Plio-Pleistocene tectonic activity is likely to have provided the opportunity for a synchronous expansion in the three endemic mammal species in this study, as well as numerous other species. Interestingly, both our Pleistocene geological reconstruction and our proposed origins of expansion in the centre of the island closely resemble maps inferred from a study of tarsier species distribution on Sulawesi [53].

Furthermore, the recent emergence of connections between Sulawesi's arms coincides with a faunal turnover on the island and the extinction of multiple species. The geological reconstruction, and in particular the recent elimination of the marine barrier at the Tempe depression separating the Southwest and Central regions, fits well with suggested replacement in tarsier species that occurred in the last ~1 My [41]. The extinction of a numerous other species found in the early to late Pleistocene (~2.5–0.8 Myr ago) palaeontological assemblages of the Southwest arm, such as dwarf elephants (*Stegodon sompoensis* and *Elephas celebensis*; [19]), also coincides with the emergence of connections with the Central region. The dispersal of our three species from the central region of Sulawesi may therefore have played a role in these extinctions.

Sulawesi's development by emergence and coalescence of islands had a significant impact on the population structure and intraspecific morphological differentiation of Sulawesi's three largest mammals and many other endemic taxa. Thus, while most of Sulawesi's extant fauna arrived relatively recently, the more ancient geological history of the island (collision of multiple fragments) might have also affected patterns of endemism. Many aspects of Sulawesi's interconnected natural and geological histories remain unresolved. Integrative

approaches that combine biological and geological data sets are therefore essential for reconstructing a comprehensive evolutionary history of Wallace's most anomalous island.

References

1. Wallace AR. 1863 On the Physical Geography of the Malay Archipelago. *Journal of the Royal Geographical Society of London* **33**, 217.
2. Wallace AR. In press. ISLAND LIFE. In *Island Life*, pp. xix–xx.
3. Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000 Biodiversity hotspots for conservation priorities. **403**, 853–858.
4. Lydekker R, Lydekker R. 1896 *A geographical history of mammals*. By R. Lydekker. Cambridge,: The University press,.
5. Musser GG. 1987 The mammals of Sulawesi. *Biogeographical evolution of the Malay Archipelago*, 73–93.
6. Smith RB, Silver EA. 1991 Geology of a Miocene collision complex, Buton, eastern Indonesia. *Geol. Soc. Am. Bull.* **103**, 660–678.
7. Hall R. 1996 Reconstructing Cenozoic SE Asia. In *Tectonic Evolution of SE Asia* (eds R Hall, DJ Blundell), pp. 153–184.
8. Hamilton W. 1979 Tectonics of the Indonesian Region: Geological Survey Professional Paper 1078, US. *Government Printing Office*
9. Davidson JW. 1991 The geology and prospectivity of Buton Island, Southeast Sulawesi, Indonesia. *Indonesian Petroleum Association, Proceedings 20th annual convention, Jakarta 1991 I*, 209–234.
10. Moss SJ, Wilson MEJ. 1998 Biogeographic implications from the Tertiary palaeogeographic evolution of Sulawesi and Borneo. In Hall, R. & Holloway, J. D. (eds.) *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, The Netherlands, 133–163.
11. Hall R. 1998 The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *Evolution*
12. Hall R. 2013 The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *J. Limnol.* **72**, 1–17.
13. Spakman W, Hall R. 2010 Surface deformation and slab–mantle interaction during Banda arc subduction rollback. *Nat. Geosci.* **3**, 562–566.
14. Hall R. 2011 Australia-SE Asia collision: plate tectonics and crustal flow. In *The SE Asian gateway: history and tectonics of Australia-Asia collision* (eds R Hall, MA Cottam, MEJ Wilson), pp. 75–109.
15. Michaux B. 1996 The origin of southwest Sulawesi and other Indonesian terranes: a biological view. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **122**, 167–183.

16. de Boer AJ, Duffels JP. 1996 Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: a geotectonic explanation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **124**, 153–177.
17. 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* **66**, 2252–2271.
18. Evans BJ, Supriatna J, Andayani N, Setiadi MI, Cannatella DC, Melnick DJ. 2003 Monkeys and toads define areas of endemism on Sulawesi. *Evolution* **57**, 1436–1443.
19. van den Bergh GD, de Vos J, Sondaar PY. 2001 The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **171**, 385–408.
20. Miller KG *et al.* 2005 The Phanerozoic record of global sea-level change. *Science* **310**, 1293–1298.
21. Macdonald AA, Burton JA, Leus K. 2008 *Babirusa babirusa*. *The IUCN Red List of Threatened Species*
22. Macdonald, A., Leus, K., Masaaki, I. & Burton, J. 2016 *Babirusa togeanensis*. *IUCN Red List of Threatened Species*. (doi:10.2305/iucn.uk.2016-1.rlts.t136472a44143172.en)
23. Leus, K., Macdonald, A., Burton, J. & Rejeki, I. 2016 *Babirusa celebensis*. *IUCN Red List of Threatened Species*. (doi:10.2305/iucn.uk.2016-1.rlts.t136446a44142964.en)
24. Frantz L, Meijaard E, Gongora J, Haile J, Groenen MAM, Larson G. 2016 The Evolution of Suidae. *Annual review of animal biosciences* **4**, 61–85.
25. Meijaard E, Groves C. 2002 Upgrading three subspecies of babirusa (*Babirusa* sp.) to full species level. *Asian Wild Pig News* **2**, 33–39.
26. Semiadi G, Mannullang B, Burton JA, Schreiber A, Mustari AH. 2008 *Bubalus depressicornis*. *The IUCN Red List of Threatened Species*
27. Burton JA, Wheeler P, Mustari A. 2016 *Bubalus depressicornis*. *The IUCN Red List of Threatened Species*
28. Groves CP. 1969 Systematics of the anoa (Mammalia, Bovidae). *Beaufortia* **17**, 1–12.
29. Burton JA, Hedges S, Mustari AH. 2005 The taxonomic status, distribution and conservation of the lowland anoa *Bubalus depressicornis* and mountain anoa *Bubalus quarlesi*. *Mamm. Rev.* **35**, 25–50.
30. Frantz LA *et al.* 2013 Genome sequencing reveals fine scale diversification and reticulation history during speciation in *Sus*. *Genome Biol.* **14**, R107.
31. Groves CP. 1984 Of mice and men and pigs in the Indo-Australian Archipelago. *Canberra Anthropology* **7**, 1–19.
32. Rozzi R. 2017 A new extinct dwarfed buffalo from Sulawesi and the evolution of the

- subgenus *Anoa*: An interdisciplinary perspective. *Quat. Sci. Rev.* **157**, 188–205.
33. Aubert M *et al.* 2014 Pleistocene cave art from Sulawesi, Indonesia. *Nature* **514**, 223–227.
 34. Gongora J *et al.* 2011 Rethinking the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). *Zool. Scr.* **40**, 327–335.
 35. dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z. 2012 Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc. Biol. Sci.* **279**, 3491–3500.
 36. Goldstein DB, Ruiz Linares A, Cavalli-Sforza LL, Feldman MW. 1995 An evaluation of genetic distances for use with microsatellite loci. *Genetics* **139**, 463–471.
 37. Sun JX, Mullikin JC, Patterson N, Reich DE. 2009 Microsatellites are molecular clocks that support accurate inferences about history. *Mol. Biol. Evol.* **26**, 1017–1027.
 38. Evin A, Cucchi T, Cardini A, Strand Vidarsdottir U, Larson G, Dobney K. 2013 The long and winding road: identifying pig domestication through molar size and shape. *J. Archaeol. Sci.* **40**, 735–743.
 39. Abang Mansyursyah Surya Nugraha and Robert Hall. In press. Late Cenozoic palaeogeography of Sulawesi, Indonesia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
 40. Evans BJ, Supriatna J, Andayani N, Melnick DJ. 2003 Diversification of Sulawesi macaque monkeys: decoupled evolution of mitochondrial and autosomal DNA. *Evolution* **57**, 1931–1946.
 41. Driller C, Merker S, Perwitasari-Farajallah D, Sinaga W, Anggraeni N, Zischler H. 2015 Stop and Go - Waves of Tarsier Dispersal Mirror the Genesis of Sulawesi Island. *PLoS One* **10**, e0141212.
 42. Merker S, Driller C, Perwitasari-Farajallah D, Pamungkas J, Zischler H. 2009 Elucidating geological and biological processes underlying the diversification of Sulawesi tarsiers. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 8459–8464.
 43. Burton JA, Nietsch A. 2010 Geographical Variation in Duet Songs of Sulawesi Tarsiers: Evidence for New Cryptic Species in South and Southeast Sulawesi. *Int. J. Primatol.* **31**, 1123–1146.
 44. Shekelle M, Meier R, Wahyu I, Ting N, Others. 2010 Molecular phylogenetics and chronometrics of Tarsiidae based on 12S mtDNA haplotypes: evidence for Miocene origins of crown tarsiers and numerous species within the Sulawesi clade. *Int. J. Primatol.* **31**, 1083–1106.
 45. McGuire JA, Linkem CW, Koo MS, Hutchison DW, Lappin AK, Orange DI, Lemos-Espinal J, Riddle BR, Jaeger JR. 2007 Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. *Evolution* **61**, 2879–2897.
 46. Pritchard JK, Stephens M, Donnelly P. 2000 Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.
 47. Evans BJ, McGuire JA, Brown RM, Andayani N, Supriatna J. 2008 A coalescent

framework for comparing alternative models of population structure with genetic data: evolution of Celebes toads. *Biol. Lett.* **4**, 430–433.

48. Geer A van der. 2010 *Evolution of island mammals : adaptation and extinction of placental mammals on islands*. Wiley-Blackwell.
49. Evin A, Dobney K, Schafberg R, Owen J, Vidarsdottir US, Larson G, Cucchi T. 2015 Phenotype and animal domestication: A study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evol. Biol.* **15**, 6.
50. Kruska D, Röhrs M. 1974 Comparative--quantitative investigations on brains of feral pigs from the Galapagos Islands and of European domestic pigs. *Z. Anat. Entwicklungsgesch.* **144**, 61–73.
51. McIntosh GH, Pointon A. 1981 The Kangaroo Island strain of pig in biomedical research. *Aust. Vet. J.* **57**, 182–185.
52. Burton JA, Macdonald AA. 2008 *Sus celebensis*. *The IUCN Red List of Threatened Species* (doi:10.2305/IUCN.UK.2008.RLTS.T41773A10559537.en)
53. Reed CA. 1970 : Taxonomy and Evolution of the Monkeys of Celebes (Primates: Cercopithecidae) . Jack Fooden. *Am. Anthropol.* **72**, 1564–1565.

Acknowledgments

All data associated with this manuscript are available on Dryad (DOI TBD). We thank Joshua Schraiber and Erik Meijaard for valuable comments. L.A.F.F., J.H, A.L., A. H-B and G.L. were supported by a European Research Council grant (ERC-2013-StG-337574-UNDEAD) and Natural Environmental Research Council grants (NE/K005243/1 and NE/K003259/1). L.A.F.F. was supported by a Junior Research Fellowship (Wolfson College, University of Oxford). P.G. S.G., J.v.d.H, C.A. and D.O. were supported by Flemish government structural funding. A.R was supported by a Marie Curie Initial Training Network (BEAN—Bridging the European and Anatolian Neolithic, GA no. 289966) awarded to M.G.T. M.G.T. is supported by a Wellcome Trust Senior Research Fellowship (GA no. 100719/Z/12/Z). B.J.E was supported by the Natural Science and Engineering Research Council of Canada. This work received additional support from the University of Edinburgh Development Trust, the Roslin Institute, the Balloch Trust and the Stichting Dierentuinen Helpen (Consortium of Dutch Zoos). Additional support was also provided by The Rufford Small Grant, Royal Geographical Society, London, the Royal Zoological Society of Scotland and The University of Edinburgh Birrell-Gray Travel Award. We also thank the National

Museums of Scotland for logistic support, and the Negaunee Foundation for their continued support of a curatorial preparator. We are also indebted to the Indonesian Ministry of Forestry, Jakarta (PHKA), Sulawesi's Provincial Forestry Departments (BKSDA); the Indonesian Institute of Science (LIPI); Museum of Zoology, Research Center for Biology, Cibinong (LIPI); and the project's long-standing Indonesian sponsor, Ir. Harayanto MS, Bogor Agricultural University (IPB) for sample collection/permission.

Figure legends

Figure 1: Time to the most recent common ancestor (TMRCA) for three mammal species on Sulawesi. **a.** Posterior densities of the TMRCA estimates for Anoa, Babirusa, and Sulawesi warty pig inferred using a Bayesian molecular clock based on mitochondrial DNA sequences. **b.** Distribution of the average squared distances computed from microsatellite data from Babirusa and Sulawesi warty pig.

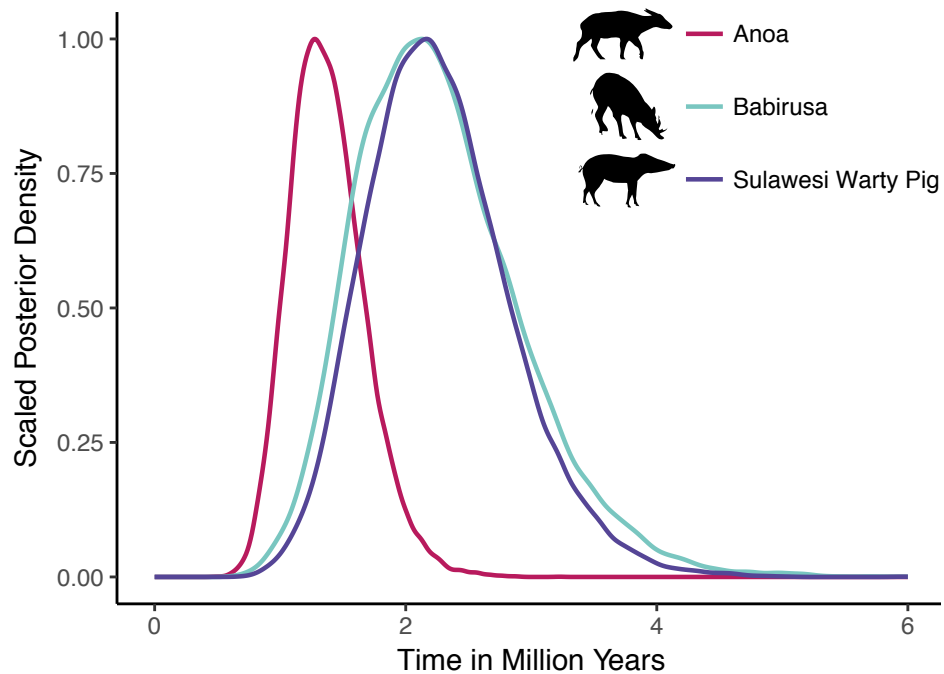
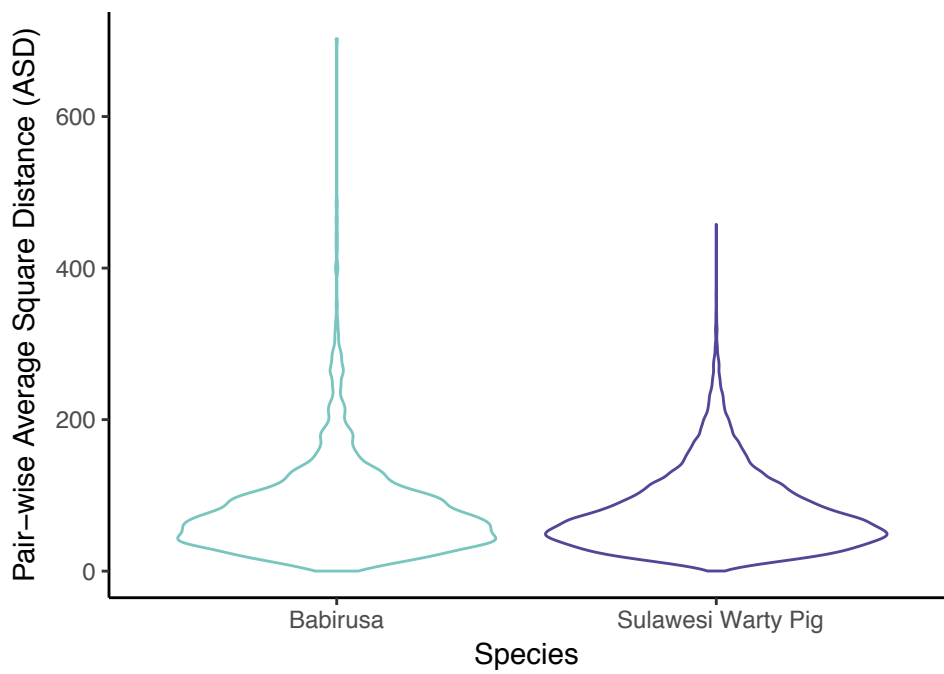
Figure 2: Population morphological variation inferred from geometric morphometric data. **a.** Neighbour-joining network based on Mahalanobis distances measured from second and third lower molar shapes and visualisation of population mean shape. **b.** Variation of third molar size per population (log centroid size).

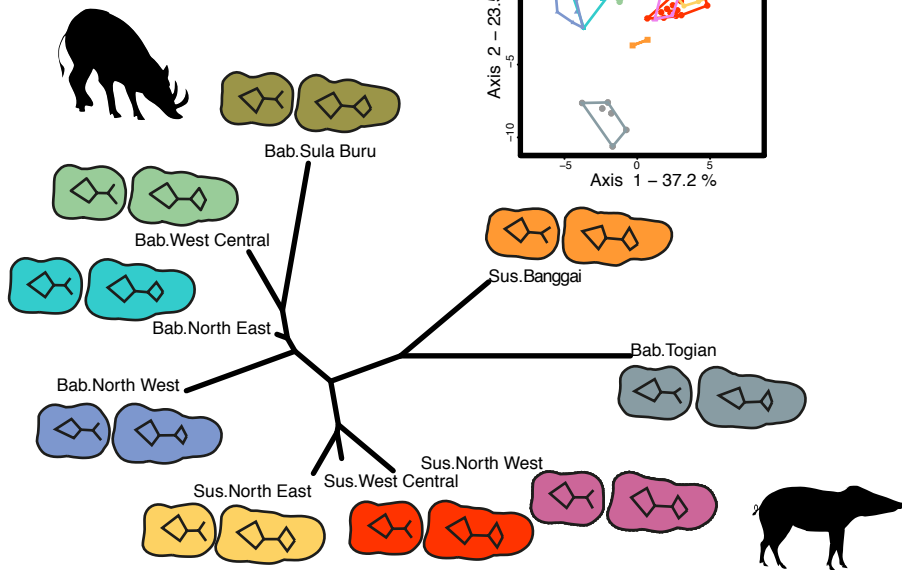
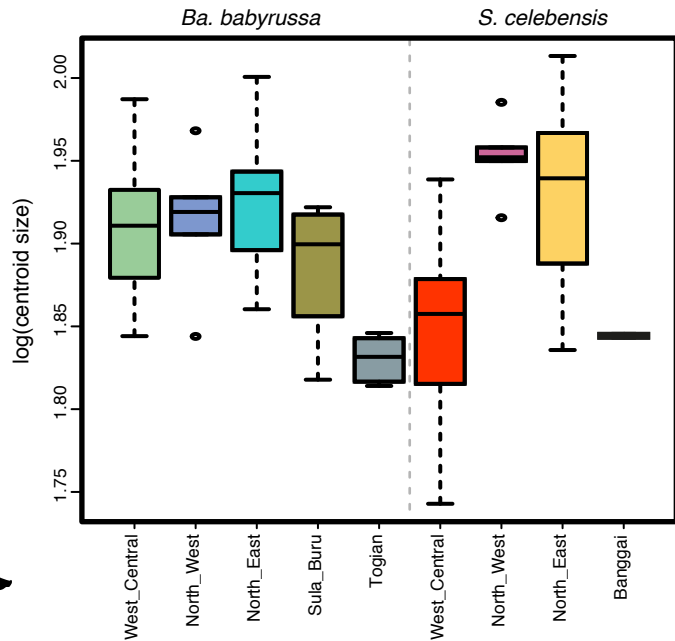
Figure 3: Geological maps of Sulawesi and the geographical origin of expansion. **a.** Reconstruction of Sulawesi over the last 5 Myr (adapter from [39]) and potential origin of expansion of **b.** Anoa, **c.** Babirusa, and **d.** Sulawesi warty pig. Low correlation values (between distance and extrapolated genetic diversity; see *Supplementary Material*) represent most likely origin of expansion.

Figure 4: Population structure and geographic patterning of three mammal species on Sulawesi inferred from mitochondrial and microsatellite DNA. **a.** to **c.**, A tessellated projection of sample haplogroups in each region of endemism, and phylogeny of **a.** Anoa **b.** Babirusa, and **c.** Sulawesi warty pig. Each region is

labelled with the number of samples used for the projection. The projection extends over regions with no samples (e.g. the Southwest peninsula for Babirusa and Anoa) and the population membership affinities for these regions are therefore less reliable. Red and blue stars on the phylogenetic trees correspond to posterior probabilities greater than 0.9 and 0.7, respectively. **d. to f.**, Tessellated projection of the STRUCTURE analysis, using the microsatellite data, for **d.** Anoa, **e.** Babirusa, and **f.** Sulawesi warty pig. The best K value for each species was used ($K=5$ for Anoa; $K=6$ for Babirusa; $K=5$ for Sulawesi warty pig; *Supplementary Material* Figure S8). NE=North East; NC=North Central; NW=North West; TO=Togian; BA=Banggai Archipelago; EC=East Central; WC=West Central; SU=Sula; BU=Buru; SE=South East; SW= South West; BT=Buton.

Figure 5: Posterior distribution of the current population size (N_e) of each species as inferred via approximate Bayesian computation.

a.**b.**

a.**b.**

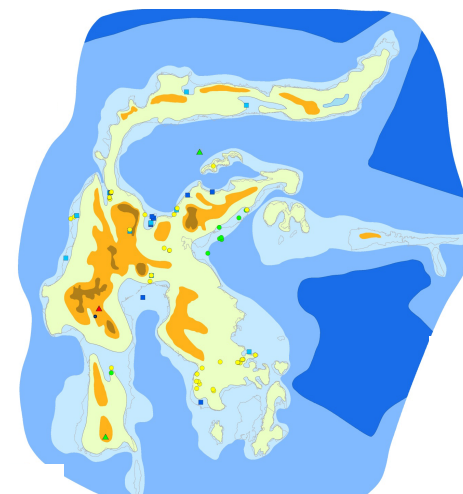
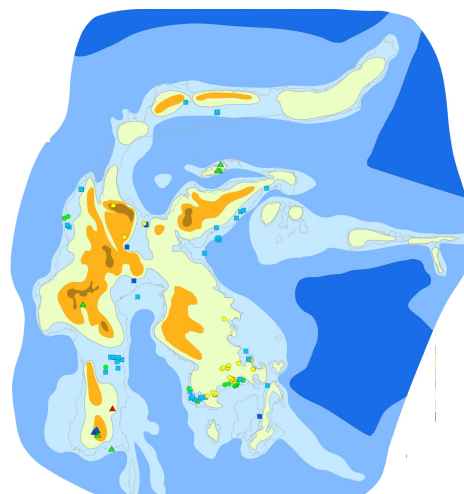
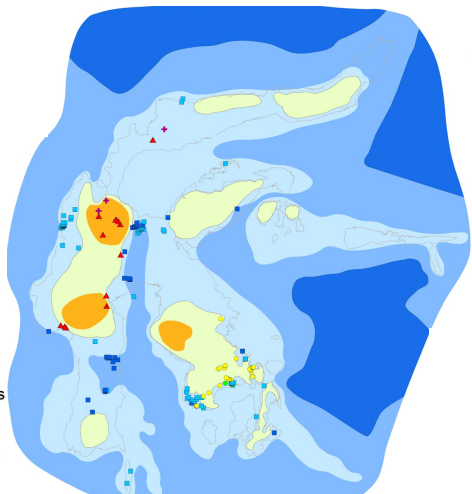
a.

Pliocene (4Ma)

Pleistocene (2Ma)

Pleistocene (1Ma)

Topography-Bathymetry

**b.****c.****d.**