

# Contributions to Mammalogy and Zooarchaeology of Wallacea

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# Late Quaternary Mammal Introduction and Extinction Records from Archaeological Cave Deposits in Timor-Leste

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**ABSTRACT.** Humans have influenced island biotas in the last few millennia through widespread forest clearances and the introduction of commensals and pest species, causing the extinction of island endemics around the world. This is particularly evident in Timor, where more than 40,000 years of human habitation produced few if any extinctions until the last few thousand years when Timor lost most of its endemic murids. We present new records and dates for endemic rodents and introduced fauna from archaeological cave deposits in Timor-Leste that captures this human-mediated transition. We discuss the chronology of faunal introductions and losses at these sites, and compare the Timor records to other records in surrounding islands. We find no directly dated evidence for significant overlap between the introduction of exotics and extinction of murid endemics at ecological timescales, although determining true extinction and introduction ages will require direct dating and modelling of taxon occurrences, which may bring extinction and introduction closer together in time. Nevertheless, we suggest that, based on current data, the almost complete loss of Timor's endemic forests were the primary driving force in rodent extinctions.

**ABSTRAK** [Bahasa Indonesia]. Manusia telah memengaruhi keragaman biota pulau dalam beberapa milenium terakhir melalui pembabatan hutan yang luas dan introduksi spesies komensal dan hama, yang menyebabkan kepunahan hewan endemik pada beberapa pulau di seluruh dunia. Hal ini terutama terlihat di Timor, di mana lebih dari 40.000 tahun umur hunian manusia yang hanya menyebabkan sedikit atau hampir tidak ada kepunahan, sampai beberapa ribu tahun terakhir ketika Timor kehilangan sebagian besar tikus endemiknya. Kami menyajikan data dan penanggalan baru terkait tikus endemik dan fauna yang diintroduksi ke dalam pulau berdasarkan pada temuan dari gua arkeologi di Timor-Leste yang merekam perubahan yang disebabkan oleh manusia. Kami membahas kronologi introduksi fauna dan dampak negatif di lokasi-lokasi ini, dan membandingkan data di Timor dengan data lain di pulau-pulau sekitarnya. Kami

**Keywords:** rodent, rat, pig, dog, exotic fauna, *Melomys*, *Komodomys*

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tidak menemukan bukti penanggalan yang dapat dicocokkan korelasinya antara waktu pengenalan fauna eksotis dan kepunahan tikus endemik dalam skala waktu ekologis, walaupun menentukan usia kepunahan dan introduksi fauna yang sesungguhnya akan memerlukan penanggalan secara langsung dan pemodelan kemunculan taksonomi, yang mungkin dapat menunjukkan waktu kepunahan dan introduksi lebih dekat. Meskipun demikian, berdasarkan data yang ada saat ini, kami berpendapat bahwa hampir hilangnya hutan endemik di Timor merupakan faktor utama dalam kepunahan tikus.

REZUMU [Tetum language]. Emar fó ona influénsia ba biota insulár sira iha miléniu hirak liubá, liuhusi tesi ai no hamate floresta (ai-laran) iha fatin barak no liuhusi hatama espésie komensál sira no kuit (praga), hodi provoka estinsaun ba espésie endémika insulár iha mundu tomak. Prosesu ida ne'e ita bele haree liuliu iha Timor, iha ne'ebé, durante tinan rihun 40 resin ho prezensa emar nian, estinsaun sira la iha, ka iha uitoan de'it, maibé iha tinan rihun balun ikus ne'e, Timor lakon maioria husi ninia murídeu (balada maktohik ka roedór) endémiku sira. Ami aprezena rejistu no data foun sira kona-ba roedór endémiku sira no kona-ba fauna ne'ebé hatama ona. Dadus sira ne'e ami rekolle iha depózitu arkeolójiku sira iha fatuk-kuak Timor-Leste nian, ne'ebé hatudu tranzisaun ida ne'e, ne'ebé akontese tanba prezensa emar nian. Ami diskute kronolojia kona-ba introdusaun (hatama) no perda (lakon) sira fauna nian iha fatin sira ne'e, no ami kompara rejistu sira husi Timor ho rejistu husi illa sira ne'ebé besik. Ami la hetan prova sira ho data ne'ebé bele hatudu duni sobrepozisaun (akontese iha tempu hanesan) maka'as entre introdusaun (hatama) espésie ezótika sira no estinsaun (lakon nafatin) husi murídeu endémiku sira iha eskala tempu ekolójika nian sira, maske definisaun ho loloos kona-ba idade estinsaun no introdusaun prezisa data saun (atribui data) direta no modelasaun konaba okorrénsia (mosu) *táxones* (grupu ka divizaun iha sistema biolójiku) nian, no definisaun ida ne'e bele hatudu katak estinsaun no introdusaun akontese iha tempu besik. Maske nune'e, ami sujere katak, bazeia ba dadus ne'ebé oras ne'e daudaun iha, lakon kuaze total husi floresta (ai-laran) endémika Timor nian maka razaun prinsipál ba estinsaun roedór sira nian.

## Introduction

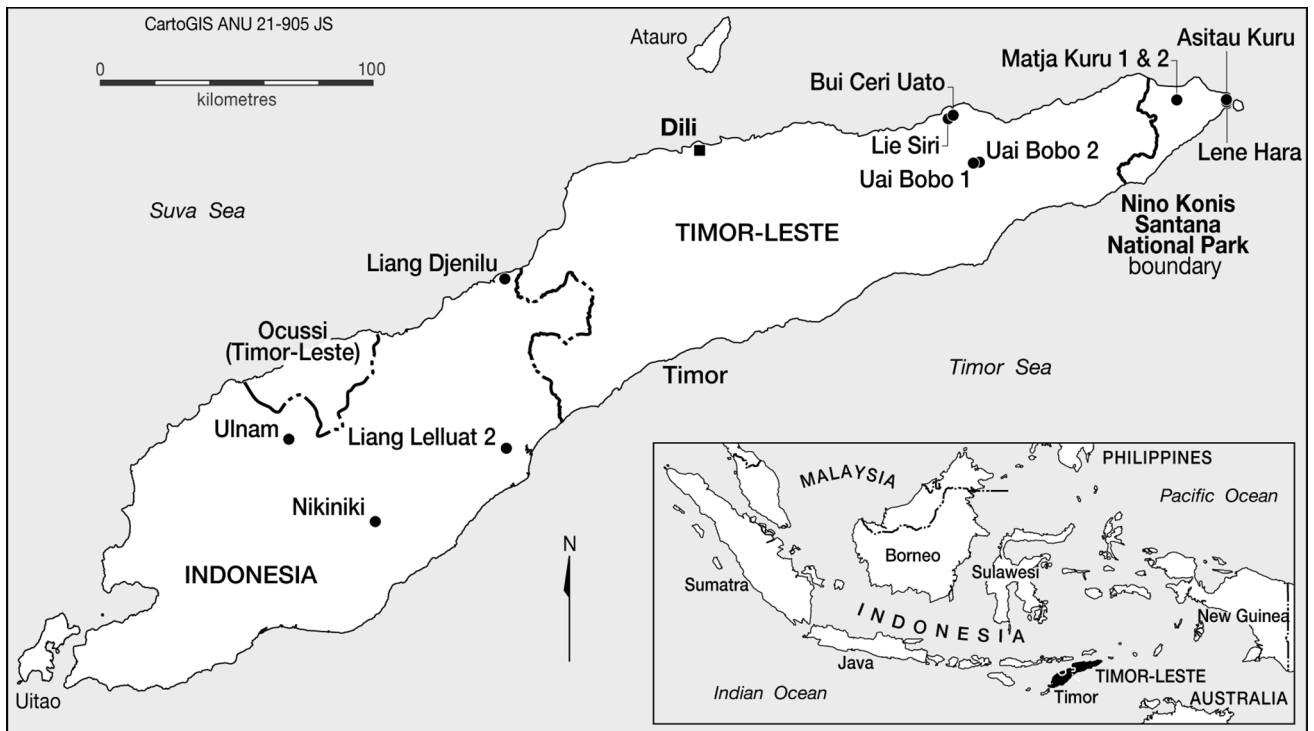
Humans have had a disproportional impact on island biotas over the last few millennia (Ceballos & Ehrlich, 2018; Louys *et al.*, 2021; Nogué *et al.*, 2021), and the widespread introduction of commensals and pest species have been implicated in the extinction of island endemics around the world (Wood *et al.*, 2017; Castilla-Beltrán *et al.*, 2021). However, based on current archaeological and palaeontological records, humans and other hominins may have had more limited impacts on island ecosystems prior to the widespread adoption of agriculture, maritime trade, and domestication (Leppard, 2014; Rozzi *et al.*, 2023; Louys *et al.*, 2021; Wood *et al.*, 2017), but this record is not well resolved for earlier periods of the Pleistocene. On the island of Timor, more than 40,000 years of human habitation produced very few extinctions (Hawkins *et al.*, 2017; Louys *et al.*, 2021); although an example of the latter includes a crane (*Grus* sp.) that likely became extinct in the Late Pleistocene (Meijer *et al.*, 2019). It was only in the last few thousand years that Timor lost a disproportionate amount of its endemic biota (Aplin & Helgen, 2010).

Prehistoric excavations on Timor documenting some of these losses began in rockshelters near Nikiniki, southwest Timor (Fig. 1), by Alfred Bühler in 1935 (Sarasin, 1936) (no local names of the rockshelters are provided and they are referred to as “Abri” [rockshelter] I, II, and III). Bühler uncovered pottery fragments and domestic animals that were likely Holocene in age, as well as giant rat fragments from Abri II which were subsequently described by Schaub (1937) as the extinct species *Coryphomys buehleri*. In 1938, Willems of the Oudheidkundige recovered relatively recent archaeological material from Ulnam Cave on the slopes of Gunung Mutis located NW of Nikiniki (Oudheidkundig Verslag, 1939: 12). Two additional caves, Liang Leluat II and Liang Djenilu, excavated by Verhoeven in 1954, produced more Holocene material, including blades, scrapers, and worked points (Verhoeven, 1959).

Older deposits on Timor were first identified at Lene Hara cave in the eastern part of the island by the Portuguese anthropologist Antonio de Almeida in 1963. The site contained an 80 cm deep cultural assemblage with marine shells and stone artefacts found throughout the sequence, but with pottery fragments restricted to the surface (Fig. 1). A brief report on the stone artefacts described them as typologically “pre-Neolithic” (Almeida & Zybszweski, 1968). However, the site was never dated, and none of the fauna was properly described. In 1966, Glover visited the site and photographed Almeida’s trench, which was still open (Glover, 1969). Glover made a small cutting on the edge of the trench, which confirmed Almeida’s observation that pottery was absent below the surface (Glover, 1969).

Glover conducted additional excavations between 1966–1967 at Uai Bobo 1 and 2, Lie Siri, and Bui Ceri Uato in eastern Timor and found large amounts of prehistoric terrestrial faunal remains that, together, provided a baseline cultural sequence for the island (Glover, 1986) (Fig. 1). Glover (1986: appendix 2) presented new giant murids from his excavations, with initial identification of murid cranial remains made by Dan Witter, with further work and tabulation undertaken by Jack Mahoney, as described in Glover’s (1986) Appendix 2. Mammalogist Guy Musser of the American Museum of Natural History subsequently agreed to take over the study of the fossil rodents, and he later passed on the material to Kristofer Helgen, who studied the collection with mammalogist and zooarchaeologist Kenneth P. Aplin (KPA). In addition to *Coryphomys*, three undescribed genera of giant rats were recognized in Glover’s monograph. Pending formal description, these were designated “Large murid, genus A” (Glover, 1986: plate 49), “Large murid, genus B” (Glover, 1986: plate 50), and “Large murid, genus C” (Glover, 1986: plate 51). These are hereafter referred to as Genus A, B, and C, respectively. Genus C is absent from Bui Ceri Uato but otherwise all three genera are present in all of Glover’s sites.

Following the annexation of Timor-Leste by Indonesia



**Figure 1.** Map of Timor island showing the location of all the sites discussed in the text. Produced by CartoGIS Services, The Australian National University.

in 1975, archaeological research paused until The East Timor Archaeological Project (ETAP) was initiated in 2000 (O'Connor *et al.*, 2002). The ETAP initiated new surveys to locate other prospective caves and middens in eastern Timor-Leste and opened a test excavation at Lene Hara (O'Connor *et al.*, 2002). Renewed excavation at Lene Hara focused on a 1 × 1 m test pit situated adjacent to Almeida's trench near the southern entrance (Square A). This test pit at Lene Hara and the first excavations at Matja Kuru caves 1 and 2 and Jerimalai rockshelter (now known as Asitau Kuru) under ETAP revealed human occupation dating back at least 40,000 years, associated with a diverse marine and terrestrial zooarchaeological record (O'Connor, 2007; O'Connor *et al.*, 2002; O'Connor *et al.*, 2010; O'Connor & Aplin, 2007; Samper Carro *et al.*, 2023; Shipton *et al.*, 2019; Veth *et al.*, 2005).

Ken Aplin played a significant role in analysing faunal material from Timor, including material from the caves described above (O'Connor & Aplin, 2007). For example, a thorough revision of *Coryphomys* based on faunal material from Matja Kuru caves 1 and 2 and Asitau Kuru, as well as specimens previously excavated by Glover (1986) from the sites mentioned above, revealed a new species of giant murine, *Coryphomys musseri* (Aplin & Helgen, 2010). Descriptions of additional giant rat genera and species first identified in Glover (1986) have been ongoing, with descriptions of Glover's Genus A, B, and C and their constituent species currently in preparation.

In addition to these findings, KPA also analysed a sample of the terrestrial faunal components of Lene Hara, Matja Kuru 1 and 2, and Asitau Kuru, tabulating numbers of identified specimens of mostly terrestrial fauna for each excavated unit (EU) of select excavation squares dating from the Late Pleistocene to the recent. These records span several important faunal events such as the introduction

of domestics and commensals to the island, as well as the extinction of the giant rat fauna. Before a description of these results could be published, KPA passed away in 2019. Here, we present KPA's records (except for Matja Kuru 2), new date estimates for giant rat faunal material, and new chronological models for Glover's and ETAP sites. We use these to examine and describe late Quaternary introductions and extinctions on Timor and compare them to other faunal records in surrounding islands.

## Methods

### Geochronology

Three approaches to determining the first and last appearance dates (FAD and LAD, respectively) for faunal accumulations and geochronological events at Asitau Kuru, Bui Ceri Uato, Lene Hara, Lie Siri, Matja Kuru 1, Uai Bobo 1, and Uai Bobo 2 were applied. First, specimens representing either extinct or introduced taxa were directly dated using radiocarbon 14 (<sup>14</sup>C) where possible (Zazzo & Saliège, 2011). Second, excavated units (EU) in which remains were found were dated using <sup>14</sup>C on marine shell and charcoal fragments, as well as optical luminescence (OSL) dating techniques on sediment samples (SI Tables) (Huntley *et al.*, 1985). Where datable material has not been reported from the first or last occurrences in EUs, the EU age was estimated by bracketing the maximum and minimum ages from the EUs above and below the EU of interest for the excavation square in which it was found. All dates and/or lab codes considered in the bracketing are indicated in the *Supplementary Information* (SI) material. All direct ages are reported as unmodelled calibrated ages, while associated and bracketing ages are reported as modelled ages, following calibration. All radiocarbon ages discussed and listed here are calibrated

ages unless otherwise indicated. For direct and associated ages based on the dating of a single sample, the median age of that sample was used for a single point estimate. Bracketing ages were based on the earliest extent of the lower date 95.4% probability range and the latest extent of the upper date range. For example, Matja Kuru 1 Square AA produced a date range of 4639–4135 cal BP and 5200–4514 cal BP at 95.4% probability for spits 3 and 5, respectively. Spit 4 is therefore bracketed between 5200 and 4135 cal BP (see Table 1 and SI).

The calibration of dates and the various modelled ages were obtained through the OxCal v4.4 online platform (Bronk Ramsey, 2009a). All dates obtained from terrestrial carbons (i.e., charcoal or bone) were calibrated with a mixed U(0,50) curve, combining the IntCal20 (Reimer *et al.*, 2020) and SHCal20 (Hogg *et al.*, 2020) curves, as recommended for dates from the Inter-Tropical Convergence Zone (Hogg *et al.*, 2020; Marsh *et al.*, 2018). All marine shell sample dates were calibrated with the Marine20 curve (Heaton *et al.*, 2020). A chronostratigraphic model for each site analysed in this study was constructed using the multi-phase Bayesian modelling applications in OxCal v4.4. This produces a series of chronostratigraphic phases which we use to interpret the site formation history. For charcoal dates in these models, we applied the Charcoal Plus t-type Outlier Model with a prior outlier probability of 10%, which is specifically designed to account for the inbuilt age of charcoal (old wood effect), while also allowing for some stratigraphic movement in an archaeological context (Bronk Ramsey, 2009b; Dee & Bronk Ramsey, 2014). The General t-type Outlier Model with a prior outlier probability of 5% was used for all other dates (i.e., bone and shell), following commonly used modelling procedures for general archaeological dates (Bronk Ramsey, 2009b; Wood *et al.*, 2016).

Each chronostratigraphic model, in addition to using all available dates, maximizes the addition of relative stratigraphic information (e.g., superpositioning, stratigraphic layers, vertical distance between samples). For Bui Ceri Uato, Lie Siri, and Uai Bobo 1 & 2, there was sufficient, comparable data to run depositional models which could interpolate “missing” ages across the stratigraphy based on age-depth correlation. In these depositional models we assume a Poisson (random) accumulation of sediment (Bronk Ramsey, 2008), calculated from the available age data by averaging the model over many values of  $k$  (Bronk Ramsey & Lee, 2013). The unit of depth used was in centimetres (cm) with a model interpolation rate set to a single date per ~5 cm for sites with reliable depth measurements (Lie Siri and Uai Bobo 2). For sites lacking reliable depths, such as Bui Ceri Uato and Uai Bobo 1, volume ( $m^3$ ) was used instead with interpolation set to one date per ~5  $cm^3$ .

For Asitau Kuru, Lene Hara, and Matja Kuru 1, neither depths nor volumes were readily available and/or informative to the model. For example, excavations at Lene Hara have produced a set of dates from different excavations distributed widely across the site which can be correlated to separate phases of occupation thanks to extensive efforts to interpret the site’s stratigraphy and sedimentary history (see SI and references therein). Due to the site’s complex depositional history (e.g., Squares A and B record phases of occupation which pre-date the entirety of the Square F sequence), individual depths associated with the different dates across the entire site do not lend themselves to a depositional model.

For such sites we simply ran chronostratigraphic multi-phase models without the age-depth interpolation. Details on model specifics and results for each site is available in the *Supplementary Information* (SI).

For each extinct or introduced species considered, their last appearance ages for each site in which they are found are shown as a horizontal bar graph. A comparison of LADs and FADs was produced using the youngest and oldest representative sample, respectively, across all sites considered herein.

## Faunal analysis

All ETAP sites were excavated in units (EU) ranging from 2 to 10 cm in depth, varying across sites, depending on squares and stratigraphic features. All excavated material was then sieved using fine-meshed sieves ( $\leq 2$  mm). Bone samples were treated in weak acetic acid to dissolve adhered carbonate and sediment in instances where specimens were obscured. All archaeological samples were sorted by broad group (i.e., reptiles, birds, fish) and mammalian elements were separated by cranial versus post-cranial remains, or samples were left as “unidentified” bone. Mammal bones were further sorted according to rodents, bats, marsupials, larger mammals (e.g., introduced taxa), and humans where possible. All diagnostic elements were identified to generic- or species-level. Rodents were identified using maxillary and mandibular fragments as well as individual teeth. When species identification was not possible, rodent elements were assigned to a size category based on visual assessment by KPA. The identification of murid material from the ETAP sites was made based on reference material available and illustrated in Glover (1986). Counts of large murid NISPs supplemented the ETAP records from Glover’s sites and were taken directly from his monograph (Glover, 1986: p. 79, 119, 156, 191). Reference to other fauna recovered by Glover is made in the discussion where appropriate.

Different taxonomic treatments of species and sites reflects KPA’s evolving interests and understanding of the faunal diversity of Timor over time. As such, it is not clear if the lists are complete for non-rodent taxa. For example, the first sites that KPA examined (Lene Hara and Matja Kuru 1) do not list humans, reptiles, bats, or sharks but did record pottery, shrews, dogs, civets, deer, and macaques. Due to this inconsistency, fish, turtle, and other marine remains are not reported here (although they are known for some sites, e.g., Matja Kuru 1 and Lene Hara). All sites discussed here list the following genera: *Melomys*, *Komodomys*, *Rattus*, *Coryphomys*, *Phalanger*, *Sus*, as well as Glover’s giant rat Genera A, B, and C. For Lene Hara and Matja Kuru 1, small and medium *Komodomys*-like specimens were initially separated; for this study, these distinctions are grouped together under the category “*Komodomys*”; this includes “*K.*” *timorensis*, reflecting KPA’s unpublished revision of *Rattus timorensis*, which re-classifies this species in the genus *Komodomys* (see also Thomson *et al.*, 2018), and a larger-bodied *Komodomys*. We treat “*K.*” *timorensis* as an extant taxon, although its taxonomic and conservation status remain to be clarified. We treat the larger-bodied *Komodomys* as a separate, extinct species; however, confirmation of this status awaits full taxonomic analysis and description.

These records more accurately represent a presence rather than presence/absence as we cannot be certain that all material

**Table 1.** FADs and LADs of select taxa considered in this study, ages presented as cal BP. Full details of the calibration and age modelling of the samples are provided in the *Supplementary Information*.

Square	Taxon	Excavation unit	Date name	Date type	Modelling	Max	Median	Min
<i>Matja Kuru I Square A</i>								
MK1 A	Giant rat indet	Spit 1	End Phase 2	Associated	Modelled	1399	1175	508
MK1 A	Giant rat indet	4	Wk-25443	Direct	Unmodelled	1525	1453	1376
MK1 A	<i>Coryphomys</i>	2	Wk-25443 and End Phase 2	Bracket	Modelled	1531	—	508
MK1 A	Genus B	2	Wk-25443 and End Phase 2	Bracket	Modelled	1531	—	508
MK1 A	Genus C	4	Wk-25443	Associated	Modelled	1531	1453	1365
MK1 A	Genus A	12	NZA-17007	Associated	Modelled	3715	3539	3370
MK1 A	Large <i>Komodomys</i>	1	End Phase 2	Associated	Modelled	1399	1175	508
MK1 A	Small <i>Melomys</i>	7	Wk-25638	Associated	Modelled	3826	3661	3565
MK1 A	Large <i>Melomys</i>	8	S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	<i>Phalanger</i>	31	Wk-31509	Direct	Unmodelled	2916	2821	2763
MK1 A	<i>Paradoxurus</i>	13	Wk-31508	Direct	Unmodelled	2919	2817	2756
MK1 A	<i>Phalanger</i>	13	NZA-17007 and ANU-11632	Bracket	Modelled	3849	—	3370
MK1 A	<i>Paradoxurus</i>	13	NZA-17007 and ANU-11632	Bracket	Modelled	3849	—	3370
MK1 A	<i>Sus</i>	12	NZA-17007	Associated	Modelled	3715	3539	3370
MK1 A	<i>Rattus rattus</i>	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	<i>Rattus exulans</i>	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	<i>Canis</i>	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	<i>Macaca</i>	8	S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
<i>Matja Kuru I Square AA</i>								
MK1 AA	Genus B	1	ANU-11834 and End Phase 2	Bracket	Modelled	4639	—	508
MK1 AA	Large <i>Komodomys</i>	1	ANU-11834 and End Phase 2	Bracket	Modelled	4639	—	508
MK1 AA	<i>Coryphomys</i>	6	ANU-11622 and ANU-11621	Bracket	Modelled	6053	—	4514
MK1 AA	Large <i>Melomys</i>	6	ANU-11622 and ANU-11621	Bracket	Modelled	6053	—	4514
MK1 AA	Genus A	7	ANU-11621	Associated	Modelled	6053	5841	5633
MK1 AA	Genus C	9	ANU-11620	Associated	Modelled	5330	5136	4880
MK1 AA	Small <i>Melomys</i>	4	ANU-11622 and ANU-11834	Bracket	Modelled	5200	—	4135
MK1 AA	<i>Rattus rattus</i>	12	ANU-11618 and ANU-11619	Bracket	Modelled	5609	—	4420
MK1 AA	<i>Paradoxurus</i>	10	ANU-11619 and ANU-11620	Bracket	Modelled	5330	—	4420
MK1 AA	<i>Phalanger</i>	8	ANU-11620 and ANU-11621	Bracket	Modelled	6053	—	4880
MK1 AA	<i>Macaca</i>	6	ANU-11621 and ANU-11622	Bracket	Modelled	6053	—	4514
MK1 AA	<i>Sus</i>	6	ANU-11621 and ANU-11622	Bracket	Modelled	6053	—	4514
MK1 AA	<i>Canis</i>	4	ANU-11622 and ANU-11834	Bracket	Modelled	5200	—	4135
<i>Lene Hara Square A</i>								
LH A	Giant rat indet.	4	ANU-11400 and OZF-213	Bracket	Modelled	3535	—	323
LH A	Genus A	9	OZF-213 and End Phase 6	Bracket	Modelled	3535	—	1582
LH A	<i>Phalanger</i>	3	Start Phase 7 and ANU-11400	Bracket	Modelled	1885	—	323
LH A	<i>Sus</i>	3	Start Phase 7 and ANU-11400	Bracket	Modelled	1885	—	323
LH A	<i>Canis</i>	5	OZF-212 and End Phase 6	Bracket	Modelled	4556	—	1582
<i>Lene Hara Square D</i>								
LH D	<i>Paradoxurus</i>	18	ANU-12059	Associated	Modelled	3815	3568	3356
LH D	<i>Rattus exulans</i>	18	ANU-12059	Associated	Modelled	3815	3568	3356
LH D	Large <i>Melomys</i>	5	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	<i>Rattus rattus</i>	13	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	<i>Phalanger</i>	11	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	<i>Sus</i>	11	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	Cervid	4	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
<i>Lene Hara Square F</i>								
LH F	Genus A	17	ANU-12042 and Transition Phase 5/6	Bracket	Modelled	4567	—	3498
LH F	Giant rat indet.	12	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	Large <i>Komodomys</i>	11	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	Large <i>Melomys</i>	7	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283
LH F	<i>Phalanger</i>	34	Wk-31507	Direct	Unmodelled	2490	2397	2341
LH F	<i>Phalanger</i>	14	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	<i>Canis</i>	15	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	<i>Rattus exulans</i>	15	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	<i>Sus</i>	6	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283
LH F	<i>Rattus rattus</i>	7	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283

Table 1. *Continued ...*

**Table 1.** *Continued.*

Square	Taxon	Excavation unit	Date name	Date type	Modelling	Max	Median	Min
<i>Asitau Kuru Square B</i>								
AK B	<i>Coryphomys</i>	19	Wk-18158 and Wk-18157	Bracket	Modelled	6092	—	4959
AK B	Genus A	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	Large <i>Melomys</i>	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	Large <i>Komodomys</i>	5	Wk-19230 and End Phase 3	Bracket	Modelled	4838	—	1258
AK B	Small <i>Melomys</i>	26	Wk-18159 and Wk-17832	Bracket	Modelled	6419	—	5590
AK B	<i>Sus</i>	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	<i>Phalanger</i>	7	Wk-19230 and End Phase 3	Bracket	Modelled	4838	—	1258
AK B	<i>Rattus exulans</i>	17	Wk-18158 and Wk-18157	Bracket	Modelled	6092	—	4959
<i>Lie Siri</i>								
Lie Siri	Giant rat indet.	Horizon VIb	ANU-172, ANU-173	Associated	Modelled	3957	—	2417
Lie Siri	Genus A	Horizon Vc	Horizon Vc	Associated	Modelled	7717	7253	6627
Lie Siri	<i>Coryphomys</i>	Horizon Va	Horizon Va	Associated	Modelled	7976	7707	7452
Lie Siri	Genus B	Horizon III	Horizon III	Associated	Modelled	8338	8027	7702
Lie Siri	Genus C	Horizon III	Horizon III	Associated	Modelled	8338	8027	7702
<i>Bui Ceri Uato</i>								
Bui Ceri Uato	Giant rat indet.	Horizon VIII	ANU-11741	Associated	Modelled	7184	6888	6592
Bui Ceri Uato	Genus A	Horizon IV	ANU-11878	Associated	Modelled	11691	11105	10686
Bui Ceri Uato	<i>Coryphomys</i>	Horizon II	ANU-11877	Associated	Modelled	12980	12734	12505
Bui Ceri Uato	Genus B	Horizon II	ANU-11877	Associated	Modelled	12980	12734	12505
<i>Uai Bobo 1</i>								
Uai Bobo 1	Genus B	Horizon V	Horizon V	Associated	Modelled	1290	765	351
Uai Bobo 1	<i>Coryphomys</i>	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
Uai Bobo 1	Genus A	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
Uai Bobo 1	Genus C	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
<i>Uai Bobo 2</i>								
Uai Bobo 2	Genus C	Horizon X	Wk-25439	Associated	Modelled	1697	1573	1521
Uai Bobo 2	<i>Coryphomys</i>	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560
Uai Bobo 2	Genus A	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560
Uai Bobo 2	Genus B	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560

was identified prior to KPA's passing. As such, reports list the minimum number of identified specimens (mNISP) rather than standard NISP counts. While the nature of the data precludes direct quantitative inter-site comparisons because we may not be comparing like-with-like, they do allow for qualitative comparisons between excavation units, squares, and sites. For Lene Hara Square A, the data was supplemented by a more detailed, previously unpublished description of the remains by KPA, which has been updated where necessary. Unfortunately, no similar descriptors by KPA of the other sites he examined is known to us.

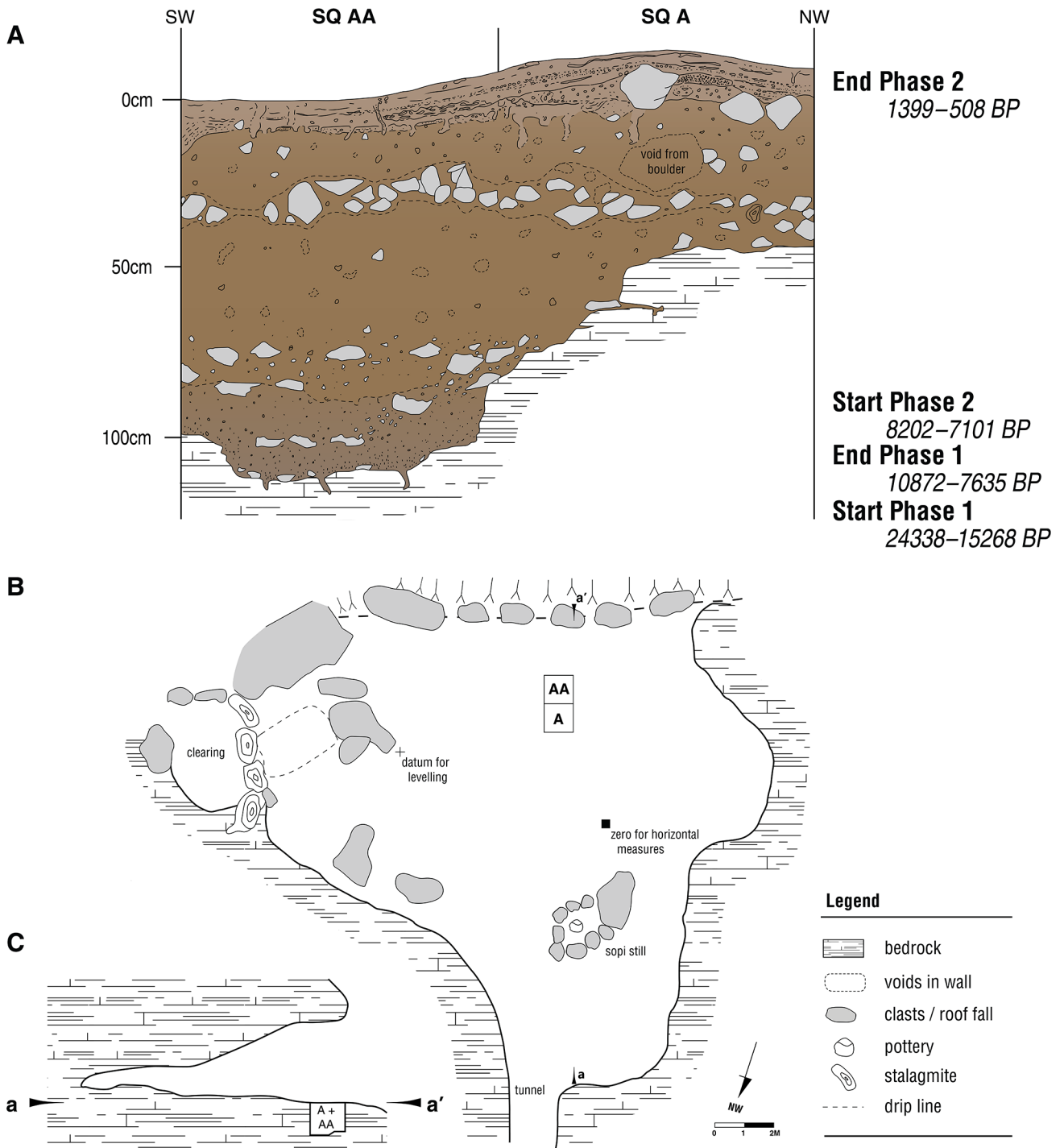
## Results

All calibrations, modelled ages, and age-depth models for the sites are presented in the SI and illustrated in Figs 2–8. A summary of the LADs and FADs are presented in Table 1 and summarized in Figs 9–11. Below, we discuss the last appearances of extinct taxa and the first appearances of the introduced taxa. There are numerous gaps in taxon presence throughout each excavation square sequence (SI). We do not consider these as genuine absences but rather, given the highly limited spatial scale sampled by each excavation combined with known taphonomic and depositional biases throughout the cave sequences (O'Connor *et al.*, 2017; Louys *et al.*, 2017; Samper Carro *et al.*, 2023), we treat the presence of each extinct taxon as continuous on the island

until at least their last dated record. Extant species are treated as continuous through to today. Readers are directed to the SI for the full range of occurrences and associated dates.

### Matja Kuru 1 Square A (Fig. 2)

The Matja Kuru 1 chronostratigraphic model revealed only one depositional phase present in Square A from approximately 7479–1175 cal BP (median ages, see SI). The distribution of dates within the square is not homogenous, with numerous instances of reversals and/or mixing. For example, marine shell, giant rat bone, and buttonquail (*Turnix* sp.) bone, all sourced from spit 8, produced median dates of 5133 (NZA-16135), 4040 (Wk-25635), and 1358 (S-ANU-55223) cal BP, respectively. Unidentified giant rat material is found from spit 1 down (i.e., the end of Phase 2 modelled at *ca.* 1175 cal BP) with the youngest direct dates between 1525 and 1376 cal BP (Wk-25443, 95.4% probability range) from spit 4. At the generic level, *Coryphomys* and Genus B are both recorded from spit 2 and Genus C from spit 4 down. Genus A is last reported from spit 12 from which a marine shell provides an associated date between 3715 and 3370 cal BP (NZA-17007, 95.4% probability range). Large *Komodomys* is found from spit 1 down (i.e., up until *ca.* 1175 cal BP, end of Phase 2). Small *Melomys* is last recovered in spit 7. This spit preserves material which has produced a modelled date of 3661 cal BP (Wk-25638, median), while the Large *Melomys* is recovered from spit 8 (which has produced



**Figure 2.** Matja Kuru 1. (A) stratigraphic section of Squares A and AA showing the start and end of each chronostratigraphic phase (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details); (B) cave site in plan view; (C) cave site in section view.

a median date: 4039 cal BP, Wk-25635). Shrews (*Crocidura* spp.) are first reported from spit 11.

In terms of introduced species, cuscus (*Phalanger orientalis*) and civet (*Paradoxurus hermaphroditus*) are first recorded from spit 13, which is bracketed by modelled ages of 3849 and 3370 cal BP (Table 1). There is also a direct date from a *Phalanger* specimen from spit 31, at 2821 cal BP (Wk-31509, median) which indicates it originated from higher in the stratigraphic sequence, and a civet

fragment from spit 13 at 2817 cal BP (Wk-31508, median). Pigs (*Sus* sp.) are first recorded from spit 12 which has a median age of 3539 cal BP (NZA-17007), followed by *R. exulans* (Pacific rat), *R. rattus* (Black rat), and dog (*Canis familiaris*) from spit 11, an undated spit but likely roughly coeval with spit 12 based on stratigraphy. Lastly, a single macaque specimen (*Macaca fascicularis*) is recorded from spit 8, which remains ambiguously dated to sometime in the mid to late Holocene.



### Matja Kuru 1 Square AA (Fig. 2)

Two depositional phases were identified in Square AA: Phase 1, a terminal Pleistocene sequence modelled as starting around 17,508 cal BP and ending around 9,501 cal BP (median, spits 21–30; see SI); and Phase 2, a Holocene sequence modelled roughly between 7479 cal BP and 1175 cal BP, and also present in Square A (Fig. 2). Genus B and large *Komodomys* are found up into spit 1. Dates obtained from the uppermost stratigraphy derive from spit 3 with an age estimate between 4639 cal BP (ANU-11834; maximum extent of the 95.4% probability range) and 508 cal BP (the end of Phase 2; minimum). *Coryphomys* and the Large *Melomys* are found in varying abundances until spit 6, which is estimated between 6053 cal BP (ANU-11621; maximum, spit 7) and 4514 cal BP (ANU-11622; minimum, spit 5). Genus A is found in varying abundances beginning in spit 25 until spit 7, from which an associated marine shell has produced a median date of 5841 cal BP (ANU-11621). Genus C is sparsely found beginning in spits 20 and 19, as well as spits 13 and 9, from which an associated marine shell has produced a LAD median date of 5136 cal BP (ANU-11620). Finally, the Small *Melomys* is found starting in spit 26, as well as in spits 24–21, 18, 16, 15, 9, and finally, spit 4, which is bracketed by dates of 5200 and 4135 cal BP (Table 1). Shrews (*Crocidura* spp.) are reported from Phase 1 in the terminal Pleistocene.

For introduced species, *R. rattus* is first reported from spit 12 with an estimated age between 5,609 and 4,420 cal BP, but becomes more abundant in spits 8 and 6–4 (Table 1). No specimens identified as *R. exulans* were reported from this square. Civets are reported from spits 10, 8, 5, and 1 and *Phalanger* is found beginning in spits 8 to 5, both of which are bracketed by reversed dates at ca. 5000 cal BP. Macaque and pig both first appear in spit 6 between 6053 and 4514 cal BP (Table 1). Finally, a single dog fragment is reported from spit 4 and bracketed between 5200 and 4135 cal BP (Table 1).

Notably, there are significant differences (Kruskal-Wallis test;  $H = 15.03$ ,  $p < 0.001$ ) in the proportion of large *Komodomys* to “*Komodomys timorensis*” in Phase 2 (average 75% of all *Komodomys* across spits) relative to Phase 1 (average 33% of all *Komodomys* across spits).

### Lene Hara Square A (Fig. 3F)

In addition to the minimum NISPs, additional previously unpublished observations by KPA from this square are provided below. The stratigraphy of this square shows evidence of disturbance, as discussed in detail in O'Connor *et al.* (2010), and evident from our age modelling for this site (see SI). As KPA's references to the original stratigraphy are no longer valid, the notes have been provided below with updates based on our current understanding of the stratigraphy and the age of this square.

*The vertebrate fauna comprises marine turtle and fish, freshwater turtle, large and small murid rodents, bats, phalanger, snakes (boids [i.e., pythons, now classified as Pythonidae] and colubroids), large and small lizards (including monitors, Varanus sp.), and the domestic pig and dog. An ‘unidentified’ category consists*

*predominantly of large chunks of finely cancellous bone that almost certainly represents fragments of marine turtle limb bones and carapace. One human incisor was recovered from spit 17. A small quantity of marine crab exoskeleton was also recovered in spit 7 and above.*

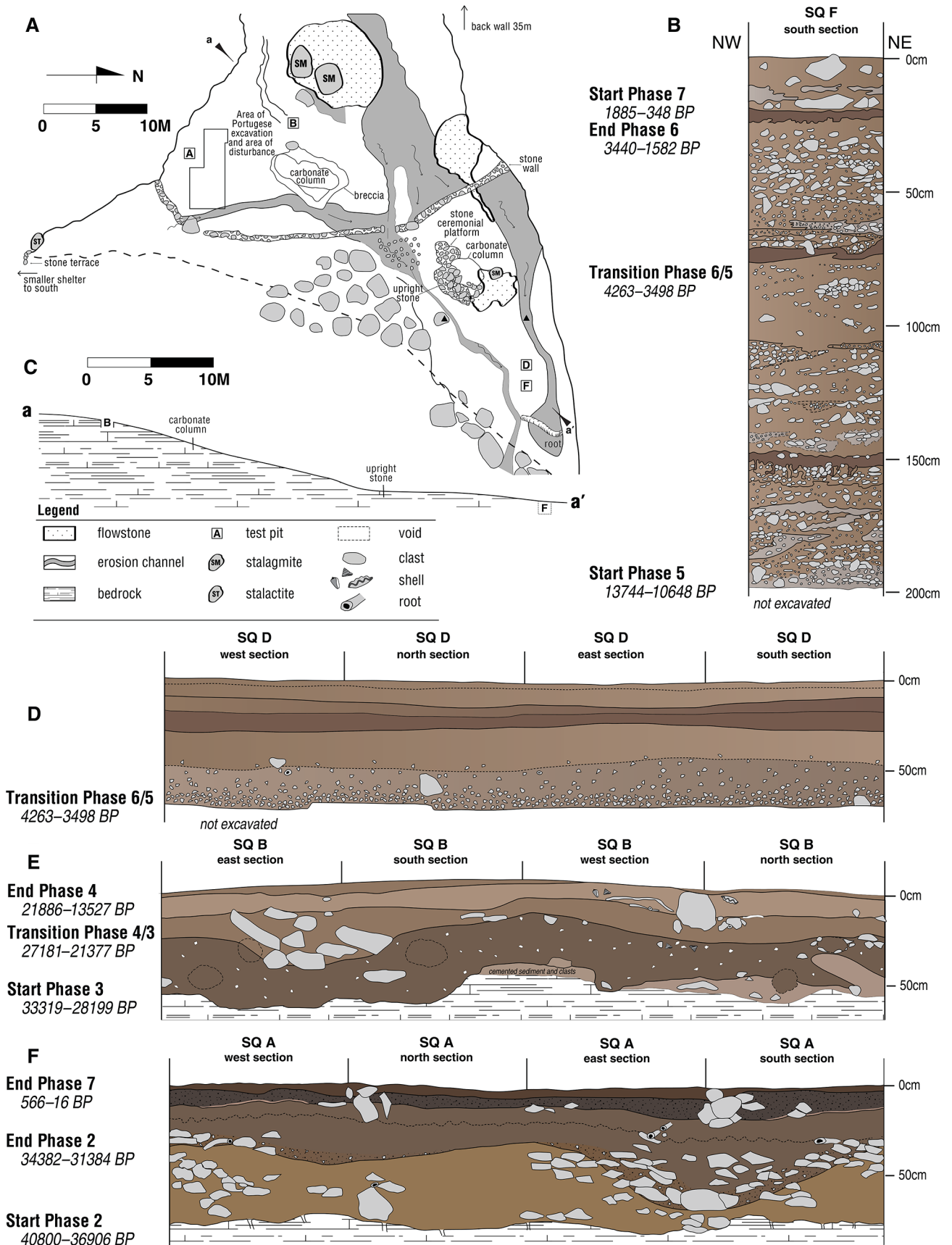
*Marine turtle occurs at all levels. The importance of this group is most likely better estimated by examining the ‘unidentified’ category in terms of bone weight—it makes up 80–90% of bone by weight from the lower levels, but from 32–62% in the more recent levels. The marine turtle is too fragmentary for identification to species but based on size and texture it most likely represents one or more species of Chelonia or Natator. Crab remains were found only in Spit 7 and above. Fish are present throughout the sequence but are nowhere abundant. Bones of terrestrial reptiles were recovered at all levels. Most of the snake remains represent moderately large pythons (two large-bodied species of the genus Python still occur on Timor) but some smaller vertebrae represent colubroid (venomous) snakes. A moderately large Varanus is represented in spits 6–8 only. Although this material clearly does not represent V. komodoensis, it is from a much larger bodied taxon than the only terrestrial monitor found on Timor today (V. timorensis). It may represent V. salvator, a large coastal dwelling monitor that occurs throughout eastern Indonesia. A freshwater chelid turtle is represented in Spit 1 by a carapace fragment.*

*A few bones of giant rats were recovered. Lene Hara Square A produced only postcranial fragments of these animals, one in each of Spits 4, 8, 9, 15, and 17. A fragmentary femur in Spit 9 is enormous and most likely represents Genus A, the largest of the Timor giant murids.*

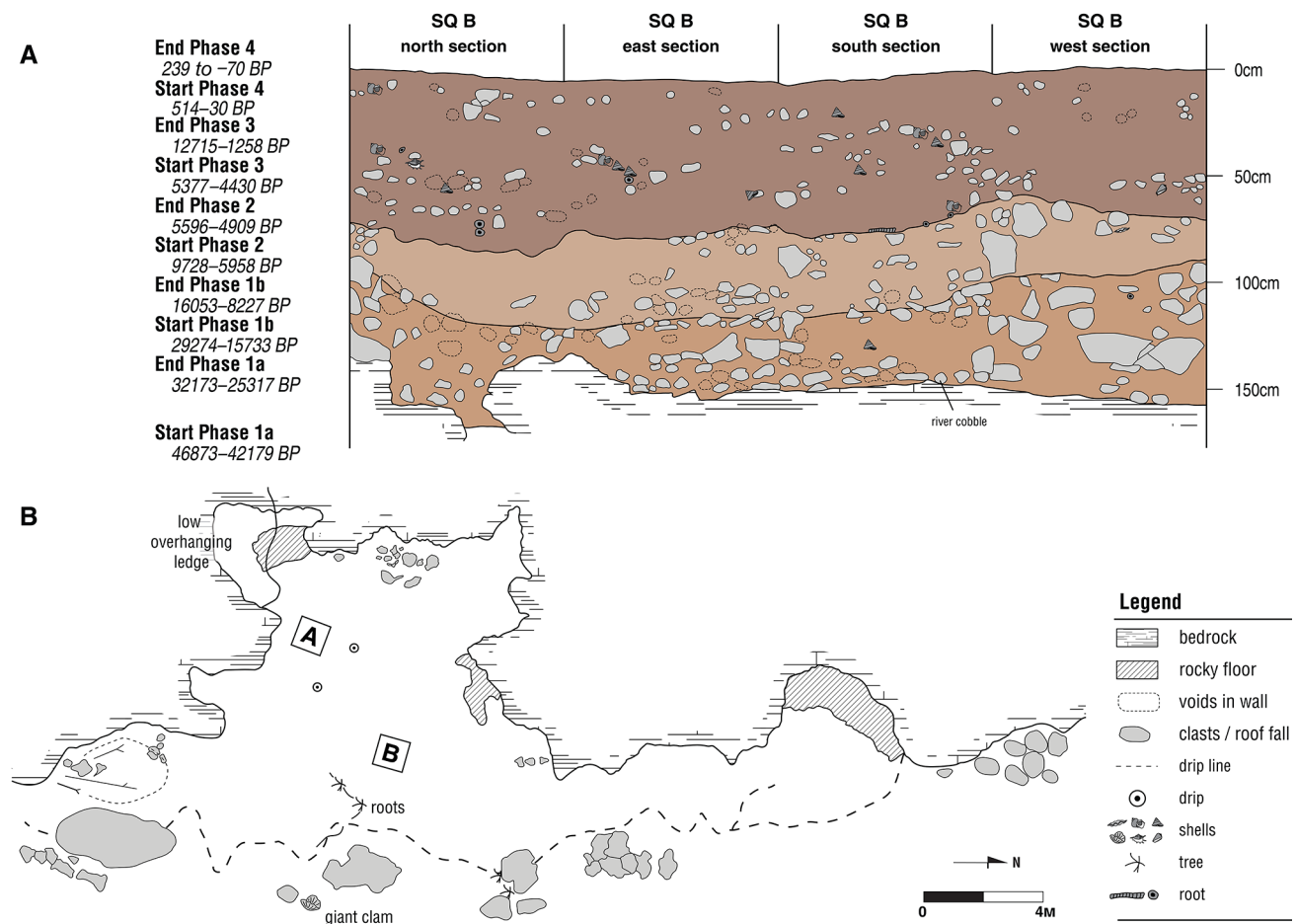
*None of the Lene Hara remains represent R. exulans, which is distinguishable from the native species by its small size and distinctive dental morphology. Two cranial fragments with teeth from Spits 3 and 10 represent an un-named endemic species that is distantly related to Rattus and was about the size of a European Black rat [these do not appear to be listed in the minimum number of identified specimens but may refer to “Komodomys timorensis or large Komodomys].*

*Several species of insectivorous bat are represented, and one larger bat that is represented only by post-cranial elements. The smaller bats and rodents might represent prey remains of a non-human predator such as a cave-roosting owl.*

*A phalanger is represented by a tibial fragment in Spit 3. Small fragments of pig and dog teeth were found in the upper levels of Test Pit A. Pig is identified from two small fragments of incisors in Spit 3 but a few of the larger, unidentified bone fragments from the upper spits might also represent this species. Dog is represented by a fragmentary right P4 from Spit 5. The P4 is a close match in size with modern Australian dingo specimens from northern Australia. —Ken Aplin.*



**Figure 3.** Lene Hara. (A) cave site in plan view; (B) stratigraphic section of Square F showing the start to end of chronostratigraphic phases 5 to 6 and start of 7; (C) transect through the site showing changes in elevation; (D) stratigraphic section of Square D showing transition chronostratigraphic phase 6/5; (E) stratigraphic section of Square B showing start to end of chronostratigraphic phases 3 and 4; (F) stratigraphic section of Square A showing start to end of chronostratigraphic phase 2 and end of phase 7 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details).



**Figure 4.** Asitau Kuru. (A) stratigraphic section of Square B showing the start and end of each chronostratigraphic phase (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details); (B) cave site in plan view.

These descriptions largely correspond to the minimum NISP, although a few points require further explanation. First, the dog remains from spit 17 likely represent disturbed material displaced from the upper spits, as marine shell associated with spit 18 is dated to 34,613 cal BP (ANU-11401), older than any domestic dog remains globally (Ovodov *et al.*, 2011). Second, if the unnamed rodent identified in these notes is in fact the large *Komodomys*, there is a transcription error (the notes indicate remains from spits 3 and 10, the NISPs list these as spits 5 and 10). Third, the first appearance of phalanger and pig likely date to sometime between 1885 and 323 cal BP (Start Phase 7 and ANU-11400, respectively—see SI), and are roughly coincident (within the context of this square) with the last appearance of giant rats and the large *Komodomys*.

#### Lene Hara Square B (Fig. 3E)

This square has only produced Pleistocene dates, with faunal material recorded in KPA's notes for spits 6–17. As such, it does not preserve the last appearance of any extinct rodent nor the first appearance of most commensals. However, there is a record of *R. rattus* from spit 7, material of which is likely older than 21,361 BP (ANU-12141). This is not likely to be an *in situ* recovery, but probably represents recently introduced surficial material. The square also preserves Genus B, “*Komodomys timorensis*,” and Large and Small *Melomys*.

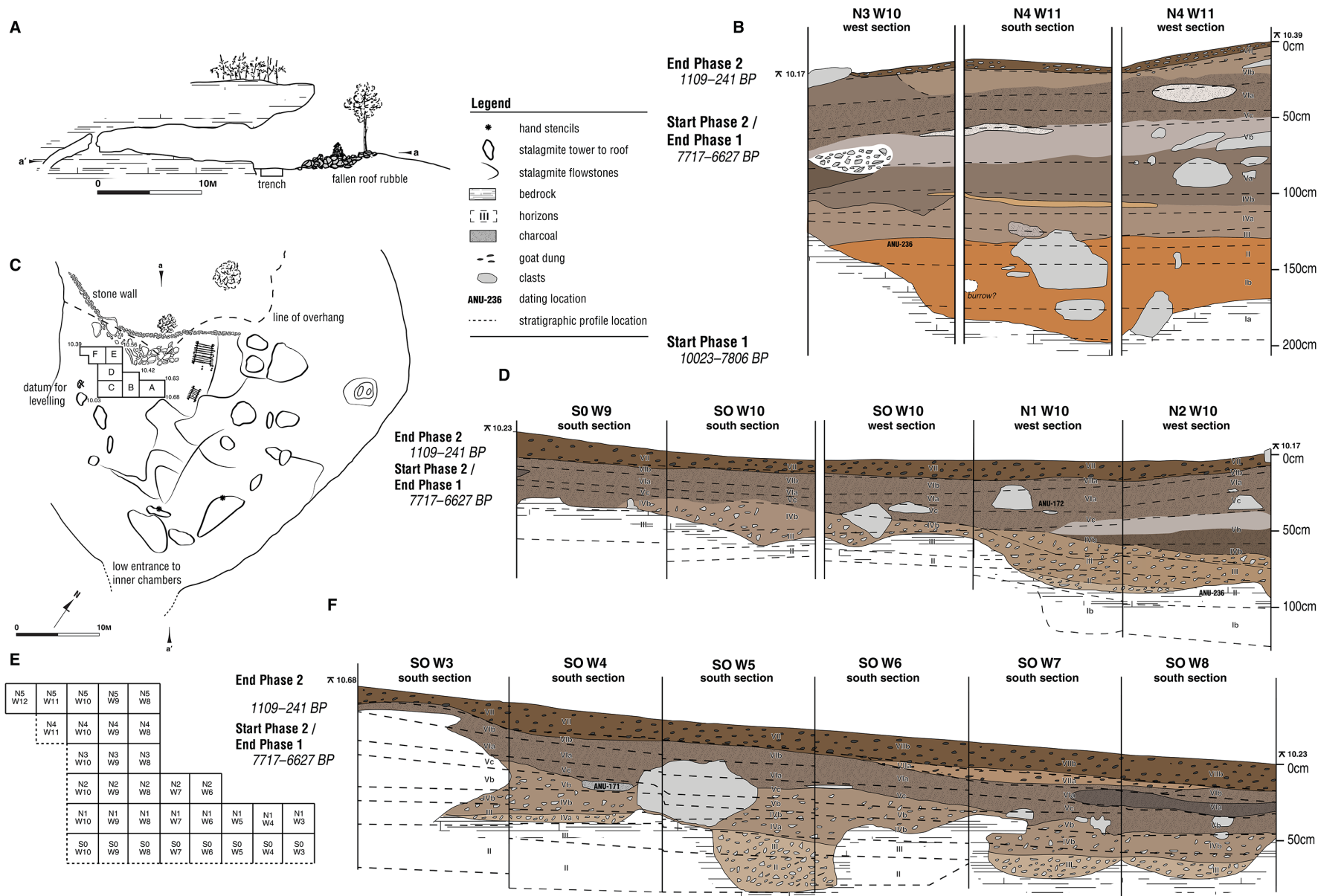
#### Lene Hara Square D (Fig. 3D)

Minimum NISPs are available for spits 1–18, dated material is available for spits 18 and 20. All of the faunal material from this square was deposited in Phase 6 (between 3834 and 2316 cal BP) or Phase 7 (between 740 and 339 cal BP) (see SI for full model). No *Komodomys* material is recorded from this square. Large *Melomys* is recovered up until spit 5. The deepest records of introduced species are for civet and Pacific rat, from spit 18 which has also produced marine shell dated to 3568 cal BP (ANU-12059). Black rat is recovered from spit 13, phalanger and pig from spit 11, and deer from spit 4. Shrew is recovered from spit 10.

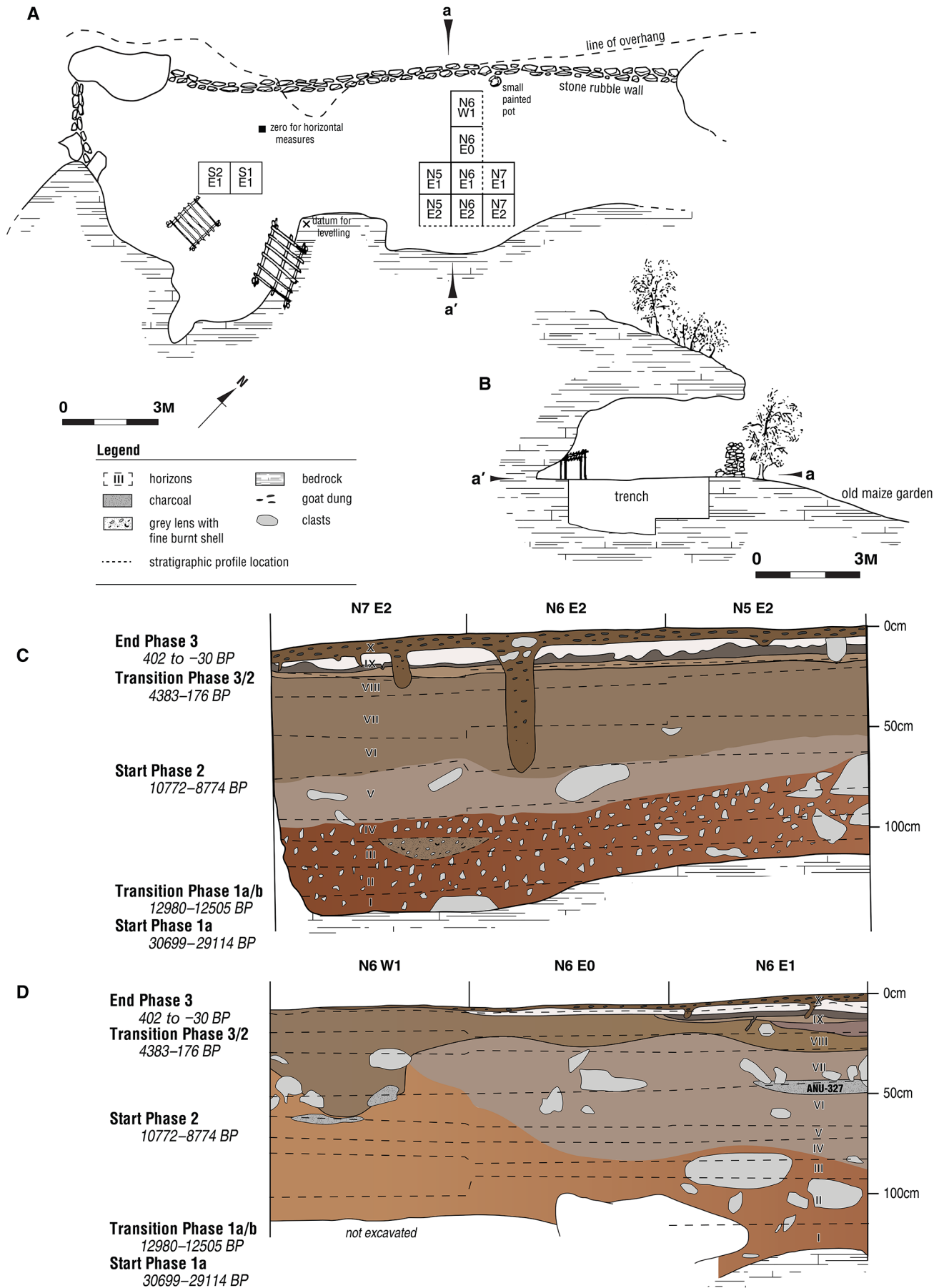
#### Lene Hara Square F (Fig. 3B)

Square F is a well stratified excavation with three major phases recognized from the dated material. Phase 5 comprises spits 45–18 and spans approximately 11,479–3834 cal BP, Phase 6 consists of spits 17–8 and dates to approximately 3834–2316 cal BP, and Phase 7, spits 7–1, spans approximately 740–339 cal BP (SI).

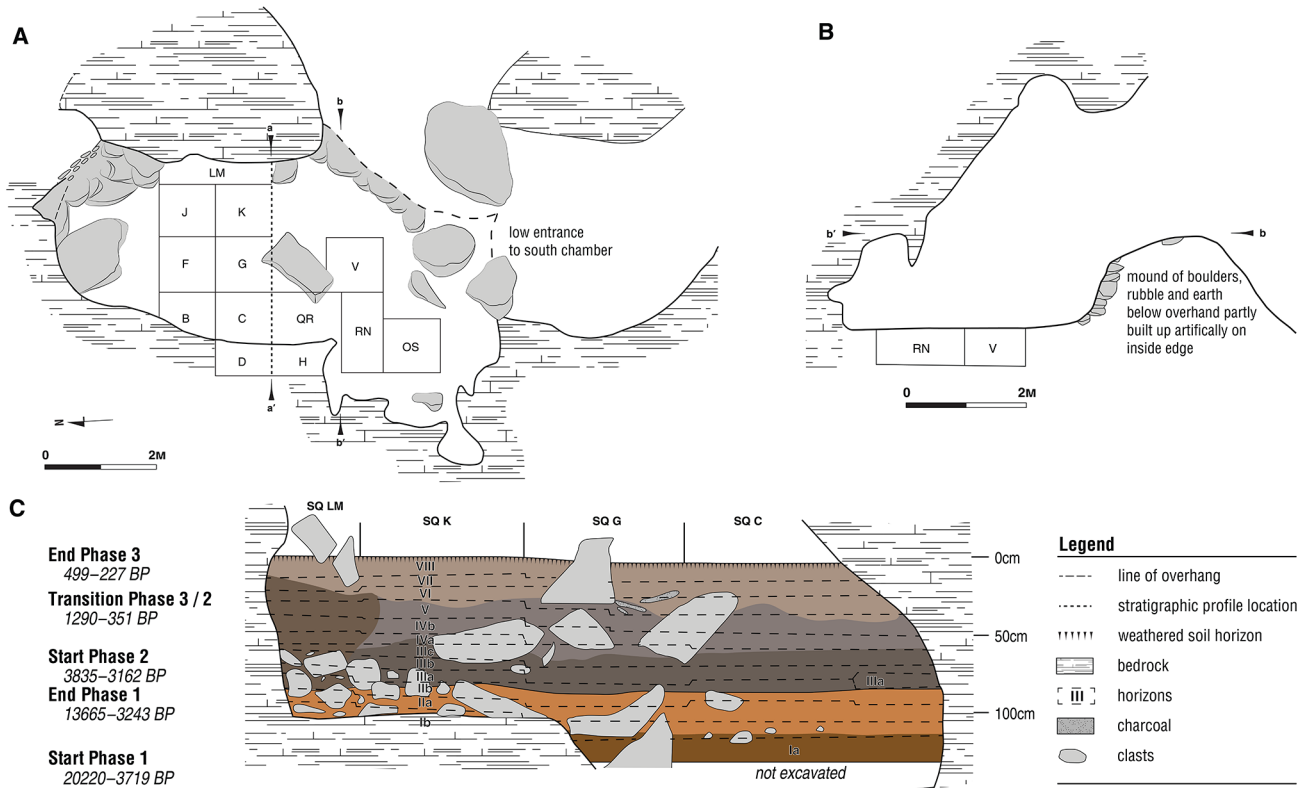
Only Genus A and unidentified giant rat are recorded in Square F. The youngest record of Genus A is from spit 17 in Phase 6, between 4567 and 3498 cal BP (Table 1). Unidentified giant rat material is found up until spit 12, likely between 3850 and 2552 cal BP (Table 1). Large *Komodomys*



**Figure 5.** Lie Siri. (A) cave site in section view; (B) stratigraphic section of Area F showing start and end of phases 1 and 2; (C) cave site in plan view; (D) stratigraphic section of south section of Areas A–C showing end of phases 1 and 2 and start of phase 2; (E) detail of excavation squares; (F) stratigraphic section of south section of Areas A–C showing end of phases 1 and 2 and start of phase 2, continued (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).



**Figure 6.** Bui Ceri Uato. (A) cave site in plan view; (B) cave site in section view; (C) stratigraphic section of south section of Squares N7E2, N6E2, N5E2 showing phases 1a to 3; (D) stratigraphic section of east section of Squares N6W1, N6E0, N6E1 showing phases 1a to 3 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).



**Figure 7.** Uai Bobo 1. (A) cave site in plan view; (B) cave site in section view; (C) stratigraphic section of Squares LM, K, G, C showing phases 1 to 3 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).

is reported to a similar age, up to spit 11; “*Komodomyss timorensis*” however is only recorded up to spit 22 in Phase 5. There is no Small *Melomys* but the Large *Melomys* is reported from spit 7, near the bottom of Phase 7 and thus between 1885 and 283 cal BP (Table 1). *Crocidura* is found to spit 6 and thus Phase 7.

The lowest occurrence of introduced species is likely the cuscus specimen from spit 34 in Phase 5; however, direct dates on this specimen indicate it is derived from younger sediments as it dates to 2397 cal BP (Wk-31507). Pacific and Black rat specimens from this spit are similarly considered introduced from younger deposits. Cuscus also occurs in spit 14, which may be older (possibly between 3850 and 2552 cal BP). A similar age range can be attributed to dog and Pacific rat material recorded in spit 15. Pig is first recorded in spit 6, i.e., between 1885 and 283 cal BP (Table 1). Finally, the Black rat is first recorded from spit 7, with a similar age range as the aforementioned date.

#### Asitau Kuru Square B (Fig. 4)

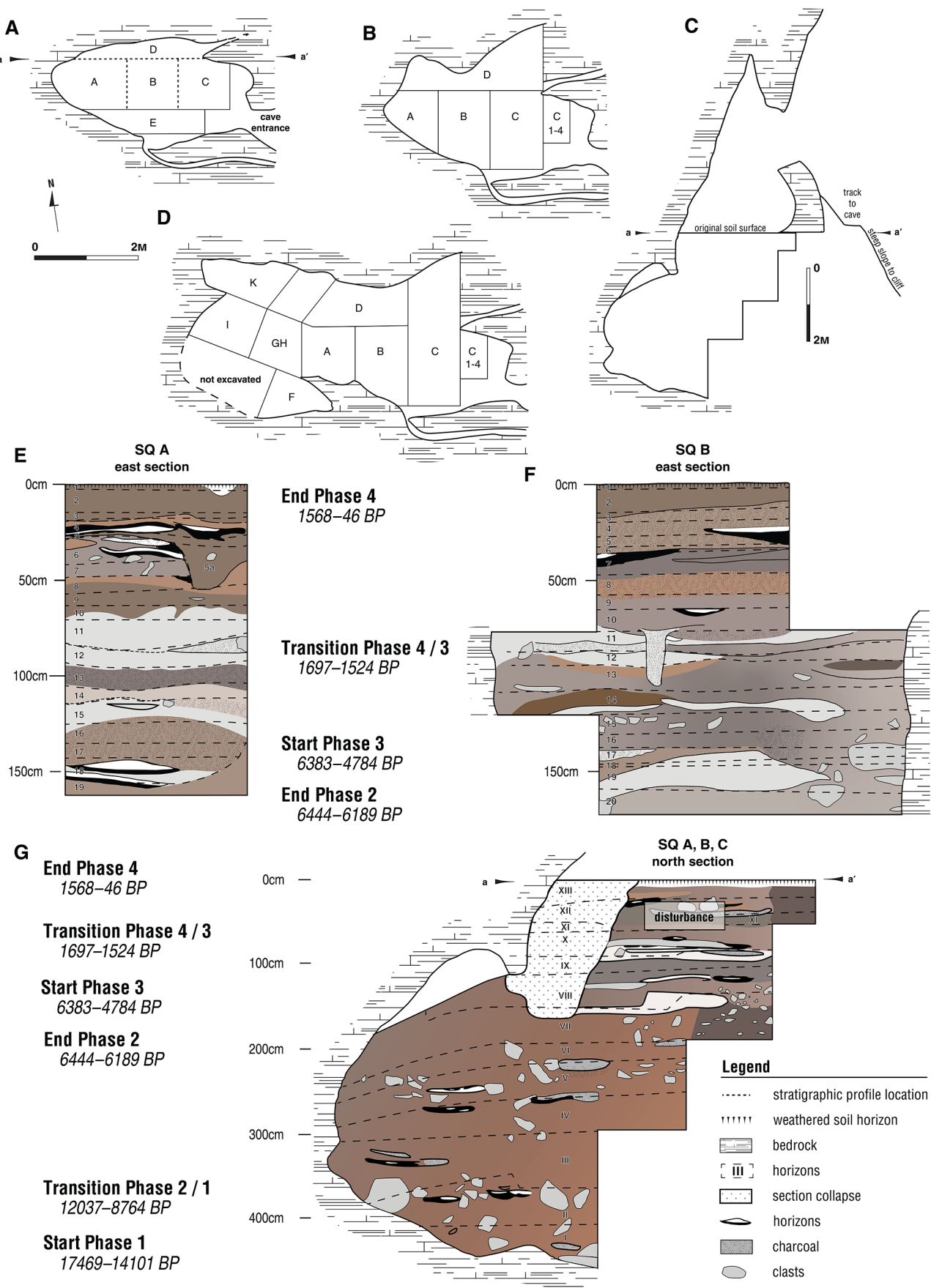
While the fauna from this site is sorted according to spits, the dates have been documented relative to depth and stratigraphic layer. Nevertheless, correlations between occurrences and dates can be made based on the depths recorded for spits. There are four phases recorded in this square. Phase 1 likely starts approximately 44,052 cal BP and continues until 14,223 cal BP. There is a hiatus, with Phase 2 starting about 6548 cal BP and continuing until 5301 cal BP. Phase 3 begins ca. 4803 cal BP through to 2308 cal BP. Finally, Phase 4 records the very recent past, 250 cal BP until present (ca. 53 cal BP) (SI).

The only giant rat records are of *Coryphomys* and Genus A. *Coryphomys* is recovered up to spit 19, which is approximately 45 cm depth, which is likely between 6092 and 4959 cal BP (Table 1). Genus A is recovered from spit 3 with an associated date of 122 cal BP. However, an outlier charcoal date from spit 4 dating to 5080 cal BP (Wk-19229) indicates disturbance in the Phase 4 stratigraphy, reflected in our suggested broad bracketing ages of 4838 cal BP (Wk-19230, spit 9) to 13 cal BP (Wk-19228, spit 3). Two additional taxa, *Komodomyss timorensis* and the Large *Melomys*, also make their final appearance in spit 3. The large *Komodomyss* is found up to spit 5 (Phase 3), and for similar reasons above is considered to date between 4838–1258 cal BP. Finally, the Small *Melomys* is recorded only in spit 26 which is around 58 cm below the surface; associated marine shells from these depths have been dated to between 6419 and 5590 cal BP (Table 1).

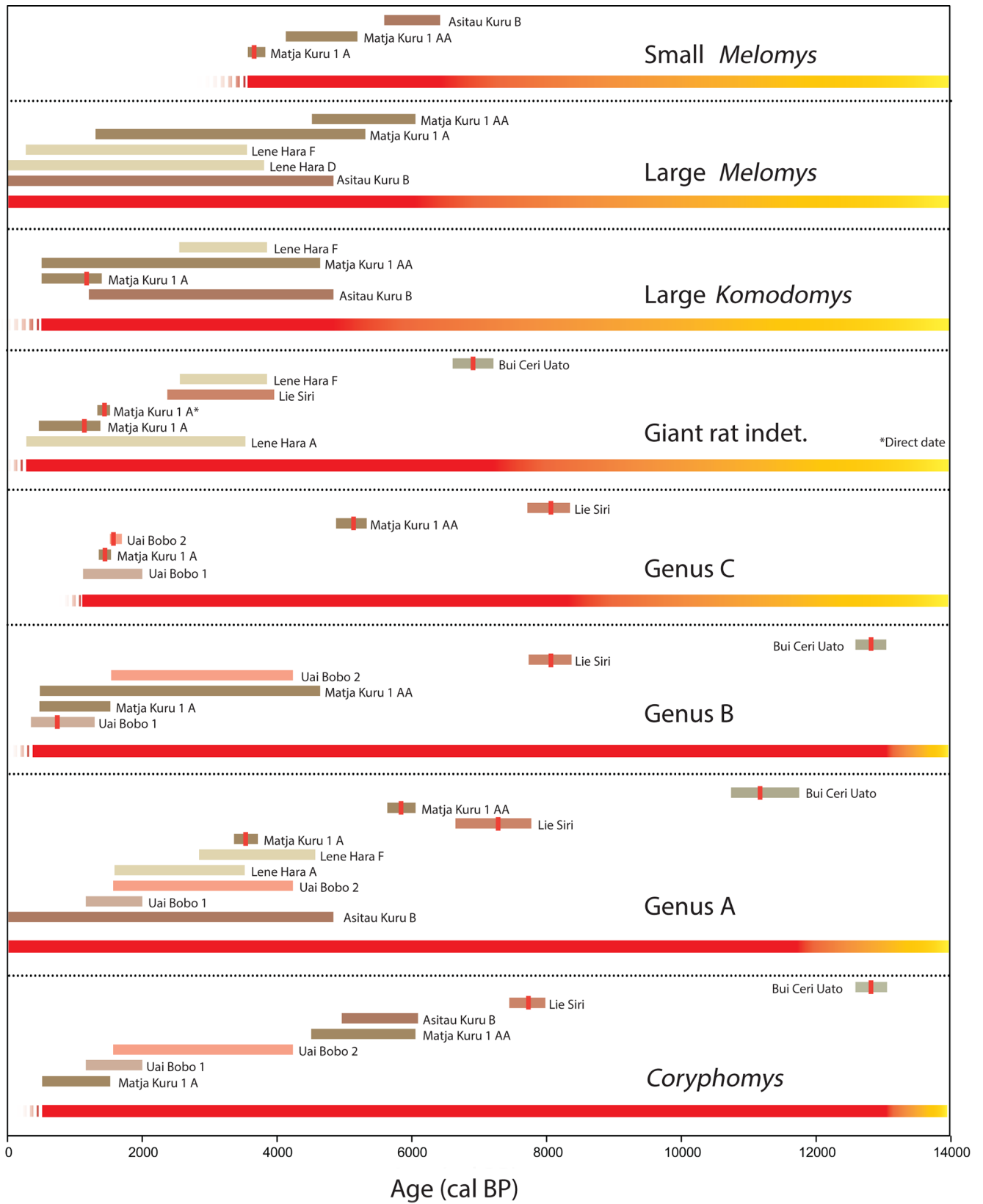
For introduced species, pig is only found in spit 3, so its age is bracketed as above. Cuscus is found as low as spit 7 (Phase 3), approximately 12–13 cm depth, and estimated at between 4838 and 1258 cal BP (Table 1). *Rattus exulans* is recorded from only spit 17, approximately 39 cm depth. Dated material from around this depth shows inverted, but roughly coeval ages, modelled at between 6092 and 4959 cal BP (Table 1).

#### Lie Siri (Fig. 5)

The stratigraphically highest unidentified giant rat material at this site is found in Glover’s horizon VIIb, which our modelling suggests is as young as 3957–2417 cal BP (Table

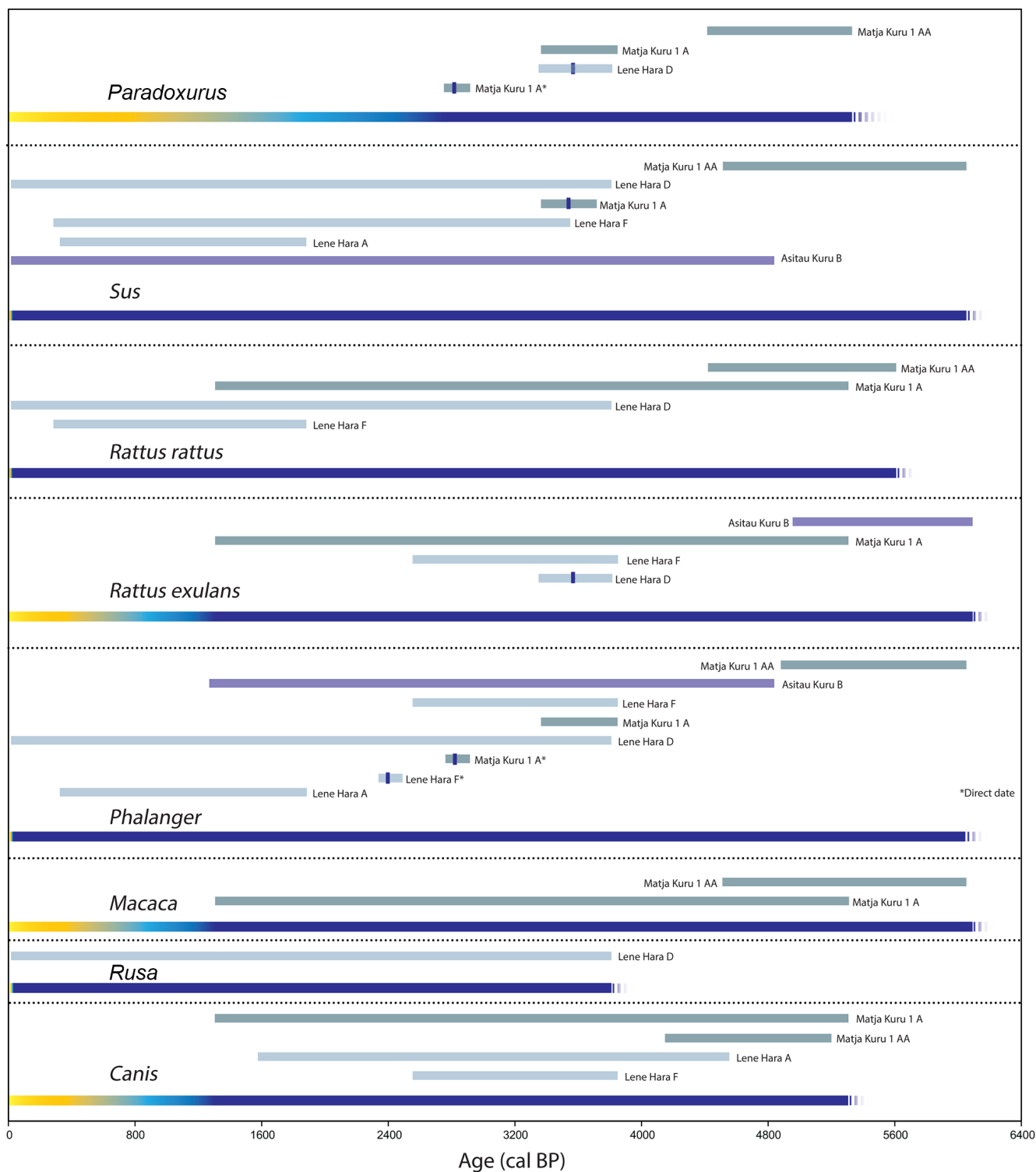


**Figure 8.** Uai Bobo 2. (A) cave site in plan view at surface; (B) cave site in plan view at 1.7m below surface; (C) cave site in section view; (D) cave site in plan view at 4.2m depth; (E, F) stratigraphic section of east section at Squares A and B showing end of phase 2 to end of phase 4; (G) stratigraphic section of north section at Squares A, B and C showing end of phases 1 to 4 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).



**Figure 9.** Last appearance dates (LADs) of select extinct fauna from the excavations considered in this study. Median ages are represented by dark vertical lines for each excavation square or site, age ranges (bracket or associated) by lighter bands. All ages in cal BP, full details in the Supplementary Information. It is assumed that all endemic species were present on Timor before their latest appearance (indicated here in graded yellow). Signor-Lipps effect indicated by dashed lines following LADs for each taxon—these are indicative only and have not been quantified.





**Figure 10.** First appearance dates (FADs) of select fauna from the excavations considered in this study. Median ages are represented by dark vertical lines for each excavation square or site, age ranges (bracket or associated) by lighter bands. All ages in cal BP, full details in the Supplementary Information. It is assumed that all introduced species are present on Timor until today (indicated here in graded yellow). Signor-Lipps effect indicated by dashed lines following FADs for each taxon—these are indicative only and have not been quantified.

1). Genus A is found in horizon Vc, which has an age-depth interpolated date of 7717–6627 cal BP (Table 1). *Coryphomys* is found in horizon Va, dated to approximately 7707 cal BP (Table 1). Genus B and Genus C are found at horizon III and below, i.e., between 8338 and 7703 cal BP (Table 1).

**Bui Ceri Uato (Fig. 6)**

The stratigraphically highest unidentified giant rat material is found in Glover’s horizon VIII at this site, which our modelling suggests is *ca.* 6888 cal BP (ANU-11741). Genus A is found in horizon IV, which is between 11,691 and 10,686 cal BP (ANU-11878). *Coryphomys* and Genus B are found in horizon II, dated to approximately 12,980 and 12,505 cal BP (ANU-11877). No Genus C material is recorded from this site.

**Uai Bobo 1 (Fig. 7)**

The stratigraphically highest giant rat material is Genus B from this site, found in Glover’s horizon V. This has age-depth modelled dates of between 1290 and 351 cal BP (Table 1). *Coryphomys*, Genus A and Genus C are all found in horizon IV, which is likely between 2000 and 1157 BP (Table 1).

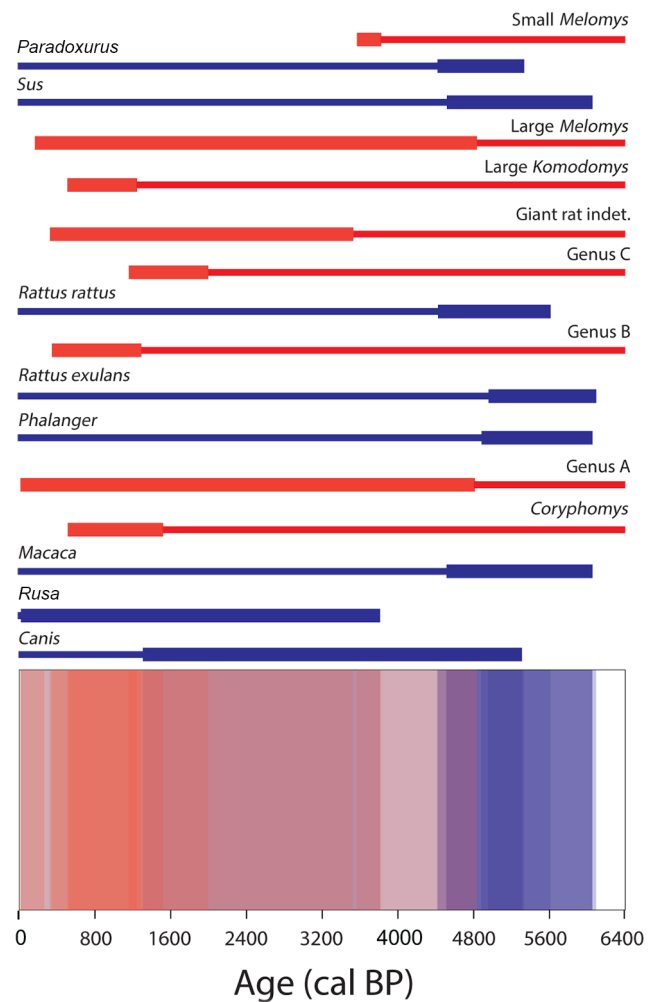
**Uai Bobo 2 (Fig. 8)**

The stratigraphically highest giant rat material is Genus C from this site, found in Glover’s horizon X, with a direct date between 1695–1522 cal BP (Wk-25439). *Coryphomys*, Genus A and Genus B are all likely recorded in horizon IX, which is modelled between 4235 and 1560 cal BP (Table 1). Two direct dates from giant rats were obtained from this horizon IX material, one on a very large murid (?Genus A) dated to 1275–1076 cal BP (Wk-25630), and another on a large murid dated to 3630–3457 cal BP (Wk-25631).

**Discussion**

Our study provides a preliminary assessment of the chronological record of extinctions and faunal introductions across several archaeological cave sites in Timor-Leste. These records, although imperfect, provide an important consideration of the sequence of major ecological events on the island. We report only ten direct dates from the taxa considered: a single cuscus specimen from Lene Hara, six dates from Matja Kuru 1 (a cuscus, a buttonquail, a civet, and three unidentified large to giant murids), and three unidentified large to giant murids from Uai Bobo 2. A further ten radiocarbon analyses on bone failed (SI). Given that all other chronologies are by association, we were not able to conduct any quantitative analyses of the Signor-Lipps effect (Signor & Lipps, 1982) on these distributions. As such, our LADs and FADs will represent under and overestimates of extinction and introduction datums, respectively. Nevertheless, they are a good starting point to discuss timings and mechanisms of extinctions on the island.

All murid extinctions likely occurred in the last 2000 years, except perhaps the Small *Melomys*, the last record of which at Matja Kuru 1 is dated to approximately 3661 cal BP (Wk-25638; Table 1). In three instances, extinctions may have occurred within the seventeenth to twentieth centuries, based on the record of Asitau Kuru Square B, Spit 3. An



**Figure 11.** Top: Summary of LADs and FADs (see Table 1) for endemic or introduced taxa considered in this study (thicker band). Cooler colours indicate faunal introductions, warmer colours faunal extinctions; thinner band indicates that endemic fauna were present before the temporal period considered here or that introduced species are still present on the island today. Bottom: Colour spectrum indicating degree of overlap between LADs and FADs for endemic and introduced species, respectively. Purple colours in the spectrum indicate considerable overlap between introduced and endemic taxa; there is little likely overlap recorded at this temporal scale.

upper age bracket for material from this spit is provided by radiocarbon sample Wk-19228, with associated age of 271–13 cal BP (Table 1), considerably younger than any other extinct giant rat material. However, of note are two additional, much lower charcoal samples, from spits 14 and 33, also dating to around this time (SI), and it is possible that all these charcoal dates are intrusive. The next closest dated material, marine shell from spit 9, provides an associated date of 4541 cal BP (Wk-19230; Table 1). This date seems more congruent with the other records from the cave deposits, and we consider these dates more likely to represent the true age of these remains. Support for this interpretation comes from the excavations at the hilltop village settlements of Ira Ara, Macapainara and Vasino at the eastern end of Timor-Leste, as well as the Leki Wakik village site near Laleia in north central Timor-Leste. These sites were occupied between the fifteenth

and mid-twentieth centuries and contained abundant faunal remains resulting from human subsistence. The assemblages contain a similar range of taxa to the earlier occupied cave sites but with a greater focus on introduced domestic species. Large endemic murids, however, are notably absent from these assemblages (see papers in O'Connor, McWilliam, & Brockwell, 2020).

If our interpretation is correct, giant rat remains from Lene Hara A and Uai Bobo 1 would then be considered the youngest material representing these taxa, and a staggered extinction scenario, from Genus C, Genus A, *Coryphomys*, and finally Genus B, the last giant rat taxa becoming extinct, may be suggested by this data. The late records of the murid extinctions, especially the Large *Melomys*, hints at the possibility that some of these species may still be extant, eking out an existence in poorly sampled remaining natural habitats. However, KPA did some modern trapping in an attempt to test this in the Nino Konis Santana National Park; one of the few remaining forested regions of Timor-Leste with some small patches of natural vegetation. He wasn't successful. Nor was Helgen, who also undertook mammal surveys and interviews with local villagers in Timor-Leste (Polhemus & Helgen, 2004; Trainor, 2010).

Faunal introductions of commensals and domesticates are not recorded prior to approximately 6000 years ago. Based on the modelled deposit ages, a suite of new taxa is recorded in the archaeological cave deposits approximately 6000 and 4800 years ago, including civets, pigs, Black and Pacific rats, cuscus, macaques, and dogs, although it must be emphasized that these oldest records are dated by association only. The oldest directly dated material from these sites—cuscus and civet—are considerably younger than the associated ages, at approximately 2800 cal BP (Table 1). Cuscus and dog remains which are directly dated from nearby Matja Kuru 2 similarly indicate introduction in the last 3000 years (O'Connor, 2015; see below), and new direct dating of a pig rib from this latter site (MK2 B16) has produced a date of 3356–3211 cal BP (S-ANU 58727, 3061 ± 21 BP). These records compare to regional faunal introductions in Wallacea and surrounding islands as follows and should be regarded as more reliable than the associated dates from the deposits.

Pigs have been recorded at about 3200 cal BP from Savidug Dune in the Batanes Islands, situated between Taiwan and Luzon (Piper *et al.*, 2013). Dogs were recovered from the same site at about 2400 cal BP. Pig remains, likely domesticate, have been recovered from Nagsabaran, Philippines, around 4400 cal BP (Amano *et al.*, 2013; Piper *et al.*, 2009) while dogs occur from 2500 cal BP (Amano *et al.*, 2013). A re-examination of the Minanga Sipakko faunal assemblage on Sulawesi has detected small numbers of domestic pig at *ca.* 3500 cal. BP (Anggraeni *et al.*, 2014). At Leang Burung 1 in South Sulawesi, Simons & Bulbeck (2004) noted the presence of introduced cervids in stratigraphic contexts in the middle Holocene but suggested that the dog and common palm civet only arrived in the late Holocene. In the Maluku, pig bones were recovered from Uattamdi at *ca.* 3260 BP (ANU-9323) to 2330 BP (ANY-9322), with dog recovered in younger levels only (Bellwood *et al.*, 1998). Pigs are present in Lapita sites in New Ireland, such as Kamgot, on Babase Island, by 3380–2950 cal BP (Matisoo-Smith, 2007).

At Liang Bua in Flores, van den Bergh *et al.* (2009) report pig, macaque, and civet by around 4000 cal BP. Deer, cattle,

dog, and horse are only found in the uppermost levels of the site (van den Bergh *et al.*, 2009). In Timor-Leste itself, a dog burial at Matja Kuru 2 is directly dated to 3064–2880 cal BP (Wk-34931) (Gonzales *et al.*, 2013). Glover (1986) reported pig between Horizons VII and XIII at Uai Bobo 2, and he attributed a similar antiquity to cuscus, civet, and bovids based on their presence in Horizon VII. Our own modelling of the dates of this horizon suggests it dates from between 7069 and 6189 cal BP (SI). O'Connor (2015) questioned the antiquity of these faunal records based on the absence of these taxa from sites known by that time and suggested that disturbance at the site may have introduced these remains into older layers—she noted that none of the Uai Bobo 2 remains had thus far been directly dated. The results of our study support O'Connor's (2015) attribution of these remains to disturbance, as none of the introductions recorded in the ETAP sites approach this antiquity, even in the least conservative interpretation of the dates. A cuscus from Matja Kuru 2 has also been directly dated, returning ages of 3381–3231 cal BP (Wk-31505; O'Connor, 2015), which correlates with the other direct dates for this taxon from Matja Kuru 1 and Lene Hara (Table 1; O'Connor, 2015). Genetic analysis of cuscus material from Timor indicates that phalangerids on the island belong to *Phalanger orientalis*; however, neither the point of origin nor the timing of divergence of these introductions are clear (Kealy *et al.*, 2020).

Louys *et al.* (2020) analysed modern Black and Pacific rat haplotype networks and craniometrics to understand dispersal of these murids into Nusa Tenggara. The two lineages examined in the Black rat species complex (RrC) points to an early dispersal into the Philippines for RrC Lineage II. RrC Lineage IV, present throughout Nusa Tenggara, suggested an original, more archaic dispersal event into the region followed by *in situ* production of genetic diversity. This was followed by a second, more recent dispersal into the islands. Louys *et al.* (2020) suggested that the Black rat arrived in Nusa Tenggara prior to the widespread dispersal of the Pacific rat from Flores, the Pacific rat's likely point of origin. The Pacific rat record followed the pattern found by others showing that, once dispersal began, a major haplotype group spread quickly through Nusa Tenggara and into the Pacific (Thomson *et al.*, 2014; Matisoo-Smith *et al.*, 2014; Hingston, 2015; West *et al.*, 2017). In Flores, Black rats do not appear in the record of Liang Luar until about 400 years ago, while Pacific rats are recorded from at least 2500 BP (St Pierre, 2011). Both species are present in the Timor sites by about 4000 cal BP, although lack of direct dates prohibits us from determining whether the species arrived together, if one preceded the other, or the exact timing of these events.

Pleistocene Timor was host to numerous endemic mammal taxa, including diverse rodent and proboscidean species (Hoojer, 1969, 1972; Aplin & Helgen, 2010). At least some of Timor's giant rodents have considerable antiquity, from at least *ca.* 165 ka (Louys *et al.*, 2017), and we consider it likely that all small-bodied endemics were present on the island prior to human arrival. Today, Timor hosts only one extant endemic rodent, "*Komodomys timorensis*", originally described from Mount Mutis in West Timor (Kitchener *et al.*, 1991), and whose current conservation status is unknown (Clayton & Kennerley, 2017). Timorese proboscideans, two species of *Stegodon*, likely became extinct in the Middle Pleistocene, well before human arrival on the island (Louys

*et al.*, 2016; Hidayah *et al.*, 2021). Murid extinctions, on the other hand, seem to have occurred only very recently. Similarly, Meijer *et al.* (2019) discuss avian extinctions on Timor, including the youngest date for an extinct large buttonquail, *Turnix* sp., directly dated to between 1395 and 1310 cal BP (S-ANU-55223, 95.4% probability range). The records from sites examined here suggest that extinction of the murid endemics did not quickly follow introduction of exotics (Fig. 10). There is a lag of several thousand years between the most likely point of exotic introductions and any ecological cascade due to those introductions. Ecological replacement and impacts are quick—on the scale of tens or perhaps at most hundreds of years (e.g., Okubo *et al.*, 1989; Morales *et al.*, 2013; Wood *et al.*, 2017). While further dating and modelling may close the gap between the dates of extinction of endemics and the introduction of invasives, implicating a principal ecological replacement extinction mechanism, based on current data we consider other extinction explanations more plausible.

Trainor (2010: 40–41) states “Timor’s landscape was probably once a mixture of tropical forests and various savanna woodlands, with agriculture and burning practices over recent millennia causing extensive forest loss.” While the exact timing of Timor’s forest loss is unknown, both Wallace (1869) and Forbes (1885) comment on the lack of tropical forest when undertaking their respective surveys in the mid to late 19th century. Wallace notes that around Kupang there was “... nothing that can be called a forest, and the whole country has a parched and desolate appearance” (Wallace, 1869: 204). Forbes (1885) noted “Indeed, life of all kinds had been exceedingly conspicuous by its absence; save a scarlet *Trichoglossus* or a cockatoo flying across our path, and a few crows at Erlura, I had seen no birds, and the vegetation since crossing the Ligoik river had been very poor indeed. A few casuarinas, acacias, gum-trees, and some rough-leaved *Compositae* being the only vegetable forms. The slopes on the other side looked somewhat more tree-dotted, however, but the bare red ground displayed itself over a large part of its area” (Forbes, 1885: 434); and “‘The land of Timor is always falling,’ is the natives’ own account of the country” (Forbes, 1885: 433). In 1932, Georg Stein conducted an expedition into the previously unexplored high mountains of Timor-Leste but was disappointed by his findings, due to the presence of villages up to an altitude of 2300 m causing forests to “entirely disappear...” (Mayr’s reconstruction of Stein’s 1931–1932 Timor expeditions; Mayr, 1944: 131). In fact, Stein documents the presence of “... only open eucalyptus groves without undergrowth” (Mayr, 1944: 131). The Nino Konis Santana National Park, in Lautem district, retains the most extensive lowland forest on the island (FAO/UNDP, 1982; Trainor, 2010), however, even here little primary forest remains (Geoff Hope pers. comm. to SOC, 2000). Stone garden walling spanning kilometres, and the remains of earlier built settlements, attest to the extensive nature of past swiddening activities within the park (O’Connor *et al.*, 2020).

Understanding the nature of vegetation changes in Timor in the last few thousand years will be paramount to reconstructing the factors driving the late Holocene extinction record of this island. Unfortunately, few palaeobotanical studies of the island exist. Oliveira’s (2008) palaeobotanical study at Bui Ceri Uato Mane in the Baucau region is one of the few that have been reported. He found

no evidence of cereal crops in Timor’s archaeological record, instead suggesting that tree crops and possibly tubers were in use throughout the Holocene. O’Connor (2015) similarly reviewed evidence for cereal in Timor’s archaeological record and found limited and contentious examples only. Louys *et al.* (2020) suggested that rice cultivation in the drier parts of Nusa Tenggara may have been coincident with the arrival of Dong Son drums, from approximately the fifth century AD, as well as metal tools.

We have previously argued that the giant rat extinctions were likely associated with the introduction of metal tools into Nusa Tenggara because these facilitated widespread forest clearance (O’Connor & Aplin, 2007; O’Connor, 2015; Louys *et al.*, 2018; Miszkiewicz *et al.*, 2020). Historical records indicate that Timor was an important centre for white sandalwood export beginning approximately 1500 AD (McWilliam, 2005; O’Connor *et al.*, 2012) and metal tools would have greatly increased production of sandalwood at the expense of native forests. Deforestation may have been exacerbated by the introduced fauna through destruction of seedlings, seeds, and defoliation in a flora which had evolved in the presence of murids, but few other terrestrial mammals. Indeed, Glover (1986: 193–194) suggests that *Celtis* sp. seeds were found throughout his sequences, but decline and disappear at the same time as the giant rats, perhaps because the seeds were collected by the murids as food. Giant rats, although not a uniform taxonomic group, nevertheless plot on the C3 end of the carbon stable isotope spectrum (i.e., browsers and/or frugivores) (Louys *et al.*, 2018; Roberts *et al.*, 2020) and would have been particularly susceptible to loss of native forests. While we do not discount the obvious impacts of introduced competitors and predators, these may have been secondary compounding factors in extinction (Bergstrom *et al.*, 2023). The combination of new metal tools, a burgeoning sandalwood trade, introduction of rice agriculture, and the ecological impacts of introduced exotics likely removed almost all of Timor’s endemic forests, and with them the giant rats that were dependent on them.

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## Supplementary Information (SI)

Supplementary Information is published separately as a figshare dataset—“Supplementary information for Late Quaternary mammal introduction and extinction records from archaeological cave deposits in Timor-Leste” (see Louys *et al.*, 2023).

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