Simultaneous extinction of Madagascar's megaherbivores correlates with late Holocene human-caused landscape transformation

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Abstract. Reconstructing the dynamics and drivers of late Quaternary megafaunal extinctions requires direct radiometric date series that are assessed within probabilistic statistical frameworks. Extinction chronologies are poorly understood for many tropical regions, including Madagascar, which had a diverse, now-extinct Holocene large vertebrate fauna including a “megaherbivore” guild of endemic hippopotami and elephant birds. Madagascar’s megaherbivores likely played vital roles in regulating ecosystem structure and nutrient cycling, but few direct dates are available for megaherbivore specimens identified to species level, with uncertainty over when and why different representatives of this guild disappeared. Here, we conduct a new investigation into Malagasy megaherbivore extinction dynamics, including 30 new AMS dates and 63 audited published dates. We use Gaussian-resampled inverse-weighted McInerny (GRIWM) analysis to estimate species-specific extinction dates for three elephant bird species (*Aepyornis hildebrandti*, *Mullerornis modestus*, *Vorombe titan*), eggshell representing *Aepyornis* or *Vorombe*, and two hippo species (*Hippopotamus lemerlei*, *H. madagascariensis*), and to estimate extinction dates for megaherbivore communities in different biomes. Megaherbivores persisted for millennia after first human arrival. Extinction date estimates vary significantly between biomes, with disappearance from dry deciduous forest over a millennium earlier than other biomes, possibly reflecting local variation in megaherbivore population densities or human pressures. However, megaherbivore communities including all elephant bird and hippo species persisted elsewhere across Madagascar until ~1200-900 BP, when they collapsed suddenly. Extinctions are closely correlated in time with intensive conversion of forests to grassland at ~1100-1000 BP, probably associated with a shift to agro-pastoralism and representing a radical change in sustainability of prehistoric human interactions with biodiversity.

Keywords: elephant bird, extinction chronology, *Hippopotamus*, Holocene, Madagascar, Quaternary extinction, radiocarbon dating

1. Introduction

Reconstructing the spatiotemporal dynamics and drivers of Late Pleistocene-Holocene megafaunal extinctions has constituted a primary question in Quaternary science for well over a century (Grayson, 1984). Multiple direct radiometric dates are required to reconstruct extinction chronologies accurately for now-extinct species, and should be analysed within probabilistic statistical frameworks that can use the temporal spacing of available dates to infer likely extinction timings (Bradshaw et al., 2012; Saltré et al., 2015). Such robust temporal frameworks are necessary before it is possible to identify temporally synchronous causal drivers that might be responsible for species losses. However, there is substantial disparity in our understanding of the temporal dynamics of late Quaternary megafaunal biodiversity loss between different biogeographic regions (Stuart, 2015), and data on extinction timings and drivers are less robust for most tropical regions due to differing preservational conditions and less comprehensive direct dating programmes (Louys et al., 2007; Turvey et al., 2013, 2021; Cooke et al., 2017; Price et al., 2018).

Madagascar's rich Holocene palaeontological record contains a remarkable endemic vertebrate fauna, including 17 species of giant lemurs, as well as elephant birds (the endemic ratite family Aepyornithidae), hippopotami, large euplerid carnivores, the enigmatic aardvark-like *Plesiorycteropus*, giant tortoises, and crocodiles (Burney et al., 2004; Goodman and Jungers, 2014; Hansford and Turvey, 2018). Although only two of the giant lemur genera, *Archaeoindris* and *Megaladapis* are likely to have exceeded the body mass threshold of >44 kg (Jungers, 2008), typically used to define Quaternary megafauna (Martin and Klein, 1984), Madagascar's Holocene fauna included a true "megaherbivore" guild comprising hippopotami (up to ~400 kg; Weston and Lister, 2009) and elephant birds, the world's largest birds (up to 860 kg; Hansford and Turvey, 2018). Whereas giant lemurs are inferred to have played important roles in seed dispersal and forest regeneration (Crowley et al., 2011; Federman et al., 2016), Madagascar's megaherbivores are likely to have been keystone species with profound top-down impacts in regulating plant community structure and composition through grazing, browsing and trampling, and biogeochemical cycling via nutrient transfer across landscapes and ecosystem boundaries (Doughty et al., 2016; Mahli et al., 2016; Shurin et al., 2020). However, all of the largest-bodied representatives of Madagascar's Holocene fauna are now extinct, with the largest surviving endemic vertebrates less than 10 kg in body mass (Goodman and Benstead, 2004). The timing of megafaunal extinctions and associated change in ecosystem functionality in Madagascar has captivated researchers ever since elephant bird bones were first brought to Europe in the nineteenth century (Burney, 1999; Burney et al., 2004; Crowley, 2010; Anderson, 2018).

Numerous hypotheses have been proposed to explain the extinction of Madagascar's large-bodied vertebrates, including non-anthropogenic climate-driven aridification, and direct or indirect human impacts associated with hunting, habitat modification, competition with introduced ruminants, or "hyperdisease" (Walker, 1967; Mahé and Sourdat, 1972; Dewar, 1984). More recently, synergistic impacts of climate change and human impacts have been proposed, which might have been spatiotemporally variable (MacPhee et al., 1997; Burney, 1999; Burney et al., 2003, 2004; Crowley, 2010; Parker-Pearson et al., 2010; Goodman and Jungers, 2014). Not all proposed hypotheses (notably complex multi-causal models) are easily falsifiable (Burney et al., 2003).

Long-term environmental archives provide a temporal framework of late Quaternary ecosystem change and human-environmental interactions in Madagascar for investigating potential drivers of regional biodiversity loss. Severe multidecadal periods of drought are recorded throughout the mid to late Holocene of the southwest Indian Ocean, with megadroughts at ~2800 and 3600 BP lasting several centuries (Li et al., 2020). In Madagascar this pattern of punctuated extreme drought is more extreme in the south and is coupled with a continuous pattern of increasing aridification from ~4200 BP onwards, although the severity and ecosystem-level impacts of this environmental change are debated (Mahé and Sourdat, 1972; Scroxton et al., 2019). Charcoal microparticulates in speleothems and sediment cores show rapid increases in the southwest at 1800-1600 BP and in the north, northwest, and central highlands at 1300-900 BP, and are interpreted as signals of human-driven deforestation (Burney, 1999; Burney et al., 2004; Crowley, 2010). Archaeological evidence for settled villages dates from 1300 BP onwards, with arrival of cattle by ~1100 BP and occupation of most of Madagascar's coasts by 900 BP (Burney et al., 2003, 2004; Crowther et al., 2016; Douglass et al., 2019), and genetic data from modern human populations indicate demographic expansion southward across Madagascar and population increase from ~1500 BP (Pierron et al., 2017). A dramatic decline in arboreal pollen and increase in grass pollen, starting at ~1100 BP and completed within a century, records a rapid, complete transition from C_3 forests to C_4 grassland (Burns et al., 2016; Crowley et al., 2017). This has been interpreted as evidence for either a peak in natural aridification or anthropogenic habitat alteration. However, $\delta^{15}N$ values in dated subfossil vertebrate bones provide no evidence of change in habitat moisture, implying that this environmental shift was associated with changing human land use (e.g., subsistence transition to agro-pastoralism, with increased use of fire to promote grass growth for cattle) rather than changing precipitation (Crowley and Samonds, 2013; Crowley et al., 2017; Hixon et al., 2018).

Until recently, human arrival in Madagascar was thought to have occurred around 2500-2000 BP, based on evidence including introduced *Cannabis* pollen and increased charcoal microparticles (Burney et al., 2004; Crowley, 2010). However, recent discoveries have challenged this interpretation. Coastal rock shelters in western Madagascar provide support for regional human presence at ~2000 BP (Douglass, 2017), and microlithic tool assemblages indicating occupation of northern Madagascar have been dated to >4000 BP (Dewar et al., 2013), although the chronological context of this evidence has been contested (Anderson et al., 2018). Human modification of extinct vertebrate bones provides evidence for even earlier regional human presence. A giant lemur (*Palaeopropithecus*) radius with cut marks has been dated to ~2400 BP (Pérez et al., 2005), and elephant bird bones showing confirmed microlithic tool marks have recently been directly dated to ~6400-6300 cal. BP (calibrated years before present) and ~10,700-10,500 cal. BP (Hansford et al., 2018).

The *Sporormiella* coprophilous fungal spore record, which represents a proxy for biomass of both mammalian and avian megaherbivores (Wood et al., 2011), indicates megafaunal declines by ~1700 BP, although with geographic variation in stratigraphic resolution (Burney et al., 2003). The archaeological record reveals an island-wide human dietary “subsistence shift” around 1050 cal. BP from giant lemurs to smaller forest-dwelling species that persist today (Godfrey et al., 2019). Large-scale radiocarbon datasets are now available for Madagascar, including numerous direct and indirect dates for many extinct species (Burney et al., 2004; Crowley, 2010). These datasets demonstrate that some giant lemur species survived until less than a thousand years ago, with direct dates of 630±50 BP and 510±80 BP available for *Megaladapis edwardsi* and *Palaeopropithecus ingens*, respectively (Burney et al., 2004). Radiometric data have been interpreted to suggest a two-phase model of spatially staggered declines across different biomes (Crowley, 2010). This model proposes that by ~2000 BP, very large species (>150 kg) declined in arid spiny bush, other large species (10-150 kg) declined in the grassland/woodland mosaic of the central highlands, and both very large and large species declined in dry deciduous forest. Large species subsequently also declined in arid spiny bush and succulent woodland by ~1000 BP. Conversely, historical and oral accounts of reported encounters with unusual animals in Madagascar have led to suggestions that some megaherbivores (both elephant birds and hippopotami) might have persisted into the post-1500 CE European historical era or even the twentieth century (Flacourt, 1658; Racault, 2007; Wright, 2014).

However, previous radiometric studies have focused largely on extinct lemurs, with fewer direct dates available for the island's megaherbivores. Previous studies have also only reported last-occurrence dates and their confidence intervals for extinct species, instead of estimating extinction dates using more complex probabilistic methods. Madagascar's megaherbivores have been the subject of recent morphology-based taxonomic revisions, which now recognise four elephant bird species in three genera (*Aepyornis hildebrandti*, *A. maximus*, *Mullerornis modestus*, *Vorombe titan*) based upon leg bone morphology (Hansford and Turvey, 2018), and two hippo species (*Hippopotamus madagascariensis* [=*H. guldbergi*], *H. lemerlei*) based upon cranial morphology (Fovet et al., 2011; Ravotovao et al., 2014) (Text S1). It is difficult to assign dates from specimens reported in the older literature to currently-recognised species, due to an incomplete understanding of wider morphological differences among these taxa and limited description of most previously dated material.

Previous assessments of megafaunal extinction chronologies using dated late Holocene samples (Burney et al., 2004; Crowley, 2010) included only three directly dated elephant bird bones, which were only identified to genus and are difficult to interpret taxonomically following recognition of the new genus *Vorombe* (Hansford and Turvey, 2018). These and other studies (Clarke et al., 2006; Parker-Pearson et al., 2010; Douglass, 2017) have instead preferentially dated elephant bird eggshell samples, many of which cannot be definitively associated with skeletally diagnosed species (Hansford and Turvey, 2018). Although more hippo skeletal material has been directly dated, these specimens have also rarely been identified to species level (Burney et al., 2004; Crowley, 2010; Crowley and Samonds, 2013). Radiometric last-occurrence dates currently available for elephant birds (taxonomically unidentified eggshell, unknown lab number, 840±80 BP; Battistini, 1963) and hippopotami ("*Hippopotamus* sp.", lab number: GaK-1506, 980±200 BP; Mahé and Sourdat, 1972) are based on uncalibrated non-AMS (accelerator mass spectrometry) radiocarbon dates obtained before 1980 (Table 1), before exclusive use of collagen and adequate pretreatment came into regular use, and would be rejected in modern radiometric auditing studies because of their known higher potential for unreliability (Stafford, 1987; Lister and Stuart, 2013).

Here, we conduct a robust new investigation into the extinction chronology, dynamics and drivers of Madagascar's megaherbivores. We present a dataset of new direct AMS dates from morphologically diagnostic skeletal elements representing currently recognised endemic elephant bird and hippo species, combined with other available audited radiocarbon dates. We analyse species-specific and biome-specific radiometric date series using Gaussian-resampled inverse-weighted McInerny (GRIWM) analysis, a probabilistic method that progressively up-weights temporal gaps between dates closer to the time a taxon disappears from the fossil record; this approach controls for the Signor-Lipps effect (Signor and Lipps, 1982), whereby it is extremely unlikely to detect the last individual of a declining taxon (Bradshaw et al., 2012; Saltré et al., 2015). This critical approach allows us to establish a high-quality temporal baseline for understanding the timing of Madagascar's megafaunal extinctions, where multiple species extinctions may have been masked by poor taxonomic resolution, and for identifying temporally synchronous environmental changes likely to have driven the extinction of the island's unique megaherbivore guild.

2. Materials and methods

We generated 30 new direct ultrafiltered AMS dates for previously undated megaherbivore skeletal elements. AMS dating was conducted at the Oxford Radiocarbon Accelerator Unit, UK.

For investigation of species-specific extinction chronologies, following radiometric auditing we also included nine additional published direct radiocarbon dates on megaherbivore skeletal elements with species-level identification, and rejected 37 further dates, following established auditing criteria (Lister and Stuart, 2013): five published before 1980; one with no clear collection locality; 31 unidentifiable to species (Tables 1-3, Table S1). We further included 24 available direct dates for eggshell fragments representing two distinct reported morphotypes: 20 dates from "thick" (~4mm) eggshell representing either *Aepyornis* or *Vorombe*, and four dates from "thin" (~2mm) eggshell, a morphotype known to represent *Mullerornis modestus* based on ancient DNA analysis (Grealy et al., 2017). Our dataset for species-specific analysis contains 62 direct calibrated dates for six identified megaherbivore species and one eggshell morphotype: *Aepyornis hildebrandti*, n=6; *A. maximus*, n=1; *Mullerornis modestus*, n=7 (including dates on bone and thin eggshell); *Vorombe titan*, n=11; "thick" eggshell, n=20; *Hippopotamus lemerlei*, n=13; *H. madagascariensis*, n=4.

For investigation of the temporal pattern of megaherbivore extinction across different biomes, we used all dated material that could be identified as either elephant bird or hippo. This included 30 additional published dates with known localities and that were identifiable as hippo or large ratite but of unknown species, which we had excluded from species-specific analysis. Our dataset for biome-level GRIWM analysis contains 92 direct calibrated dates for four biomes: arid spiny bush, 53 dates from 14 sites; succulent woodland, 16 records from four sites; dry deciduous forest, 10 records from two sites; central highlands, 13 records from three sites (Tables 2-3, Table S1).

Taxonomic identification of skeletal material followed published morphological diagnoses for hippopotami and ratites (Fovet et al., 2011; Ravotovao et al., 2014; Hansford and Turvey, 2018). We included dates from carbonate in eggshell, as this stable biomineral is suitable for accurate age estimation (Long et al., 1983; Higham, 1994). Dates were calibrated using SHCal20 (Hogg et al., 2020) implemented in OxCal version 4.4 (Bronk Ramsey, 2009). All dates were calibrated at 2σ, with date ranges reported as 95% confidence ranges. Extinction date estimates were calculated in R version 4.0 (R Development Core Team, 2011), using the GRIWM algorithm (Saltré et al., 2015), which requires a minimum of four dates for analysis.

3. Results

Species-specific GRIWM analysis was possible for all extinct megaherbivore taxa except for *Aepyornis maximus*, for which only one specimen has been dated directly. The 2σ ranges of the most recent dates for these taxa all overlap the 1200-1100 cal. BP interval: *Aepyornis hildebrandti*, 1286-1177 cal. BP; *Mullerornis modestus*, 1284-986 cal. BP; *Vorombe titan*, 1179-998 cal. BP; “thick” eggshell, 1177-805 cal. BP; *Hippopotamus lemerlei*, 1280-1114 cal. BP; *H. madagascariensis*, 1263-1070 cal. BP (Tables 2-3). Estimated extinction dates for all taxa based on GRIWM analysis overlap the 1200-900 cal. BP interval, with 95% confidence ranges separated by a maximum of 206 years between “thick” eggshell (957-885 cal. BP) and *Hippopotamus lemerlei* (1188-1163 cal. BP) (Fig. 1, Table 4).

Unlike species-specific extinction dates, extinction dates for different biomes based on GRIWM analysis show substantial variation (Fig. 2, Table 5). Estimated megaherbivore extinction dates in three biomes (arid spiny bush, succulent woodland, central highlands) are slightly temporally staggered across the ~1150-900 cal. BP interval, with 95% confidence limits for these biomes separated by a maximum of 95 years, with megafauna persisting longest in arid spiny bush (until 957-911 cal. BP). However, megaherbivore extinction is estimated to have occurred over a thousand years earlier in dry deciduous forest sites, between 2364-2078 cal. BP.

4. Discussion

Our study uses new AMS date series and probabilistic analyses to establish baselines for understanding the spatiotemporal extinction dynamics of Madagascar’s megaherbivore guild, from both a species-level perspective based upon modern taxonomic frameworks, and a community-level perspective for megaherbivores in different biomes across this huge, ecologically complex island. Previous studies have not assessed species-specific differences in extinction chronologies across Madagascar’s large vertebrates through statistical analysis of large date series, with previous conclusions about extinction timing based upon interpretation of environmental proxy records, grouped-fauna datasets or single last-occurrence dates (Burney et al., 2003, 2004; Crowley, 2010: Godfrey et al., 2019).

The most striking result of our study is the extremely close temporal correspondence in available last-occurrence dates and associated GRIWM extinction date estimates for all investigated representatives of Madagascar’s largest-bodied avian and mammalian megafauna. All 95% confidence intervals for our species-specific GRIWM estimates cluster within a narrow temporal window of approximately three centuries between ~1200-900 cal. BP. Estimates for *Mullerornis modestus*, *Vorombe titan*, “thick eggshell” (representing either *V. titan* or *Aepyornis*), and *Hippopotamus madagascariensis* in particular overlap substantially, with the oldest bound of the confidence intervals for all of these taxa postdating 1150 cal. BP. These findings comprise probabilistic analyses for all of Madagascar’s largest-bodied extinct bird and mammal species other than *Aepyornis maximus*, and demonstrate that the island’s terrestrial megaherbivore guild experienced a closely-timed multi-taxon extinction event, with species-level extinctions occurring within a narrow time window just over a millennium ago.

In contrast, our extinction date estimates for megaherbivore communities in different biomes show substantial variation, with available data suggesting the loss of megaherbivores from dry deciduous forest over a millennium before other biomes. These findings support the previous suggestion of early megafaunal declines in this biome by ~2000 BP, but contradict the hypothesis of comparable early declines in arid spiny bush and the central highlands (Crowley, 2010). Instead, our results demonstrate that megaherbivores persisted in these biomes until ~1150-900 cal. BP, with evidence for latest survival in arid spiny bush. This spatially staggered pattern of millennial-scale decline is comparable to the dynamics of large vertebrate extinctions across many other geographic regions with diverse ecosystems, for example in late Quaternary continental and island large mammal faunas in Eurasia (Diamond, 1989; Crees et al., 2016; Turvey et al., 2016; Lister and Stuart, 2019) and in recent mammal extinctions (Channell and Lomolino, 2002), where range contraction typically occurs before final extinction. Indeed, many extant Madagascar mammals also experienced pre-modern range contraction from wider prehistoric Holocene distributions (Godfrey et al., 1999; Eronen et al., 2017).

Variation in regional persistence or extirpation across Madagascar might reflect between-biome variation in megaherbivore population densities and/or local human pressures, with some evidence for both explanations. Geographic variation in *Sporormiella* spore frequencies has been considered indicative of past differences in local megaherbivore densities (Burney et al., 2003); highest values were observed in arid spiny bush sites, where we demonstrate longest persistence of megaherbivore communities. Interestingly, comparison with *Sporormiella* data also suggests the possibility of long-term megafaunal population decline within some biomes. Whereas our radiocarbon dates demonstrate that megaherbivores definitely persisted in arid spiny bush until less than a thousand years ago, the *Sporormiella* record from the arid spiny bush site of Ambolisatra declines sharply at 1705-1486 cal. BP (Burney et al., 2003). Conversely, dry deciduous forests have experienced amongst the highest levels of historical deforestation of Madagascar's biomes, consistent with increased vulnerability of local faunas and potentially with earlier disappearance of megaherbivores (Olson and Dinerstein, 2002; Waeber et al., 2015).

However, we note that whereas other biomes contain megaherbivore dates from multiple localities, all available dates from dry deciduous forest are from the cave complex of Anjohibe (Anjohibe and Lavakasaka). Megaherbivore dates from Anjohibe span much of the Holocene (Fig. 2), and younger radiometric dates are available from the site for other extinct and extant species, indicating that its preservational window extends beyond the last record of megaherbivores (Crowley and Samonds, 2013; Goodman and Jungers, 2014). However, elephant birds and hippopotami are found in relatively low frequencies in Malagasy subfossil cave contexts (Goodman and Jungers, 2014), and a single site may not represent the chronology of a large ecoregion. Further dates are therefore needed from other dry deciduous forest sites and contexts that are ecologically similar to Anjohibe (i.e., that lack the rugged karstic topography that is less amenable to megaherbivores). Furthermore, a date from elephant bird eggshell that was rejected by our auditing criteria (1150±90 BP; Mahe & Sourdat, 1972) provides an intriguing possibility of later megaherbivore survival in the dry deciduous forest biome, into the extinction window seen for other biomes. However, this evidence is contentious due to the low-quality protocols, and also because this specimen was recovered from a coastal archaeological context; elephant bird eggs are known to have been historically moved around the coastline of Madagascar by boat and used to transport liquids such as rum (Strickland, 1849).

Rapid, simultaneous island-wide "blitzkrieg-style" extinction of megafauna within centuries of first human arrival has been demonstrated for some islands (White et al., 2010), and notably for New Zealand's moa, the other group of recently extinct giant ratites (Holdaway et al., 2013; Perry et al., 2014). This contrasts markedly with our model of biome-staggered megaherbivore declines taking place over a >1000 year interval, and with species extinctions occurring many millennia later than human arrival in Madagascar, with an "extinction window" (earliest evidence of humans to last occurrence of megafauna; Burney et al., 2004) of >9000 years. Indeed, available AMS dates for extinct giant lemurs show that several taxa persisted for several hundred years beyond megaherbivore extinction, so that co-occurrence of humans and some other now-extinct Malagasy megafaunal species was even more temporally protracted than for megaherbivores (Burney et al., 2004). However, prolonged millennial-scale co-occurrence of humans and now-extinct megafauna is also seen in some other island systems, including the insular Caribbean (Cooke et al., 2017) and the "island continent" of Australia (Gillespie et al., 2006; Price et al., 2015). Between-island evaluation is required to assess variation in duration of system-specific extinction windows, in the context of local environmental conditions (e.g., existence of native mammalian predators) that might predispose faunas to vary in their vulnerability or resilience to prehistoric human interactions.

However, although our results provide evidence for millennial-scale megaherbivore range contraction and population decline, with protracted depletion across biomes, Madagascar's megaherbivore guild persisted in three of four investigated biomes (arid spiny bush, central highlands, succulent woodland) until ~1150-900 cal. BP. At this point, surviving megaherbivore communities, which still retained all elephant bird and hippo species with sufficient data to be included in this study, collapsed across the island in a sudden event. The close correlation in the timing of all megaherbivore species extinctions is also contemporaneous with the recently documented island-wide human dietary "subsistence shift", from exploiting now-extinct large endemic vertebrates alongside other resources (e.g., foraging marine resources in coastal regions; Douglass, 2017), to exploiting introduced large vertebrates and smaller endemic species (Godfrey et al., 2019). Therefore, this process likely does not represent simply an end-result of progressive attritional biodiversity loss driven by the aridification and punctuated megadroughts of the late Holocene (Li et al., 2020). Instead, we interpret the abrupt island-wide megaherbivore extinction event as a possible "delayed blitzkrieg", not in response to initial human arrival but to changing prehistoric human-environmental interactions and associated novel threats to biodiversity. In particular, these extinctions are closely correlated in time with the period of intensive habitat conversion from forests to grassland that occurred between ~1100-1000 BP, probably associated with a subsistence shift to agro-pastoralism

(Burney et al., 2003; Virah-Sawmy et al., 2010; Crowley and Samonds, 2013; Burns et al., 2016). Additional proximate extinction drivers are also possible; for example, reduction and fragmentation of forests also facilitates access for hunters (Marchant et al., 2009). We identify this radical shift in the sustainability of prehistoric human interactions with local biodiversity as the likely ultimate driver of the disappearance of Madagascar's megaherbivore guild.

Madagascar did not lose all of its native forests during the ~1100-1000 BP interval, and our data cannot rule out the possibility that tiny remnant populations of some elephant bird and/or hippo species persisted into the last millennium in restricted environmental refugia, a pattern seen in many of today's highly threatened species that had much larger historical ranges (Channell and Lomolino, 2002; Fisher and Blomberg, 2011; Turvey et al., 2015). It is even possible that such putative last survivors could have inspired historical accounts of fantastic animals persisting in remote habitat refugia, such as the second-hand seventeenth-century description of the *vouropatra* or *vorompatra*, "a large bird which haunts the Ampatres and lays eggs like those of an ostrich; the people of these regions cannot catch it, as it seeks out the most deserted place" (Flacourt, 1658). However, our results clearly demonstrate that island-wide collapse and functional extinction of Madagascar's megaherbivore guild had occurred several centuries earlier.

Our analysis of megaherbivore extinction dynamics has focused on investigation of extinction chronologies for elephant birds and hippopotami. Madagascar's Holocene record also contains at least two species of now-extinct giant tortoise (Gerlach and Canning, 1998), which may have persisted beyond the sudden crash of other megaherbivore species ~1000 years ago (Burney et al., 2004; Crowley, 2010). However, diversity and species-level identification of tortoise subfossils is unclear, and future investigation of Madagascar's megafaunal extinctions should incorporate these taxa following revision of their taxonomy. A third endemic hippo species, *Hippopotamus laloumena*, is also recognised by some authors (Faure and Guérin, 1990), but is known from very limited material, and its distinction from the extant mainland African species *H. amphibius* requires further assessment (Boisserie, 2005; Goodman and Jungers, 2014)(See also Supplementary text S1). It is also vital to determine the roles that Madagascar's extinct megaherbivores played in regulating ecosystem functionality, how ecosystems changed following removal of these keystone species, and whether any of their roles have been replaced by those of introduced species (Albert-Daviaud et al., 2020; Lundgren et al., 2020). Madagascar's wetland habitats are now highly degraded, and forest habitats are depleted of phosphorus (Du et al., 2020) and nitrogen (Gashorn et al., 2009), limiting productivity and perhaps driving low fruiting yields (Crowley et al., 2019). Understanding past megafaunal ecology using historical baselines represents an important priority for identifying restoration targets and guiding field-based environmental management in Madagascar's degraded landscapes. Although Madagascar's native megaherbivores are gone, it is still possible to use the past to inform the present and improve resilience for Madagascar's remaining threatened ecosystems and biodiversity.

Data availability. All datasets are available in Tables 2 and 3.

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References

Albert-Daviaud, A., Buerki, S., Onjalalaina, G.E., Perillo, S., Rabarijaona, R., Razafindratsima, O.H., Sato, H., Valenta, K., Wright, P.C., Stuppy, W., 2020. The ghost fruits of Madagascar: identifying dysfunctional seed dispersal in Madagascar's endemic flora. Biol. Conserv. 242, 108438.

Anderson, T., 2018. Reassembling the Strange: Naturalists, Missionaries, and the Environment of Nineteenth-Century Madagascar. Lexington Books, Lanham, MD.

Battistini, R., Verin, P., Rason, R., 1963. Le site archaeologique de Talaky. Annal. Malgaches 1, 111–153.

Berger, R., Ducote, K., Robinson, K., Walter, H., 1975. Radiocarbon date for the largest extinct bird. Nature 258, 709.

Boisserie, J.R., 2005. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistics analysis. Zool. J. Linn. Soc. 143, 1–26.

Bradshaw, C.J.A., Cooper, A., Turney, C.S.M., Brook, B.W., 2012. Robust estimates of extinction time in the geological record. Quat. Sci. Rev. 33, 14–19.

Bronk-Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.

Burney, D.A., 1999. Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In: MacPhee, R.D.E. (Ed.), Extinctions in Near Time:

Causes, Contexts, and Consequences. Kluwer Academic/Plenum, New York, pp. 145–164.

Burney, D.A., Burney, L.P., Godfrey, L.R., Jungers, W.L., Goodman, S.M., Wright, H.T., Jull, A.J.T., 2004. A chronology for late prehistoric Madagascar. J. Hum. Evol. 47, 25–63.

Burney, D.A., James, H., Grady, F., Rafamantanantsoa, J.G., Ramilisonina, Wright, H., Cowart, J., 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar. J. Biogeogr. 24, 755–767.

Burney, D.A., Ramilisonina, 1998. The kilopilopitsofy, kidoky, and bokyboky: accounts of strange animals from Belo-sur-Mer, Madagascar, and the megafaunal "extinction window." Am. Anthropol. 100, 957–966.

Burney, D.A., Robinson, G.S., Burney, L.P., 2003. *Sporormiella* and the late Holocene extinctions in Madagascar. Proc. Natl. Acad. Sci. USA 100, 10800–10805.

Burns, S.J., Godfrey, L.R., Faina, P., McGee, D., Hardt, B., Ranivoharimanana, L., Randrianasy, J., 2016. Rapid human-induced landscape transformation in Madagascar at the end of the first millennium of the Common Era. Quat. Sci. Rev. 134, 92–99.

Channell, R., Lomolino, M.V., 2002. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. J. Biogeogr. 27, 169–179.

Clarke, S.J., Miller, G.H., Fogel, M.L., Chivas, A.R., Murray-Wallace, C.V., 2006. The amino acid and stable isotope biogeochemistry of elephant bird (*Aepyornis*) eggshells from southern Madagascar. Quat. Sci. Rev. 25, 2343–2356.

Collen, B., Turvey, S.T., 2009. Probabilistic methods for determining extinction chronologies. In: Turvey, S.T. (Ed.), Holocene Extinctions. Oxford University Press, Oxford, pp. 181–191.

Cooke, S.B., Dávalos, L.M., Mychajliw, A.M., Turvey, S.T., Upham, N.S., 2017. Anthropogenic extinction dominates Holocene declines of West Indian mammals. Annu. Rev. Ecol. Evol. Syst. 48, 301–327.

Crees, J.J., Carbone, C., Sommer, R.S., Benecke, N., Turvey, S.T., 2016. Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene. Proc. R. Soc. B 283, 20152152.

Crowley, B.E., 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quat. Sci. Rev. 29, 2591–2603.

Crowley, B.E., Godfrey, L.R., 2019. Strontium isotopes support small home ranges for extinct lemurs. Frontiers Ecol. Evol. 7, 490.

Crowley, B.E., Godfrey, L.R., Bankoff, R.J., Perry, G.H., Culleton, B.J., Kennett, D.J., Sutherland, M.R., Samonds, K.E., Burney, D.A., 2017. Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. Ecography 40, 901–912.

Crowley, B.E., Godfrey, L.R., Irwin, M.T., 2011. A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. Am. J. Primatol. 73, 25–37.

Crowley, B.E., Samonds, K.E., 2013. Stable carbon isotope values confirm a recent increase in grasslands in northwestern Madagascar. Holocene 23, 1066–1073.

Crowther, A., Lucas, L., Helm, R., Horton, M., Shipton, C., Wright, H.T., Walshaw, S., Pawlowicz, M., Radimilahy, C., Douka, K., Picornell-Gelabert, L., Fuller, D.Q., Boivin, N.L., 2016. Ancient crops provide first archaeological signature of the westward Austronesian expansion. Proc. Natl. Acad. Sci. USA 113, 6635–6640.

Flacourt, É. de, 1658. Histoire de la Grande Isle Madagascar, Guillaume de Luyne, Paris.

Dewar, R.E., 1984. Recent extinctions in Madagascar: the loss of the subfossil fauna. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, AZ, pp. 574–593.

Dewar, R.E., Radimilahy, C., Wright, H.T., Jacobs, Z., Kelly, G.O., Berna, F., 2013. Stone tools and foraging in northern Madagascar challenge Holocene extinction models. Proc. Natl. Acad. Sci. USA 110, 12583–12588.

Diamond, J.M., 1989. Quaternary megafaunal extinctions: Variations on a Theme by Paganini. J. Archaeol. Sci. 16, 167–175.

Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., Svenning, J.C., 2016. Global nutrient transport in a world of giants. Proc. Natl. Acad. Sci. USA 113, 868–873.

Douglass, K., 2017. The diversity of late Holocene shellfish exploitation in Velondriake, southwest Madagascar. J. Island Coast. Archaeol. 12, 333–359.

Douglass, K., Hixon, S., Wright, H.T., Godfrey, L.R., Crowley, B.E., Manjakahery, B., Rasolondrainy, T., Crossland, Z., Radimilahy, C., 2019. A critical review of radiocarbon dates clarifies the human settlement of Madagascar. Quat. Sci. Rev. 221, 105878.

Du, E., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X., Jackson, R.B., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nature Geosci. 13, 221–226.

Eronen, J.T., Zohdy, S., Evans, A.R., Tecot, S.R., Wright, P.C., Jernvall, J., 2017. Feeding ecology and morphology make a bamboo specialist vulnerable to climate change. Curr. Biol. 27, 3384–3389.

Faure, M., Guérin, C., 1990. *Hippopotamus laloumena* nov. sp., la troisième espèce d'hippopotame holocène de Madagascar. C. R. Acad. Sci. Ser. II 310, 1299–1305.

Faure, M., Guérin, C., Ohler, A., 2015. Le statut du nom *Hippopotamus madagascariensis* Guldberg, 1883. Réponse à Rakotovao *et al*. 2014. Geodiversitas 37, 267–269.

Federman, S., Dornburg, A., Daly, D.C., Downie, A., Perry, G.H., Yoder, A.D., Sargis, E.J., Richard, A.F., Donoghue, M.J., Baden, A.L., 2016. Implications of lemuriform extinctions for the Malagasy flora. Proc. Natl. Acad. Sci. USA 113, 5041–5046.

Fisher, D.O., Blomberg, S.P., 2011. Correlates of rediscovery and the detectability of extinction in mammals. Proc. Roy. Soc. B 278, 1090–1097.

Fovet, W., Faure, M., Guérin, C., 2011. *Hippopotamus guldbergi* n. sp.: révision du statut d'*Hippopotamus madagascariensis* Guldberg, 1883, après plus d'un siècle de malentendus et de confusions taxonomiques. Zoosystema 33, 61–82.

Ganzhorn, J.U., Arrigo-Nelson, S., Boinski, S., Bollen, A., Carrai, V., Derby, A., Donati, G., Koenig, A., Kowalewski, M., Lahann, P., Norscia, I., Polowinski, S.Y., Schwitzer, C., Stevenson, P.R., Talebi, M.G., Tan, C., Vogel, E.R., Wright, P.C., 2009. Possible fruit protein effects on primate communities in Madagascar and the Neotropics. PLoS ONE 4, e8253.

Gerlach. J., Canning, L., 1998. Taxonomy of Indian Ocean giant tortoises (*Dipsochelys*). Chelonian Conserv. Biol. 3, 3–19.

Gillespie, R., Brook, B.W., Baynes, A., 2006. Short overlap of humans and megafauna in Pleistocene Australia. Alcheringa 30(S1), 163–186.

Godfrey, L.R., Jungers, W.L., Simons, E.L., Chatrath, P.S., Rakotosamimanana, B., 1999. Past and present distributions of lemurs in Madagascar. In: Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J.U., Goodman, S.M. (Eds.), New Directions in Lemur Studies. Springer, New York, pp. 19–53.

Godfrey, L.R., Scroxton, N., Crowley, B.E., Burns, S.J., Sutherland, M.R., Pérez, V.R., Faina, P., McGee, D., Ranivoharimanana, L., 2019. A new interpretation of Madagascar's megafaunal decline: The "Subsistence Shift Hypothesis". J. Hum. Evol. 130, 126–140.

Goodman, S.M., Benstead, J.P., 2004. The Natural History of Madagascar. University of Chicago Press, Chicago.

Goodman, S.M., Jungers, W.L., 2014. Extinct Madagascar. University of Chicago Press, Chicago.

Grayson, D.K., 1984. Nineteenth-century explanations of Pleistocene extinctions: A review and analysis. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, AZ, pp. 5–39.

Grealy, A., Phillips, M., Miller, G., Gilbert, M.T.P., Rouillard, J.M., Lambert, D., Bunce, M., Haile, J., 2017. Eggshell palaeogenomics: palaeognath evolutionary history revealed through ancient nuclear and mitochondrial DNA from Madagascan elephant bird (*Aepyornis* sp.) eggshell. Mol. Phylogen. Evol. 109, 151–163.

Hansford, J.P., Turvey, S.T., 2018. Unexpected diversity within the extinct elephant birds (Aves: Aepyornithidae) and a new identity for the world's largest bird. Roy. Soc. Open Sci. 5, 181295.

Hansford, J.P., Wright, P.C., Pérez, V.R., Muldoon, K.M., Turvey, S.T., Godfrey, L.R., 2020. Evidence for early human arrival in Madagascar is robust: a response to Mitchell. J. Island Coast. Archaeol. 15, 596–602.

Hansford, J., Wright, P.C., Rasoamiaramanana, A., Pérez, V.R., Godfrey, L.R., Errickson, D., Thompson, T., Turvey, S.T., 2018. Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. Sci. Adv. 4, eaat6925.

Higham, T., 1994. Radiocarbon dating New Zealand prehistory with moa eggshell: some preliminary results. Quat. Sci. Rev. 13, 163–169.

Hixon, S.W., Elliott Smith, E.A., Crowley, B.E., Perry, G.H., Randrianasy, J., Ranaivoarisoa, J.F., Kennett, D.J., Newsome, S.D., 2018. Nitrogen isotope (δ15N) patterns for amino acids in lemur bones are inconsistent with aridity driving megafaunal extinction in south-western Madagascar. J. Quat. Sci. 33, 958–968.

Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S.M., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Bronk Ramsey, C., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L., 2020. SHCal20 Southern Hemisphere Calibration, 0–55,000 years cal BP. Radiocarbon 62, 759–778.

Holdaway, R.N., Allentoft, M.E., Jacomb, C., Oskam, C.L., Beavan, N.R., Bunce, M., 2014. An extremely low-density human population exterminated New Zealand moa. Nature Comms 5, 5436.

Jungers, W.L., Demes, B., Godfrey, L.R., 2008. How big were the “giant” extinct lemurs of Madagascar? In: Fleagle, J.G., Gilbert, C.C. (Eds.), Elwyn Simons: A Search for Origins. Springer, New York, pp. 343–360.

Li, H., Sinha, A., André, A.A., Spötl, C., Vonhof, H.B., Meunier, A., Kathayat, G., Duan, P., Voarintsoa, N.R.G., Ning, Y., Biswas, J., Hu, P., Li, X., Sha, L., Zhao, J., Edwards, R.L., Cheng, H., 2020. A multimillennial climatic context for the megafaunal extinctions in Madagascar and Mascarene Islands. Science Adv. 6, eabb2459.

Lister, A.M., Stuart, A.J., 2013. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis*: reply to Kuzmin. Quat. Sci. Rev. 62, 144–146.

Lister, A.M., Stuart, A.J., 2019. The extinction of the giant deer *Megaloceros giganteus* (Blumenbach): new radiocarbon evidence. Quatern. Int. 500, 185–203.

Long, A., Hendershott, R., Martin, P., 1983. Radiocarbon dating of fossil eggshell. Radiocarbon 25, 533–539.

Louys, J., Curnoe, D., Tong, H., 2007. Characteristics of Pleistocene megafauna extinctions in Southeast Asia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 243, 152–173.

Lundgren, E.J., Ramp, D., Rowan, J., Middleton, O., Schowanek, S.D., Sanisidro, O., Carroll, S.P., Davis, M., Sandom, C.J., Svenning, J.C., Wallach, A.D., 2020. Introduced herbivores restore Late Pleistocene ecological functions. Proc. Natl. Acad. Sci. USA 117, 7871–7878.

MacPhee, R.D.E., Burney, D.A., 1991. Dating of modified femora of extinct dwarf hippopotamus from southern Madagascar: implications for constraining human colonization and vertebrate extinction events. J. Archaeol. Sci. 18, 695–706.

MacPhee, R.D.E., Marx, P.A., 1997. The 40,000-year plague: humans, hypervirulent diseases, and first-contact extinctions. In Goodman, S.M., Patterson, B.D. (Eds.), Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C., pp. 169–217.

Mahé, J., Sourdat, M., 1972. Sur l'extinction des vertébrés subfossiles et l'aridification du climat dans le sud-ouest de Madagascar. Bull. Soc. Géol. France 14, 295–309.

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Natl. Acad. Sci. USA 113, 838–846.

Marchant, R., Brewer, S., Webb, T., Turvey, S.T., 2009. Holocene deforestation: a history of human-environmental interactions, climate change, and extinction. In: Turvey, S.T. (Ed.), Holocene Extinctions. Oxford University Press, Oxford, pp. 213–233.

Marden, L., 1967. Madagascar: island at the end of the earth. Nat. Geo. 132, 443–487.

Martin, P.S., Klein, R.G., 1984. Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, AZ.

Muldoon, K.M., Crowley, B.E., Godfrey, L.R., Rasoamiaramanana, A., Aronson, A., Jernvall, J., Wright, P.C., Simons, E.L., 2012. Early Holocene fauna from a new subfossil site: a first assessment from Christmas River, south central Madagascar. Madag. Conserv. Dev. 7, 23–29.

Olson, D.M., Dinerstein, E., 2002. The Global 200: priority ecoregions for global conservation. Ann. Missouri Bot. 89, 199–224.

Parker-Pearson, M., Godden, K., Ramilisonina, Retsihisatse, Schwenninger, J.L., Heurtebize, G., Radimilahy, C., Smith, H., 2010. Pastoralists, Warriors and Colonists: The Archaeology of Southern Madagascar. Archaeopress, Oxford.

Parker Pearson, M., Godden, K., Ramilisonina, Schwenninger, J.L., Smith, H., 1995. The Central Androy Survey: Third Report. University of Sheffield, Sheffield and Musée d'Art et d'Archéologie, Antananarivo.

Pérez, V.R., Godfrey, L.R., Nowak-Kemp, M., Burney, D.A., Ratsimbazafy, J., Vasey, N., 2005. Evidence of early butchery of giant lemurs in Madagascar. J. Hum. Evol. 49, 722–742.

Perry, G.L., Wheeler, A.B., Wood, J.R., Wilmshurst, J.M., 2014. A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes). Quat. Sci. Rev. 105, 126–135.

Pierron, D., Heiske, M., Razafindrazaka, H., Rakoto, I., Rabetokotany, N., Ravololomanga, B., Rakotozafy, L.M.A., Rakotomalala, M.M., Razafiarivony, M., Rasoarifetra, B., Raharijesy, M.A., Razafindralambo, L., Ramilisonina, Fanony, F., Lejamble, S., Thomas, O., Abdallah, A.M., Rocher, C., Arachiche, A., Tonaso, L., Pereda-Loth, V., Schiavinato, S., Brucato, N., Ricaut, F.X., Kusuma, P., Sudoyo, H., Ni, S., Boland, A., Deleuze, J.F., Beaujard, P., Grange, P., Adelaar, S., Stoneking, M., Rakotoarisoa, J.A., Radimilahy, C., Letellier, T., 2017. Genomic landscape of human diversity across Madagascar. Proc. Natl. Acad. Sci. USA 114, E6498–E6506.

Price, G.J., Louys, J., Cramb, J., Feng, Y., Zhao, J., Hocknull, S.A., Webb, G.E., Nguyen, A.D., Joannes-Boyau, R., 2015. Temporal overlap of humans and giant lizards (Varanidae; Squamata) in Pleistocene Australia. Quat. Sci. Rev. 125, 98–105.

Price, G.J., Louys, J., Faith, J.T., Lorenzen, E., Westaway, M.C., 2018. Big data little help in megafauna mysteries. Nature 558, 23–25.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Racault, J.M., 2007. Memories of the Great Ocean: Travel Relationships to French-Speaking Literatures of the Indian Ocean. Presses Paris-Sorbonne, Paris.

Rakotovao, M., Lignereux, Y., Orliac, M.J., Durantho, F., Antoine, P.O., 2014. *Hippopotamus lemerlei* Grandidier, 1868 et *Hippopotamus madagascariensis* Guldberg, 1883 (Mammalia, Hippopotamidae): anatomie crânio-dentaire et révision systématique. Geodiversitas 36, 117–161.

Saltré, F., Brook, B.W., Rodríguez-Rey, M., Cooper, A., Johnson, C.N., Turney, C.S.M., Bradshaw, C.J.A., 2015. Uncertainties in dating constrain model choice for inferring extinction time from fossil records. Quat. Sci. Rev. 112, 128–137.

Samonds, K.E., Crowley, B.E., Rasolofomanana, T.R.N., Andriambelomanana, C., Andrianavalona, H.T., Ramihangihajason, T.N., Rakotozandry, R., Nomenjanahary, Z.B., Irwin, M.T., Wells, N.A., Godfrey, R.R., 2019. A new late Pleistocene subfossil site (Tsaramody, Sambaina basin, central Madagascar) with implications for the chronology of habitat and megafaunal community change on Madagascar's Central Highlands. J. Quat. Sci. 34, 379–392.

Sauer, E.G.F., 1972. Ratite eggshells and phylogenetic questions. Bonn. Zool. Beitr. 23, 3–48.

Scroxton, N., Burns, S.J., McGee, D., Godfrey, L., Ranivoharimanana, L., Faina, P., 2019. The impact of the 4.2 kyr event in the Indian Ocean basin: major drying or insignificant event? AGUFM, GC11G-1132.

Shurin, J.B., Aranguren-Riaño, N., Negro, D.D., Lopez, D.E., Jones, N.T., Laverde-R, O., Neu, A., Ramos, A.P., 2020. Ecosystem effects of the world's largest invasive animal. Ecology 101, e02991.

Signor, P.W., Lipps, J.H., 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. In: Silver, L.T., Schultz, P.H. (Eds.), Geological Implications of Impacts of Large Asteroids and Comets on the Earth. Geological Society of America, Boulder, CO, pp. 291–296.

Stafford, T.W., Jull, A.J.T., Brendel, K., Duhamel, R.C., Donahue, D., 1987. Study of bone radiocarbon dating accuracy at the University of Arizona NSF accelerator facility for radioisotope analysis. Radiocarbon 29, 24–44.

Strickland, H.E., 1849. Supposed existence of a giant bird in Madagascar. Ann. Mag. Nat. Hist. 2(4), 338–339.

Stuart, A.J., 2015. Late Quaternary megafaunal extinctions on the continents: a short review. Geol. J. 50, 338–363.

Turvey, S.T., Crees, J.J., Di Fonzo, M.M.I., 2015. Historical data as a baseline for conservation: reconstructing long-term faunal extinction dynamics in Late Imperial–modern China. Proc. Roy. Soc. B 282, 20151299.

Turvey, S.T., Sathe, V., Crees, J.J., Jukar, A.M., Chakraborty, P., Lister, A.M., 2021. Late Quaternary megafaunal extinctions in India: how much do we know? Quat. Sci. Rev. 252, 106740.

Turvey, S.T., Tong, H., Stuart, A.J., Lister, A.M., 2013. Holocene survival of Late Pleistocene megafauna in China: A critical review of the evidence. Quat. Sci. Rev. 76, 156–166.

Turvey, S.T., Hansford, J., Brace, S., Mullin, V., Gu, S., Sun, G., 2016. Holocene range collapse of giant muntjacs and pseudo-endemism in the Annamite large mammal fauna. J. Biogeogr. 43, 2250–2260.

Virah-Sawmy, M., Willis, K.J., Gillson, L., 2010. Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. J. Biogeogr. 37, 506–519.

Waeber, P.O., Wilmé, L., Ramamonjisoa, B., Garcia, C., Rakotomalala, D., Rabemananjara, Z.H., Kull, C.A., Ganzhorn, J.U., Sorg, J.P., 2015. Dry forests in Madagascar: neglected and under pressure. Int. Forest. Rev. 17(S2), 127–148.

Walker, A., 1967. Patterns of extinction among the subfossil Madagascar lemuroids. In: Martin, P.S., Wright, H.E. Jr (Eds.), Pleistocene Extinctions: The Search for a Cause. Yale University Press, New Haven, CT, pp. 407–424.

Weston, E.M., Lister, A.M., 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. Nature 459, 85–88.

White, A.W., Worthy, T.H., Hawkins, S., Bedford, S., Spriggs, M., 2010. Megafaunal meiolaniid horned turtles survived until early human settlement in Vanuatu, southwest Pacific. Proc. Natl. Acad. Sci. USA 107, 15512–15516.

Wood, J.R., Wilmshurst, J.M., Worthy, T.H., Cooper, A., 2011. *Sporormiella* as a proxy for non-mammalian herbivores in island ecosystems. Quat. Sci. Rev. 30, 915–920.

Wright, P.C. 2014. For the Love of Lemurs: My Life in the Wilds of Madagascar. Lantern Books, New York.

Table 1. Rejected pre-1980 radiocarbon dates for Madagascar megaherbivores. Key: GaK, Gakushuin University, Japan; UCLA, University of California Los Angeles.

Lab. number	**Collection locality**	**Material**	**Reported species**	**Date (BP)**	**Reference**
UCLA-1983	Fort Dauphin	Eggshell	*Aepyornis maximus*	1000±150	Berger et al. (1975)
N/A	Irodo	Eggshell	*Aepyornis maximus*	1150±90	Mahé and Sourdat (1972)
N/A	Manambovo	Eggshell	*Aepyornis maximus*	840±80	Battistini et al. (1963)
N/A	“south Madagascar”	Eggshell	*Aepyornis maximus*	2930±85	Marden (1967)
N/A	Tulear	Eggshell	*Aepyornis maximus*	5210±140	Sauer (1972)
GaK-1506	Itampolo	Bone	*Hippopotamus* sp.	980±200	Mahé and Sourdat (1972)

Table 2. Accepted radiocarbon dates available for elephant bird species used in species-specific or biome-specific extinction date analyses. Key: CAMS, Center for Accelerator Mass Spectroscopy, Lawrence Livermore National Laboratory; Hela, Hela Dating Laboratory, Helsinki University; MNHN, Museum National d'Histoire Naturelle, Paris; NHMUK, Natural History Museum, London; NHMW, Naturhistorisches Museum, Vienna; NZA, Rafter Radiocarbon Lab, Lower Hutt, New Zealand; OxA, Oxford Radiocarbon Accelerator Unit; OZF, ANTARES AMS Facility, Menai, Australia; PSU, Pennsylvania State University; UB, Queens University, Belfast; UIO, Natural History Museum, University of Oslo; USNM, National Museum of Natural History/Smithsonian Institution; ZIUU, Zoologiska Museum, Uppsala Universitet; Beta, Beta Analytic. * indicates field or excavation grid numbers.

Lab. number	**Locality**	**Biome**	**Specimen number**	**Material**	**Date (BP)**	**Calibrated date, 2σ (BP)**	**Reference**
1. *Aepyornis hildebrandti*							
UB29724	Antsirabe	Central highlands	UIO A31834	Tibiotarsus	5282±39	6182-5916	This paper
OxA-34327	Antsirabe	Central highlands	NHMW 2014/0238/0006	Tibiotarsus	3112±31	3371-3175	This paper
OxA-33537	Antsirabe	Central highlands	NHMW 2014/0238/0037	Tibiotarsus	2177±27	2301-2012	This paper
OxA-34758	Masinandraina	Central highlands	ZIUU 34(A46)	Tarsometatarsus	1537±25	1418-1312	Hansford and Turvey (2018)
OxA-34325	Antsirabe	Central highlands	NHMW 2014/0238/0003	Tibiotarsus	1485±28	1400-1296	This paper
OxA-34328	Antsirabe	Central highlands	NHMW 2014/0238/0012	Tibiotarsus	1349±28	1286-1177	This paper
2. *Aepyornis maximus*							
Hela-1774 UB-31590	Ilakaka	Succulent woodland	USNM A605209	Tibiotarsus	9428±53	10,991-10,427	Hansford and Turvey (2018)
3. *Mullerornis modestus*							
UB29726	Lamboharana	Arid spiny bush	MNHN MAD 6768	Tibiotarsus	5597±40	6443-6283	Hansford and Turvey (2018)
β-55094 CAMS-3547	Lavakasaka	Dry deciduous forest	HFJ-92-15*	Eggshell	2380±70	2701-2141	Burney et al. (1997)
OxA-8271	Talakay	Arid spiny bush	AND33-97*	Eggshell	1825±30	1814-1609	Parker Pearson et al. (2010)
OxA-8273	Talakay	Arid spiny bush	AND2-97*	Eggshell	1780±35	1725-1564	Parker Pearson et al. (2010)
OxA-34274	Velondriake	Arid spiny bush	PSU TONY10B3_S_1*	Eggshell	1677±27	1588-1426	Douglass (2017)
Beta-103349	Ankilibehandry	Succulent woodland	BSM-95-10*	Tibiotarsus	1280±60	1270-1070	Burney et al. (1997)
UB-29725	Southwest coast	-	MNHN MAD 6662	Tibiotarsus	1296±32	1284-986	Hansford et al. (2018)
4. *Vorombe titan*							
OxA-34776	Ampoza-Ankazoabo	Arid spiny bush	NHMUK PV A2142	Femur	3381±24	3685-3486	Hansford and Turvey (2018)
OxA-34774	Ampoza-Ankazoabo	Arid spiny bush	NHMUK PV A2145	Tibiotarsus	2744±25	2867-2754	This paper
OxA-33534	Ampoza-Ankazoabo	Arid spiny bush	MNHN MAD 377	Femur	2540±26	2736-2434	This paper
OxA-34775	Ampoza-Ankazoabo	Arid spiny bush	NHMUK PV A2144	Tibiotarsus	2509±23	2717-2369	This paper
OxA-33532	Ampoza-Ankazoabo	Arid spiny bush	MNHN MAD 368	Femur	2499±25	2708-2365	This paper

OxA-33531	Ampoza-Ankazoabo	Arid spiny bush	MNHN MAD 364	Femur	2470±24	2700-2353	Hansford and Turvey (2018)
OxA-33533	Ampoza-Ankazoabo	Arid spiny bush	MNHN MAD 6770	Tarsometatarsus	2112±25	2104-1933	This paper
OxA-33572	Ankilibehandry	Succulent woodland	MNHN MAD 8813	Tarsometatarsus	2047±29	2039-1885	This paper
OxA-33573	Ankilibehandry	Succulent woodland	MNHN MAD 6655	Tibiotarsus	1503±29	1405-1303	This paper
OxA-33536	Ankilibehandry	Succulent woodland	MNHN MAD 383	Tarsometatarsus	1442±24	1353-1276	This paper
OxA-33535	Andolonomby	Arid spiny bush	MNHN 1906-16-67	Tibiotarsus	1237±24	1179-998	Hansford et al. (2018)
5. Thick eggshell							
OxA-34217	Velondriake	Arid spiny bush	PSU TONY1SE_2_1*	Eggshell	9420±83	11,068-10,293	Douglass (2017)
OxA-8279	Talakay	Arid spiny bush	MAD-97/16*	Eggshell	6238±45	7252-6954	Parker Pearson et al. (2010)
OZF856	Faux Cap	Arid spiny bush	9691C*	Eggshell	4635±105	5582-4970	Clarke et al. (2006)
OZF855	Faux Cap	Arid spiny bush	9691B*	Eggshell	4510±98	5443-4850	Clarke et al. (2006)
OxA-8280	Talakay	Arid spiny bush	MAD-97/19*	Eggshell	4461±70	5289-4861	Parker Pearson et al. (2010)
OZF854	Faux Cap	Arid spiny bush	9691A*	Eggshell	3447±63	3835-3486	Clarke et al. (2006)
OxA-5077	Maroaloke	Arid spiny bush	A2*	Eggshell	2246±57	2345-2057	Parker Pearson et al. (1995)
OxA-8281	Talakay	Arid spiny bush	MAD-97/45*	Eggshell	2246±56	2344-2059	Parker Pearson et al. (2010)
OxA-5075	Maroaloke	Arid spiny bush	A1*	Eggshell	1941±48	1992-1720	Parker Pearson et al. (1995)
OxA-34215	Velondriake	Arid spiny bush	PSU TONY2A9_S_1*	Eggshell	1929±47	1983-1708	Douglass (2017)
OxA-34216	Velondriake	Arid spiny bush	PSU TONY2B8_1_1*	Eggshell	1920±49	1983-1703	Douglass (2017)
OxA-5076	Maroaloke	Arid spiny bush	A8*	Eggshell	1838±60	1875-1570	Parker Pearson et al. (1995)
OxA-8274	Talakay	Arid spiny bush	AND1-97*	Eggshell	1716±56	1704-1426	Parker Pearson et al. (2010)
Beta-90099	Belo-sur-Mer	Succulent woodland	BSM-95-6*	Eggshell	1710±78	1744-1373	Burney et al. (1997)
OxA-8269	Talakay	Arid spiny bush	AND5-97*	Eggshell	1613±51	1575-1352	Parker Pearson et al. (2010)
OZF514	Faux Cap	Arid spiny bush	9691E*	Eggshell	1458±48	1409-1181	Clarke et al. (2006)
OxA-5078	Maroaloke	Arid spiny bush	A10*	Eggshell	1281±40	1271-1061	Parker Pearson et al. (1995)
OxA-8268	Bevala	Arid spiny bush	AND 29-97*	Eggshell	1234±40	1261-978	Parker Pearson et al. (2010)
OxA-8272	Talakay	Arid spiny bush	AND4-97*	Eggshell	1147±61	1179-910	Parker Pearson et al. (2010)
OxA-8270	Talakay	Arid spiny bush	AND6-97*	Eggshell	1114±56	1177-805	Parker Pearson et al. (2010)
6. Unknown species							
NZA-16995	Masinandraina	Central highlands	ZIUU MAS-5	Tibiotarsus	4496±40	5295-4884	Burney et al. (2004)
β-67659	Itampolo-ve	Arid spiny bush	UA HFJ-92-12*	Bone	1880±70	1927-1588	Burney et al. (1997)

Table 3. Accepted radiocarbon dates available for *Hippopotamus* species used in species-specific or biome-specific extinction date analyses. Key: AA, NSF-Arizona AMS Facility, Tuscon; CAMS, Center for Accelerator Mass Spectroscopy, Lawrence Livermore National Laboratory; CVB, Centre ValBio, Ranomafana Madagascar: Hela, Hela Dating Laboratory, Helsinki University; MNHN, Museum National d'Histoire Naturelle, Paris; NHMUK, Natural History Museum, London; OxA, Oxford Radiocarbon Accelerator Unit; Pta, Stephan Woodborne Quaternary Research Dating Unit (QUADRU), Pretoria; TO, IsoTrace Laboratory, University of Toronto; UA: Universite d'Antananarivo; Beta, Beta Analytic.; ZIUU, Zoologiska Museum, Uppsala Universitet. * indicates field or excavation grid numbers.

Lab. number	**Locality**	**Biome**	**Specimen number**	**Material**	**Date (BP)**	**Calibrated date, 2σ (BP)**	**Reference**
1. *Hippopotamus lemerlei*							
OxA-19325	Lamboharana	Arid spiny bush	NHMUK PV M82187	Cranium	3895±27	4410-4153	This paper
OxA-19316	Itampolo-ve	Arid spiny bush	NHMUK PV M4935	Cranium	3359±28	3681-3455	This paper
OxA-19318	Ampoza-Ankazoabo	Succulent woodland	ZIUU-3972	Cranium	2566±27	2747-2490	This paper
OxA-19319	Ampoza-Ankazoabo	Succulent woodland	ZIUU-3973	Cranium	2547±26	2740-2464	This paper
OxA-19321	Ampoza-Ankazoabo	Succulent woodland	NHMUK PV M82190	Cranium	2386±26	2490-2157	This paper
OxA-19315	Itampolo-ve	Arid spiny bush	NHMUK PV M4934	Cranium	2189±27	2305-2016	This paper
OxA-19317	Itampolo-ve	Arid spiny bush	NHMUK PV M4937	Mandible	1657±25	1568-1421	This paper
OxA-19322	Anavoha	Arid spiny bush	MNHN MAD 8818	Cranium	1583±24	1519-1365	This paper
OxA-19323	Lamboharana	Arid spiny bush	MNHN MAD 7914	Cranium	1404±24	1310-1180	This paper
OxA-19314	Andolonomby	Arid spiny bush	MNHN MAD 1076	Cranium	1360±25	1290-1177	This paper
OxA-19324	Lamboharana	Arid spiny bush	MNHN MAD 8823	Mandible	1349±25	1284-1177	This paper
OxA-19313	Andolonomby	Arid spiny bush	MNHN MAD 1060	Mandible	1338±26	1285-1176	This paper
OxA-19320	Ampoza-Ankazoabo	Succulent woodland	MNHN M7918	Cranium	1325±24	1280-1114	This paper
2. *Hippopotamus madagascariensis*							
OxA-19462	Antsirabe	Central highlands	NHMUK PV M5141	Cranium	3358±27	3680-3455	This paper
OxA-19464	Antsirabe	Central highlands	NHMUK PV M7093	Cranium	2857±27	3060-2805	This paper
OxA-19465	Antakara	Arid spiny bush	MNHN MAD 7352	Cranium	1298±24	1268-1080	This paper
OxA-19463	Antsirabe	Central highlands	NHMUK PV M5142	Mandible	1280±24	1263-1070	This paper
3. Unknown species							
CAMS 173568	Tsaramody	Central highlands	Not given	Phalanx	14,580±460	18,811-16,550	Samonds et al. (2019)
Hela-1828	Ilakaka	Succulent woodland	CVB, not given*	Bone	9655±60	11,184-10,751	Muldoon et al. (2012)
CAMS 142559	Anjohibe	Dry deciduous forest	UA 4917	Mandible	6310±60	7324-6995	Crowley and Samonds (2013)
Beta-64961 CAMS-8648	Anjohibe	Dry deciduous forest	UA HFJ-93-2-B*	Bone	5300±60	6262-5912	Burney et al. (1997)

CAMS 144110	Anjohibe	Dry deciduous forest	UA 9570	Cranium	4815±40	5594-5329	Crowley and Samonds (2013)
CAMS 143194	Anjohibe	Dry deciduous forest	UA 3591	Scapula	4055±40	4795-4310	Crowley and Samonds (2013)
Beta-55093 CAMS-3562	Anjohibe	Dry deciduous forest	UA HJF-92-11	Bone	3730±70	4283-3833	Burney et al. (1997)
CAMS 143195	Anjohibe	Dry deciduous forest	UA 3560	Pelvis	3455±25	3823-3574	Crowley and Samonds (2013)
CAMS 143120	Anjohibe	Dry deciduous forest	UA 1992-M-395*	Unknown	3095±30	3365-3165	Crowley and Samonds (2013)
CAMS 142896	Taolambiby	Arid spiny bush	A subzero SE 180-200*	Mandible	2905±40	3153-2866	Crowley (2010)
CAMS 143068	Anjohibe	Dry deciduous forest	UA 3558	Pelvis	2890±40	3148-2851	Crowley and Samonds (2013)
CAMS 143059	Taolambiby	Arid spiny bush	AB-1 330-440*	Vertebra	2855±35	3061-2790	Crowley (2010)
Pta-7728	Ampoza-Ankazoabo	Succulent woodland	Not given	Unknown	2760±60	2965-2739	Burney et al. (2004)
CAMS 142640	Taolambiby	Arid spiny bush	B1 2.1 m (cm)*	Vertebra	2745±40	2925-2745	Crowley (2010)
CAMS 243052	Ampoza-Ankazoabo	Succulent woodland	UA B3-13	Pelvis	2660±40	2854-2538	Crowley (2010)
CAMS 143193	Anjohibe	Dry deciduous forest	Uncatalogued (UA)	Bone fragment	2635±40	2844-2496	Crowley and Samonds (2013)
CAMS 142566	Taolambiby	Arid spiny bush	A1-B1 2.5 m*	Rib	2550±30	2742-2437	Crowley (2010)
CAMS 142918	Taolambiby	Arid spiny bush	AB-1 280 cm*	Vertebra	2540±30	2737-2430	Crowley (2010)
NZA-16996 R-28139/7	Ampoza-Ankazoabo	Succulent woodland	AMO-1	Bone	2517±40	2723-2366	Burney et al. (2004)
CAMS 142567	Taolambiby	Arid spiny bush	A1-B1 2.2 m*	Rib	2470±25	2701-2353	Crowley (2010)
GrA-11626	Ampoza-Ankazoabo	Succulent woodland	Not given	Unknown	2370±50	2682-2145	Burney et al. (2004)
CAMS 143060	Taolambiby	Arid spiny bush	A12.20 M*	Tibia	2300±50	2352-2135	Crowley (2010)
CAMS 142636	Ankilibehandry	Succulent woodland	SQ234. Oh *	Tooth root	2275±35	2339-2137	Crowley (2010)
TO-1438	Lamboharana	Arid spiny bush	MNHN MAD 1710	Unknown	2020±300	2720-1319	MacPhee et al. (1991)
AA-2895	Andolonomby	Arid spiny bush	MNHN MAD 1711	Unknown	1970±50	1999-1746	MacPhee et al. (1991)
CAMS 143150	Antsirabe	Central highlands	unidentified A*	Rib	1800±35	1807-1577	Crowley (2010)
TO-1437	Lamboharana	Arid spiny bush	MNHN MAD 1709	Bone	1740±50	1728-1432	MacPhee et al. (1991)
CAMS 142734	Taolambiby	Arid spiny bush	A1-B1 2.4 m*	Vertebra	1440±30	1356-1186	Crowley (2010)
CAMS 142540	Antsirabe	Central highlands	unidentified A1*	Rib	1260±25	1259-1062	Crowley (2010)

Table 4. Taxon-specific GRIWM extinction date estimates for Madagascar elephant bird and *Hippopotamus* species.

Megafaunal taxon	**Samples**	**Extinction date estimate (BP)**	**Extinction date estimate (CE)**
Aepyornis hildebrandti	6	1223-1118	727-832
Mullerornis modestus	7	1124-1031	826-919
Vorombe titan	11	1106-939	844-1011
"thick" eggshell	20	957-885	993-1065
Hippopotamus lemerlei	13	1188-1163	762-787
Hippopotamus madagascariensis	4	1132-1050	818-900

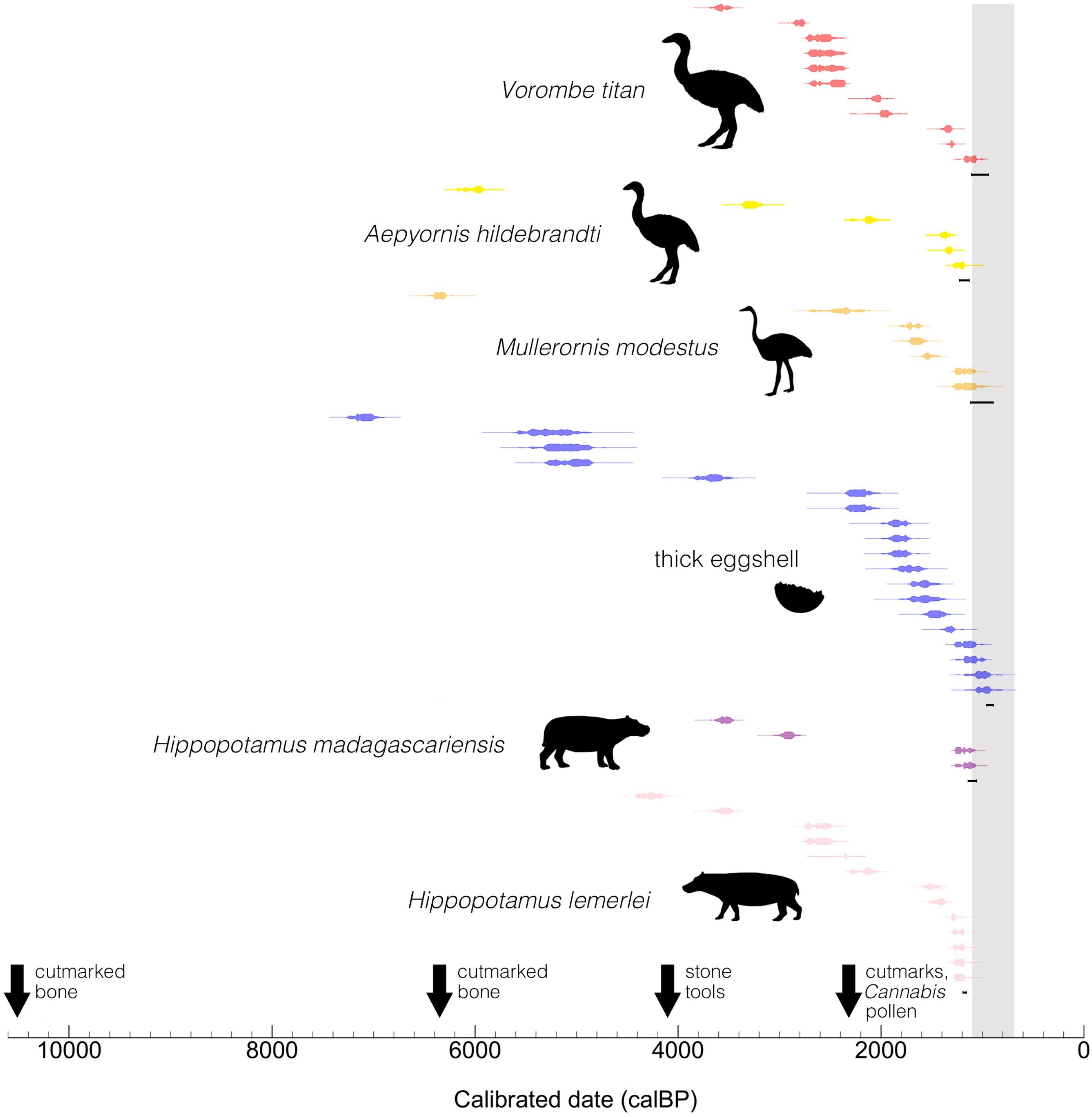
Table 5. GRIWM extinction date estimates for megaherbivore communities in different Madagascar biomes.

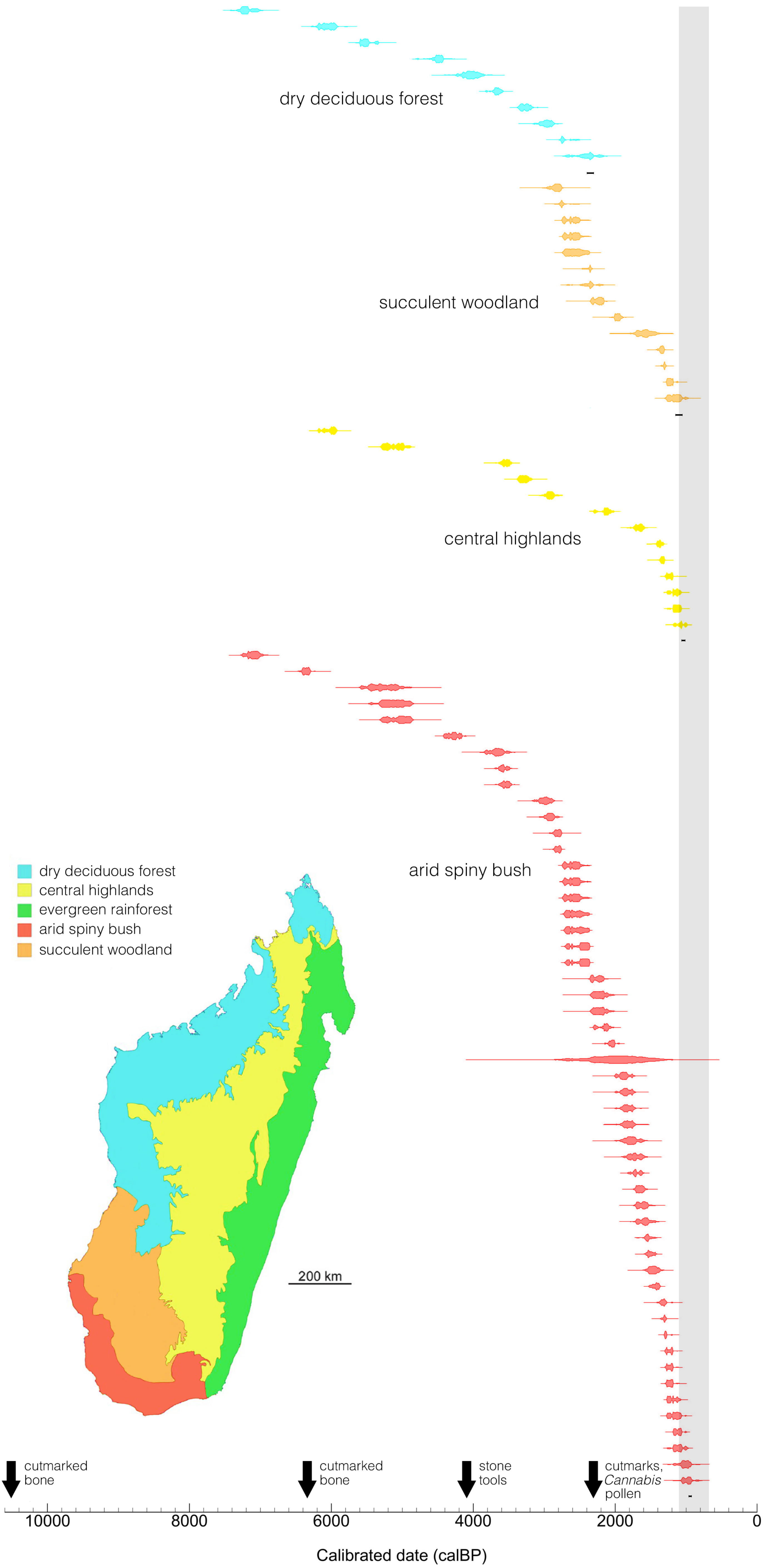
Biome	**Taxa**	**Samples**	**Extinction date estimate (BP)**	**Extinction date estimate (CE/BCE)**
Arid spiny bush	*Aepyornis* sp., *H. lemerlei*, *H. madagascariensis*, *M. modestus*, *V. titan*, thick eggshell	53	957-911	993-1039 CE
Central highlands	*A. hildebrandti*, *Aepyornis* sp., *H. madagascariensis*, *Hippopotamus* sp.	13	1109-1045	841-905 CE
Succulent woodland	*M. modestus*, *V. titan*, *H. lemerlei*, *Hippopotamus* sp., thick eggshell	16	1133-1052	817-898 CE
Dry deciduous forest	*M. modestus*, *Hippopotamus* sp.	10	2364-2078	414-128 BCE

FIGURE LEGENDS

Figure 1. Species-specific AMS date series for Madagascar's extinct megaherbivores, calibrated using OxCal 4.4 and SHCal20. Estimated species extinction dates based on GRIWM analysis shown by black bars below each date series. Vertical grey band indicates approximate timing of inferred human subsistence transition to agro-pastoralism (decline in arboreal pollen and increase in grass pollen) from Burns et al. (2016). Different types of dated evidence for earlier human presence in Madagascar from Burney et al. (2003), Dewar et al. (2013), and Hansford et al. (2018).

Figure 2. Biome-specific AMS date series for Madagascar's extinct megaherbivore communities, calibrated using OxCal 4.4 and SHCal20. Estimated biome-specific extinction dates based on GRIWM analysis shown by black bars below each date series. Vertical grey band indicates approximate timing of inferred human subsistence transition to agro-pastoralism (decline in arboreal pollen and increase in grass pollen) from Burns et al. (2016). Different types of dated evidence for earlier human presence in Madagascar from Burney et al. (2003), Dewar et al. (2013), and Hansford et al. (2018).


Vorombe titan
Aepyornis hildebrandti
Mullerornis modestus
thick eggshell
Hippopotamus madagascariensis
Hippopotamus lemerlei
cutmarked bone
cutmarked bone
stone tools
cutmarks, *Cannabis* pollen
10000
8000
6000
4000
2000
0
Calibrated date (calBP)


dry deciduous forest
succulent woodland
central highlands
arid spiny bush
dry deciduous forest
central highlands
evergreen rainforest
arid spiny bush
succulent woodland
200 km
cutmarked bone
cutmarked bone
stone tools
cutmarks, *Cannabis* pollen
10000
8000
6000
4000
2000
0
Calibrated date (calBP)

TEXT S1: NOMENCLATURE OF MALAGASY HIPPOS

Grandidier (1868) established the name *Hippopotamus lemerlei* for a fossil hippopotamus from Madagascar. Guldberg (1883), describing new fossil material from Madagascar, proposed the name *H. madagascariensis*. However, Fovet *et al*. (2011: 33) show from Guldberg's text that he was not intending to define a new species, but merely to give *lemerlei* a new name that he considered more appropriate. Nonetheless, Guldberg's *H. madagascariensis* has its own type material and his paper satisfies the criteria of Article 12 of the International Code of Zoological Nomenclature (ICZN, 1999) for availability of names published before 1931.

Subsequently, Stuenes (1989) and Faure & Guerin (1990) showed clearly that there were in fact two distinct species of fossil hippopotami from Madagascar. Stuenes (1989) designated a specimen studied by Grandidier as lectotype of *lemerlei*, and another illustrated by Guldberg as lectotype of *H. madagascariensis*. The latter name was subsequently used by most authors for the species additional to *H. lemerlei* (Weston & Lister 2009).

Fovet *et al*. (2011) and Faure *et al*. (2015), however, consider *madagascariensis* an unavailable name in the meaning of ICZN (1999), since Guldberg had intended it merely as a 'replacement name' for *lemerlei*. Article 11.6 of the Code states: "A name which when first published in an available work was treated as a junior synonym of a name then used as valid is not thereby made available". But paragraph 11.6.1 continues: "However, if such a name published as a junior synonym had been treated before 1961 as an available name and either adopted as the name of a taxon or treated as a senior homonym, it is made available thereby". The Code adds that the authorship and date of the taxon is that of its first publication. Several authors between 1883 and 1961 (e.g., Major 1902) clearly used the name *madagascariensis* as the valid name for a taxon, so *Hippopotamus madagascariensis* Guldberg, 1883 remains an available name.

Distinct from its nomenclatural availability is the taxonomic validity of *H. madagascariensis* as a species separate from *H. lemerlei*. Fovet *et al*. (2011) and Faure *et al*. (2015) are of the opinion that the lectotypes of *lemerlei* and *madagascariensis*, selected by Stuenes (1989), are of the same species, rendering *madagascariensis* a junior subjective synonym of *lemerlei.* They proposed a new name, *Hippopotamus guldbergi* Fovet *et al*., 2011, with a skull at NHMUK as the holotype, for the 'second species' on Madagascar. We, however, agree with Stuenes (1989) and Rakotovao *et al*. (2014: 153-5) that the lectotype crania of *H. madagascariensis* and *H. lemerlei* are distinct and represent the two taxa now abundantly documented from Madagascar (e.g., Weston & Lister 2009). The *madagascariensis* lectotype clearly lacks the distinctive bulbous swelling to the upper rim of the orbit seen in *lemerlei*, as well as having a shorter muzzle relative to the size of the braincase. These are among the few characters reliably separating the two species.

In consequence, we retain the names *Hippopotamus lemerlei* Grandidier, 1868 and *H. madagascarensis* Guldberg, 1883 for the two common fossil hippopotamus species on Madagascar. *H. guldbergi* Fovet *et al*. (2011) is treated as a junior subjective synonym of

H. madagascariensis Guldberg, 1883. Since the Guldberg specimen chosen by Stuenes (1989) as lectotype of *madagascariensis* is lost, Rakotovao *et al*. (2014) proposed another specimen as lectotype, but the Code (Articles 73.2.2 and 74.1.1) makes clear that a lectotype, once selected, cannot be changed even if lost. The lectotype selected by Stuenes (1989) remains valid and was fortunately illustrated in detail by Guldberg (1883) and reprinted by Fovet *et al*. (2011).

A third species, *H. laloumena* Faure & Guérin, 1990, with type specimen from Mananjary on the east coast of Madagascar, is known only from a mandible and some foot bones (Faure *et al*. 2010). It is close in size to small individuals of *H. amphibius* (Weston & Lister 2009), and was initially described as the subspecies *H. amphibius standini* Monnier & Lamberton, 1922 (considered a *nomen nudum* by Faure & Guerin 1990). It has been suggested that the remains are modern importations of *H. amphibius* (Boisserie, 2005; Goodman & Jungers, 2014), possibly based on some modern hippo bones curated in Malagasy museums. However, the type mandible of *H. laloumena* is heavily mineralised, indicating considerable antiquity, while foot bones from the Belobaka locality were excavated from a deposit tentatively dated to around 20 ka BP (Faure *et al*. 2010). This implies that a larger species of hippopotamus colonised the island on one or more occasions before historical times (Weston & Lister 2009). This animal might indeed represent a subspecies of *H. amphibius* (no diagnostic cranial material is yet known), but due to a degree of body size scaling and the probable antiquity of this specimen, we retain its separate taxonomic status as *H. laloumena*.

REFERENCES

Boisserie, J.R., The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): A review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society* **143**, 1-26 (2005).

Goodman, S.M., Jungers, W.L., *Extinct Madagascar* (University of Chicago Press, 2014).

Faure, M., Guérin, C., *Hippopotamus laloumena* nov. sp., la troisième espèce d'hippopotame Holocène de Madagascar. *Comptes Rendus de l'Académie des Sciences, Paris, série II* **310**, 1299-1305 (1990).

Faure, M., Guérin, C., Genty, D., Gommery, D., Ramanivosoa, B., Le plus ancien hippopotame fossile (*Hippopotamus laloumena*) de Madagascar (Belobaka, Province de Mahajanga). *Comptes Rendus Palevol* **9**, 155-162 (2010).

Faure M., Guérin C., Ohler A., Le statut du nom *Hippopotamus madagascariensis* Guldberg, 1883. Réponse à Rakotovao *et al.* 2014. *Geodiversitas* **37**, 267-269 (2015).

Fovet, W., Faure, M., Guérin, C., *Hippopotamus guldbergi* n. sp.: Révision du statut d'*Hippopotamus madagascariensis* Guldberg, 1883, après plus d'un siècle de malentendus et de confusions taxonomiques. *Zoosystema* **33**, 61-82 (2011).

Grandidier, A., Sur les découvertes zoologiques faites récemment à Madagascar. *Annales des Sciences naturelles, Zoologie et Paléontologie, série 5*, **10**, 375-378 (1868).

Gildberg, G.A., Undersøgelser over en subfossil flodhest fra Madagascar. *Christiana Videnskabs-Selskab Forhandlinger* **6**, 1-24 (1883).

ICZN, *International Code of Zoological Nomenclature, Fourth Edition* (1999). https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/the-code-online/

Major, C.J.F., Some account of a nearly complete skeleton of *Hippopotamus madagascariensis* Guld., from Sirabé, Madagascar, obtained in 1895. *Geological Magazine IX*, **455**, 193-199 (1902).

Monnier, L., Lamberton, C., Note sur des ossements subfossiles de la region de Mananjary. *Bulletin de l'Académie Malgache* **3**, 211-213 (1922).

Rakotovao, M., Lignereux, Y., Orliac, M.J., Duranthon, F., Antoine, P.O., *Hippopotamus lemerlei* Grandidier, 1868 et *Hippopotamus madagascariensis* Guldberg, 1883 (Mammalia, Hippopotamidae): Anatomie crânio-dentaire et révision systématique. *Geodiversitas* **36**, 117-161 (2014).

Stuenes, S., Taxonomy, habits and relationships of the subfossil Madagascan hippopotami *Hippopotamus lemerlei* and *H. madagascariensis*. *Journal of Vertebrate Paleontology* **9**, 241-268 (1989).

Weston, E.M., Lister, A.M., Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature* **459**, 85-89 (2009).

Table S1. Rejected radiocarbon dates. Key: GaK, Gakushuin University, Japan; UCLA, University of California Los Angeles.

Lab. number	Collection locality	Material	Reported species	Date (BP)	Reference
UCLA-1983	Fort Dauphin	Eggshell	*Aepyornis maximus*	1000±150	1
N/A	Irodo	Eggshell	*Aepyornis maximus*	1150±90	2
N/A	Manambovo	Eggshell	*Aepyornis maximus*	840±80	3
N/A	“south Madagascar”	Eggshell	*Aepyornis maximus*	2930±85	4
N/A	Tulear	Eggshell	*Aepyornis maximus*	5210±140	5
GaK-1506	Itampolo	Bone	*Hippopotamus* sp.	980±200	2

REFERENCES

1. Berger, R., Ducote, K., Robinson, K., Walter, H., Radiocarbon date for the largest extinct bird. *Nature* **258**, 709 (1975).
2. Mahé, J., Sourdat, M., Sur l’extinction des vertébrés subfossiles et l’aridification du climat dans le sud-ouest de Madagascar. *Bull. Soc. Géol. France* **14**, 295-309 (1972).
3. Battistini, R., Verin, P., Rason, R., Le site archaeologique de Talaky. *Annal. Malgaches* **1**, 111-153 (1963).
4. Marden, L., Madagascar: Island at the end of the earth. *National Geographic Magazine* **132**, 443-487 (1967).
5. Sauer, E.G.F., Ratite eggshells and phylogenetic questions. *Bonner Zoologische Beitrage* **23**, 3-48 (1972).