

Paleoecological evidence for late Holocene aridification from the Taolambiby subfossil site of southwestern Madagascar

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Abstract

Taolambiby, a key subfossil site in southwestern Madagascar, has yielded many bones of extinct large lemurs and associated fauna in excavations spanning more than a century. In 2004 our group collected a 4.4 m sediment profile from deposits near prior excavations. Our aim was to use sedimentological and palynological inferences to examine the interaction between climate change and human activities, in order to better understand how each may have contributed to local extirpations. The basal age of this profile was ca. 3500 cal yr BP. Lithology of the excavated and cored material showed many changes in sediment regime, reflecting the variable nature of the basin's hydrology. After ca. 1500 cal yr BP, the record shows successive drying of the site and subsequent erosion and redeposition. After this time, pollen and spores were not preserved but charcoal particles continued to provide a record of local and regional fires up to the present. Between 340 and 250 cm below surface, pollen was well-preserved, showing evidence for a mixture of mesic and xeric vegetation, including many trees, shrubs, forbs, and ferns, most still found in the adjacent Bezà Mahafaly Special Reserve. This pollen record, spanning the period from ca. 3000 - 1500 cal yr BP, shows evidence for increased wetness at the beginning of the period and subsequent aridification. Coprophilous fungus spores (*Sporormiella*) are high during this same interval, suggesting the local presence of abundant megafauna, but decline with increasing aridification.

Charcoal values peak as *Sporormiella* declines, and charcoal decreases afterward. Although these results are consistent with hypotheses invoking a human role in megafaunal extinctions and vegetation change, the coincidence of increasingly dry conditions by the middle of the first millennium CE points to a role for climate change at this site, increasing the severity of human impacts and accelerating local extirpations.

Key words: extinctions, aridification, fire history, *Sporormiella*, palynology

Résumé détaillé

Taolambiby, un site subfossile clé du Sud-ouest de Madagascar, a permis de récupérer de nombreux os de grands lémurien éteints et de la faune associée lors de fouilles qui ont duré plus d'un siècle. En 2004, notre groupe a recueilli un profil sédimentaire de 4,4 m dans des dépôts situés à proximité des fouilles antérieures. L'âge basal de ce profil était d'environ 3500 ans calendaires BP. La lithologie des matériaux excavés et carottés a montré de nombreux changements dans le régime sédimentaire, reflétant la nature variable de l'hydrologie du bassin et, après ca. 1500 ans BP, l'assèchement successif du site, l'érosion et la redéposition qui s'ensuivent. Après cette période, le pollen et les spores n'ont pas été préservés, mais les particules de charbon ont continué à fournir un enregistrement des incendies locaux et régionaux jusqu'à aujourd'hui. Entre 340 et 250 cm sous la surface, le pollen était bien préservé, montrant des signes d'un mélange de végétation mésique et xérique, y compris de nombreux arbres, arbustes, plantes herbacées et fougères, dont la plupart se trouvent encore dans la réserve adjacente de Bezà Mahafaly. Ce registre pollinique, qui couvre la période d'environ 3000 à 1500 ans calendaires BP, montre des preuves d'une humidité accrue au début de la période et d'une aridification ultérieure. Les spores de champignons coprophiles (*Sporormiella*) sont élevées pendant ce même intervalle, ce qui suggère la présence locale d'une mégafaune abondante, mais elles diminuent avec une croissance de l'aridification. Les valeurs de microcharbons atteignent un pic lorsque *Sporormiella* décline, et le charbon de bois diminue ensuite. Bien que ces résultats soient conformes

aux hypothèses invoquant un rôle humain dans les extinctions de la mégafaune et les changements de végétation, la coïncidence de conditions de plus en plus sèches au milieu du premier millénaire de notre ère indique un rôle du changement climatique sur le site, augmentant la gravité des impacts humains et accélérant les disparitions locales.

Les preuves paléoécologiques suggèrent que le bassin éphémère contenant les riches dépôts subfossiles de Taolambiby a réagi au forçage climatique de la fin de l'Holocène. Après une période sèche vers 3500 ans BP, des conditions plus humides sont revenues, d'abord en affouillant le bassin et en déposant de galets de quartz, puis en commençant à accumuler du sable fin et des débris humiques dans un marais saisonnier. Vers 2700 ans BP, des conditions de plus en plus mésiques sont évidentes sur le site, avec suffisamment d'eau permanente dans le bassin pour accumuler des sédiments typiques de cette région d'un lac peu profond, et avec la préservation d'os et d'abondants restes de plants et de fortes concentrations de spores de champignons coprophiles. Sur les hauteurs environnantes, les broussailles épineuses et les buissons à feuilles caduques ont largement cédé la place à des arbres plus mésiques, mais toujours adaptés à la sécheresse saisonnière. Pendant cette période humide, les incendies se sont multipliés dans les environs.

Vers 1500 ans BP, le climat était à nouveau aride, de sorte que les forêts sèches et mésiques ont cédé la place à des buissons xériques et à une végétation ligneuse adaptée au feu. Le bassin lui-même est redevenu un marais saisonnier et a fini par s'assécher presque complètement et a commencé à s'éroder. Les os modifiés par l'homme confirment que des personnes se trouvaient sur le site au milieu du premier millénaire de notre ère, et peut-être même un millénaire plus tôt. Taolambiby montre des preuves d'une multiplicité d'effets délétères sur la mégafaune subfossile du site, dont plusieurs impacts humains, probablement exacerbés par une aridification croissante.

Mots clés : extinctions, aridification, historique des incendies, *Sporormiella*, palynologie

Introduction

Despite the large number of studies focusing on the rich bone deposits of Taolambiby, southwestern Madagascar (summarized in Perez *et al.*, 2005; Goodman & Jungers, 2014; Anderson *et al.*,

2018), most investigators have not addressed the stratigraphic provenance of the materials collected and none have included studies of associated microfossils. Stratigraphic analyses of pollen, spores, and charcoal particles, coupled with radiocarbon dating and sediment description, have enriched our understanding of many other classic subfossil sites (Burney *et al.*, 2004), but to date have not addressed the changes in context at Taolambiby that might edify the well-documented late Holocene decline of the subfossil megafauna of the island.

Studies of the paleoenvironmental context of the late Holocene extinction event in Madagascar have proved critical (although as yet not definitive) in evaluating the many competing hypotheses proposed to explain the island's loss of terrestrial vertebrates larger than 10 kg. These hypotheses span a range of potential causes, from aridification (Virah-Sawmy *et al.*, 2009) to fire, overhunting, and hypervirulent disease (see Burney, 1999, for a summary of the expectations of each). In addition to these older, primarily single-cause hypotheses, two more recent hypotheses have invoked more nuanced explanations, involving the interaction of several factors, notably the Synergy Hypothesis (Burney *et al.*, 2004) and the Subsistence Shift Hypothesis (Godfrey *et al.*, 2019). Under the former, it is proposed that a human-driven decline in megafauna, coupled with late Holocene drying, precipitated a series of environmental state shifts whereby loss of megafaunal grazers led to major changes in fire ecology and ultimately, deleterious changes in vegetation type. In the latter hypothesis, the same impacts occur but the primary driver was not human arrival, but major changes in human subsistence strategies, notably a fundamental shift in lifeways from hunter-gatherer to sedentary agriculturalist and pastoralist. One major uncertainty has been the date of initial human settlement, an issue that has become not more, but less settled in recent years, with a departure from an emerging consensus that people arrived roughly two millennia ago (Burney *et al.*, 2004; Crowley, 2010) to recent estimates ranging from as early as ca. 11,000 yr BP (Hansford *et al.*, 2018, 2020) to as recently as 1300 yr BP (Anderson *et al.*, 2018; but see Douglass *et al.*, 2019). Further uncertainty has arisen recently with increasing evidence that although no island-wide climate change can be conveniently invoked to explain the timing of extinctions throughout the island, increased

aridification in the late Holocene may indeed complicate the picture for the drier southwestern part of the island (see Faina *et al.*, 2021).

Although the present study cannot resolve these important questions—indeed, no single site is likely to close the case—we present evidence that the fossil-rich site of Taolambiby does show evidence for severe climate change at the same time that human impacts were evident at this site and in the broad region.

Materials and methods

Location and site characteristics

The name of the site, Taolambiby, means literally “animal bones” in Malagasy, and some variation of it crops up frequently as a minor place name throughout Madagascar at sites containing large bone fossils, from Jurassic dinosaurs to the late Holocene subfossil megafauna. By far the most famous is the site 20 km east-northeast of the small town of Betioky-Sud in southwestern Madagascar (Figure 1). The site is

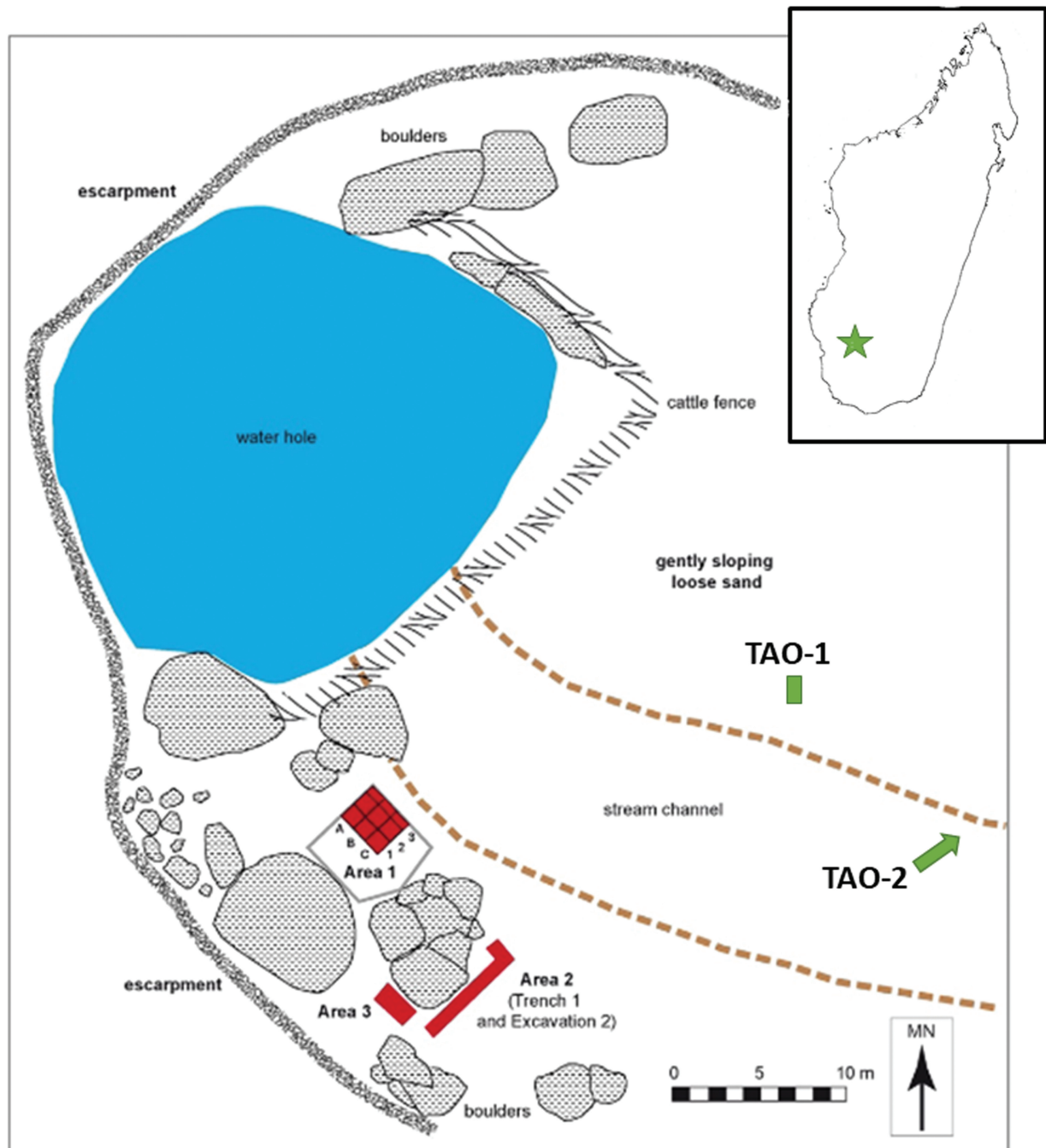


Figure 1. Location of Taolambiby subfossil site in southwestern Madagascar. Sediment profile TAO-1 was collected at 23°40.213'S 44°34.408'E, 190 m above sea-level. TAO-2 indicates location of dated bone sample collected from wall of adjacent stream channel. Also shown are excavations of Anderson *et al.* (2018) labeled as Areas 1-3. Map adapted from Anderson *et al.* (2018, Supplement 1).

directly downhill from a series of low erosion scarps on weakly cemented calcarenite at ca. 200 m above sea-level. It lies due west of areas of lower elevation, culminating in the flood plain of the Sakamena River, a seasonal drainage channel that feeds into the large Onilahy River. Between the fossil locality and the river are two parcels of land with native vegetation and extant lemurs under protection, known collectively as the Bezà Mahafaly Special Reserve.

The basin appears to be related to a semicircular feature on the hillside that formed from spring seepage resulting in slope collapse. Most likely the area behind the small pond on the site has a horizontal or gently sloping impervious layer (an aquitard or aquiclude) that has, at least during wetter periods, produced a perched water table. As the topography eroded, by perhaps the mid-Holocene it had exposed an outcrop that allowed this water to create an artesian spring on the site. Over the centuries, this small seepage pond has apparently increased in size during periods of relatively high precipitation, scouring out, during flood events in particular, a shallow basin. In response to higher annual rainfall, a marsh or even a pond might be expected to form on the site. During drier periods, the site would dry out and sediments would undergo desiccation, and perhaps deflation and redeposition, within the small basin and downslope.

The layers containing bones of extinct and extant late Holocene animals are in a topographic low, shaped like a cul-de-sac, opening east-southeast. There is a small pond below the headwall, with a seasonal drainage into a ravine that cuts through the deposits, exposing some of the bone layers that are closer to the surface. The surface zone is heavily disturbed by livestock, and some fine sediments near the surface are almost certainly spoil piles from previous excavations by Lamberton (1933) and perhaps others. Most other early investigators, however, report merely picking bones out of the layers exposed by erosion, or give no provenance information (Methuen, reported in Walker, 1967; Godfrey *et al.*, 2001).

The site we chose for developing a sediment profile (TAO-1, Figure 1) is on the north side of the stream channel, on a flat area outside the modern flood zone and southeast of an area of gently sloping loose sand that we judged to be likely spoil piles as they resemble those of early 20th century investigators that have been re-excavated and screened in more recent times at other sites (Burney, 1999; Burney *et al.*, 2008). Until the late 20th century, the operative method was to dig a large pit, sometimes well below

the water table, and pile the sediment alongside, often apparently with little or no screening. We also inspected an area of the ravine adjacent to our profile site (TAO-2, Figure 1), finding bones of extinct and extant animals in a dark sandy layer that might have been a source of previous finds exposed by erosion.

Sampling methods

The primary purpose of this field work was to generate a stratigraphic profile of a sediment column judged most likely to contain a continuous and minimally disturbed sediment sequence that reached the bottom of the organic layers. It was assumed, based on previous experience, that to reach the deepest bone-bearing layers with certainty, we needed to be in a position close to the inferred center of the geomorphic depression defined by the semi-circular scarp forming the headwall, and as far as possible from sources of colluvial breakdown and alluvial deposition. We sounded the approximate center of the basin that would have contained the larger pond believed by previous investigators (Raison & Vérin, 1967) to have once covered the site.

The uppermost layers were excavated by trowel, as a 1 X 2 m trench. The water table was reached at 267 cm below the surface datum. At this point, to prevent contamination and hole collapse, a two-handed open-drive sampler or gouge corer was employed to make a 20 cm diameter hole in the center of the pit, down to 345 cm. At that depth, a 10 cm diameter bucket auger was used down to the apparent bottom of organic deposits, recovering at the base (441 cm below surface) a sample of the underlying rock (see Burney, 2018, for a description of coring techniques employed).

Sediment types were described in the field and with subsequent lab examination. Colors were assigned via soil chart (Munsell Color, 1990). Textures were classified from sediment smears in the lab via light microscopy at 10X and 100X.

Comparative modern vegetation data were compiled from personal observation at the adjacent Bezà Mahafaly Special Reserve, with reference to the MadCat database (2020) for current nomenclature, and vegetation descriptions published in Ratsirarson *et al.* (2001), Rasoazanabary and Godfrey (2016), and Phillipson *et al.* (2018).

Dating and microscopy

AMS ¹⁴C dating was applied to plant macrofossils from four levels in the organic-rich parts of the core

(Table 1). Samples for radiocarbon dating were pretreated with hot HCl to remove carbonates, followed by NaOH to remove secondary organic acids, followed by a second HCl treatment. One bone collagen date was also obtained from an extinct lemur specimen found in the TAO-2 site near the profile. The bone sample was washed with deionized water, the surface scraped free of the outermost layers, and then gently crushed. Dilute, cold HCl was repeatedly applied and replenished until the mineral fraction was eliminated. The demineralized bone was then dissected and inspected for rootlets. Any rootlets present were also removed when replenishing the acid solutions. Collagen residue was then pretreated with NaOH to ensure the absence of secondary organic acids.

AMS ^{14}C determinations were corrected for isotopic fractionation from $\delta^{13}\text{C}$ readings from IRMS. Radiocarbon dates were converted to calendar years

(cal yr BP) using the High Probability Density Range Method (Bronk Ramsey, 2009) and the SHCAL20 calibration curve (Hogg *et al.*, 2020).

Table 2 presents all currently available ^{14}C dates for bones of extinct megafauna from Taolambiby. These include materials collected from the TAO-1 pit and reported in Crowley (2010). Current calibrations are included from the SHCAL20 calibration curve (Hogg *et al.*, 2020).

For pollen, spore, and charcoal determinations, slides were prepared from small subsamples collected at 10 cm intervals throughout the profile. The rest of the sediment was screened down to 1.6 mm mesh, and all small bones, seeds, wood, snail shells, and other biological materials were saved in sterile containers. Pollen and spore extraction procedures followed standard techniques described in Faegri *et al.* (1989). Counts ranged from ca. 200 to >1000 in each level included in the analysis. Charcoal pieces

Table 1. Radiocarbon dates from TAO-1 sediment profile.

Depth (cm) in profile ¹	Material	^{14}C LAB #	Conventional ^{14}C age $\pm 1\sigma$	2 σ cal yr BP range ²	2 σ cal yr CE/BCE	$\delta^{13}\text{C}$ (‰) ³
250-251	Plant fibers	Beta-462710	1580 $\pm$ 30	1524-1356	426-594 CE	-25.5
290-291	Tree bark	Beta-205893	2470 $\pm$ 40	2545-2351 (60.6%) 2705-2629 (21.1%) 2619-2555 (13.8%)	596-402 BCE 756-680 BCE 670-606 BCE	-27.7
330-331	Wood fragment	Beta-205894	2740 $\pm$ 40	2882-2744 (93.5%) 2920-2905 (1.9%)	933-795 BCE 971-956 BCE	-27.8
415-416	Plant fibers	Beta-462711	3350 $\pm$ 30	3594-3451 (88.3%) 3636-3600 (6.0%) 3680-3671 (1.1%)	1645-1502 BCE 1687-1651 BCE 1731-1722 BCE	-26.2

¹ Depth from soil surface at profile site TAO-1. See Figure 2.

² Calibrated by High Probability Density Range Method (Bronk Ramsey, 2009) from Database SHCAL20 (Hogg *et al.*, 2020).

³ Measured by Infrared Mass Spectrometry.

Table 2. Radiocarbon dates for extinct megafauna from Taolambiby.

Taxon	Specimen or Field #	Laboratory #	Conventional age (yr BP $\pm 1\sigma$)	Mean calibrated age (yr BP $\pm 2\sigma$)	Date source
<i>Aldabrachelys</i> sp.	Burney exp. A1-B1 2.4 m	CAMS 143057	1540 $\pm$ 45	1395 $\pm$ 90	Crowley (2010)
	Burney exp. A1 1.1-1.2 m	CAMS 143108	1745 $\pm$ 30	1618 $\pm$ 83	Crowley (2010)
	Burney exp. A1-B1 2.5 m	CAMS 142638	2535 $\pm$ 30	2578 $\pm$ 153	Crowley (2010)
	Burney exp. A1-B1 2.5 m	CAMS 143099	2605 $\pm$ 30	2628 $\pm$ 133	Crowley (2010)
	Burney exp. A1 2.3 m	CAMS 143098	3025 $\pm$ 35	3193 $\pm$ 138	Crowley (2010)
	Burney exp. A1-B1 2.7 m	CAMS 143050	2500 $\pm$ 25	2555 $\pm$ 155	Crowley (2010)
	Not given	GaK 1651	2290 $\pm$ 90	2248 $\pm$ 243	Mahé & Sourdats (1972)
<i>Archaeolemur majori</i>	Anderson exp. UA 1283	OxA-26159	1218 $\pm$ 27	1078 $\pm$ 98	Anderson <i>et al.</i> (2018)
	UA 1283	CAMS 143106	2565 $\pm$ 40	2608 $\pm$ 143	Crowley (2010)
	UA 1287	CAMS 143058	1385 $\pm$ 25	1243 $\pm$ 63	Crowley (2010)
<i>Cryptoprocta spelea</i>	UA 10543	CAMS 143062	3115 $\pm$ 30	3290 $\pm$ 85	Crowley (2010)
	UA 10544	CAMS 142717	2005 $\pm$ 30	1933 $\pm$ 68	Crowley (2010)

Taxon	Specimen or Field #	Laboratory #	Conventional age (yr BP $\pm 1\sigma$)	Mean calibrated age (yr BP $\pm 2\sigma$)	Date source
<i>Hippopotamus</i> sp.	Anderson exp.	OxA-27173	1257 $\pm$ 29	1120 $\pm$ 60	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-27175	1749 $\pm$ 29	1630 $\pm$ 70	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-27305	1242 $\pm$ 24	1118 $\pm$ 58	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-X-2494-47	1231 $\pm$ 27	1120 $\pm$ 50	Anderson <i>et al.</i> (2018)
	Burney exp. A1-B1 2.5 m	CAMS 142566	2550 $\pm$ 30	2603 $\pm$ 138	Crowley (2010)
	Burney exp. A subzero SE	CAMS 142896	2905 $\pm$ 40	3008 $\pm$ 143	Crowley (2010)
	Burney exp. A1-B1 2.2 m	CAMS 142567	2470 $\pm$ 25	2528 $\pm$ 173	Crowley (2010)
	Burney exp. A1-B1 2.4 m	CAMS 142734	1440 $\pm$ 30	1313 $\pm$ 43	Crowley (2010)
	Burney exp. A1-B1 2.8 m	CAMS 142918	2540 $\pm$ 30	2600 $\pm$ 140	Crowley (2010)
	Burney exp. B1 2.1 m	CAMS 142640	2745 $\pm$ 40	2815 $\pm$ 70	Crowley (2010)
	Burney exp. A1 2.2 m	CAMS 143060	2300 $\pm$ 50	2243 $\pm$ 108	Crowley (2010)
	Burney exp. A1 3.3-4.4 m	CAMS 143059	2855 $\pm$ 35	2953 $\pm$ 108	Crowley (2010)
	Burney exp.	CAMS 150585	2620 $\pm$ 110	2615 $\pm$ 265	Godfrey & Crowley (2016)
<i>Megaladapis edwardsi</i>	UA 4191	CAMS 142800	3005 $\pm$ 30	3123 $\pm$ 123	Crowley (2010)
	UA 4203	CAMS 143104	2165 $\pm$ 30	2153 $\pm$ 143	Crowley (2010)
<i>M. madagascariensis</i>	OUMNH 5105	AA-45961-T-16042	2713 $\pm$ 44	2800 $\pm$ 75	Burney <i>et al.</i> (2004)
	UA 4192	CAMS 143114	2945 $\pm$ 30	3052 $\pm$ 118	Crowley (2010)
	UA 4193	CAMS 143107	2290 $\pm$ 25	2243 $\pm$ 98	Crowley (2010)
	UA 4194	CAMS 142716	3025 $\pm$ 40	3133 $\pm$ 133	Crowley (2010)
	UA 4195	CAMS 143196	2600 $\pm$ 30	2625 $\pm$ 130	Crowley (2010)
	UA 4202	CAMS 143129	2645 $\pm$ 30	2743 $\pm$ 43	Crowley (2010)
<i>Pachylemur insignis</i>	Anderson exp.	OxA-X-2500-22	1283 $\pm$ 24	1165 $\pm$ 95	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26160	1234 $\pm$ 27	1115 $\pm$ 60	Anderson <i>et al.</i> (2018)
	UA 2914	CAMS 143148	2685 $\pm$ 30	2788 $\pm$ 63	Crowley (2010)
	UA 2915	CAMS 142798	2185 $\pm$ 30	2173 $\pm$ 133	Crowley (2010)
	UA 2924	CAMS 142731	2915 $\pm$ 30	3012 $\pm$ 133	Crowley (2010)
	UA 2931	CAMS 143105	2215 $\pm$ 30	2205 $\pm$ 120	Crowley (2010)
	UMASS TAO-66-73	CAMS 144109	1265 $\pm$ 30	1150 $\pm$ 85	Crowley (2010)
<i>Palaeopropithecus ingens</i>	Anderson exp.	OxA-26630	2112 $\pm$ 26	2050 $\pm$ 55	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26631	2445 $\pm$ 27	2522 $\pm$ 178	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26632	2506 $\pm$ 27	2560 $\pm$ 155	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26633	2431 $\pm$ 28	2517 $\pm$ 178	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26634	2452 $\pm$ 26	2523 $\pm$ 178	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26635	2069 $\pm$ 26	1988 $\pm$ 68	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26636	2080 $\pm$ 26	1993 $\pm$ 68	Anderson <i>et al.</i> (2018)
	Anderson exp.	OxA-26637	2871 $\pm$ 27	2960 $\pm$ 105	Anderson <i>et al.</i> (2018)
	OUMNH 14346j	AA-45960-T-16041A	2325 $\pm$ 43	2250 $\pm$ 110	Burney <i>et al.</i> (2004)
	UA 1083	CAMS 143056	2510 $\pm$ 30	2565 $\pm$ 155	Crowley (2010)
	UA 1088	CAMS 142568	2720 $\pm$ 35	2803 $\pm$ 63	Crowley (2010)
	UA 1090	CAMS 142797	2150 $\pm$ 30	2070 $\pm$ 65	Crowley (2010)
	UA 1091	CAMS 143061	2120 $\pm$ 30	2063 $\pm$ 68	Crowley (2010)
	UA 4480	CAMS 143103	1990 $\pm$ 25	1913 $\pm$ 83	Crowley (2010)
	UA PP17	CAMS 142900	2615 $\pm$ 30	2630 $\pm$ 130	Crowley (2010)
	UA 8862 PP68	CAMS 142732	2995 $\pm$ 30	3115 $\pm$ 120	Crowley (2010)
	OUMNH	CAMS 150587	1940 $\pm$ 120	1833 $\pm$ 273	Crowley & Godfrey (2013)

Key to abbreviations:

AA: University of Arizona Accelerator Mass Spectrometry Laboratory (USA)

Anderson exp.: Expedition reported in Anderson *et al.* (2018).

Burney exp.: Expedition reported in this paper and Crowley (2010).

CAMS: Center for Accelerator Mass Spectrometry (USA)

GaK: Gakushuin University (Japan)

OxA: Oxford Radiocarbon Accelerator Unit (England)

OUMNH: Oxford University Museum of Natural History (England)

UA: Université d'Antananarivo (Madagascar)

were measured via grid reticule as described in Swain (1973). "Microcharcoal" included all particles up to 125 μm ; larger pieces were classified as "macrocharcoal." Concentrations were measured via an exotic spike, using darkly acetylated *Lycopodium* tablets containing a known quantity of spores (Faegri *et al.*, 1989).

Pollen percentages were calculated with a base of total terrestrial pollen and fern spores. Aquatic/paludal pollen types and *Sporormiella* spores were calculated against the raw sum. Of identified terrestrial pollen and fern spores, 22 types occurred at 2% or more in at least one level. These were used for cluster analysis and pollen zonation, employing constrained incremental sum-of-squares (CONISS; Grimm, 1987). Zones were selected on the basis of distinct clusters and outliers.

Results

Sediment descriptions and ages

The TAO-1 sediment profile was complex, with 12 recognizable sedimentary units in 441 cm (Figure 2), including evidence for sediment hiatuses and redeposition in the upper half of the profile and between the pollen zones recognized (see "Pollen

and spores" below). A comprehensive age model from the available radiocarbon dates was not constructed since the key assumption (linear age-depth relationship) was not justified for this profile. In a case like this, dates from plant macrofossils or other materials without inherent age problems may be suitable for determining the age of materials at the same level but interpolating ages for samples between and beyond dates is not a reliable approach, since stratigraphic evidence shows some sediments have been lost or redeposited. For this reason, dates were obtained from plant macrofossils at levels directly associated with stratigraphic events described, (see Burney *et al.*, 2001; Burney, 2002, for other examples that use this approach for dating episodically deposited sediments).

The surface layer, down to 20 cm, is a bioturbated modern soil, weakly developed and containing dry leaf litter at the surface, grading into a sandy humic detrital zone. This is underlain by a more consolidated very light gray sandy silt that, at 70 cm, becomes a very light-yellow silty sand. At ca. 90 cm sediments show evidence of alternate wetting and drying, with reddish brown drying cracks and reddish brown drying cracks. This layer also contains shell fragments from native land snails. Below this is

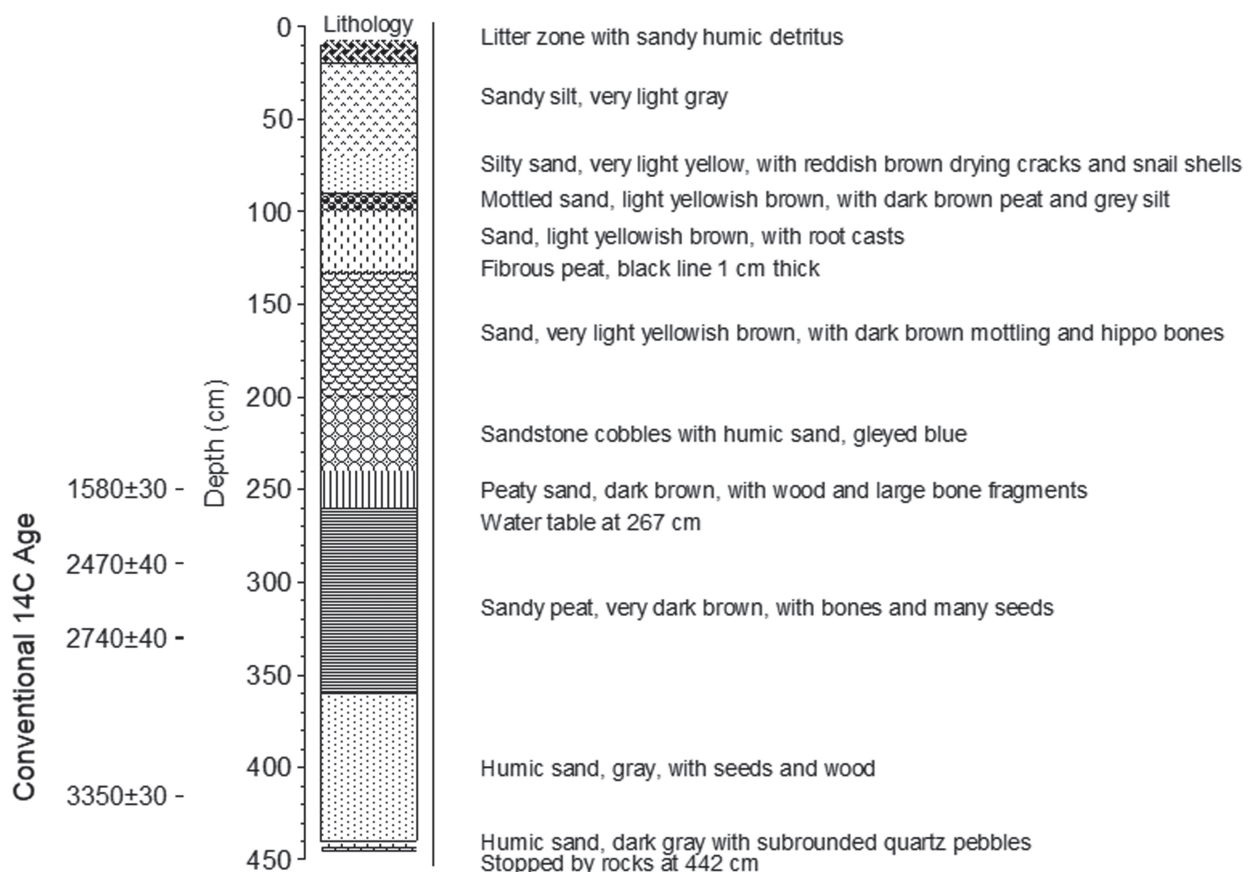


Figure 2. Stratigraphic section from TAO-1.

a 10 cm layer of mottled sand, light yellowish brown, coarsely mixed with dark brown peat and grey silt. From 100–132 cm there is a uniform light yellowish brown sand with very little organic matter except for small vertical root casts. At 133 cm there is a 1 cm-thick line of black fibrous peat, quite distinct. This appears in the 2 m wall profile to be essentially level, as if deposited in standing water, whereas the layers above show lateral variation and are perhaps lenses or wedges of sediment deposited through either human disturbance (e.g., excavation spoil) or colluviation. Below this level down to 200 cm is a light yellowish-brown sand with dark brown mottling (organic staining) and fragments of bone, including abraded hippo bones. This layer is highly similar, and at similar depth, to a layer exposed in the adjacent ravine, where we obtained a cranial fragment (TAO-05-1; Beta-205892) from the orbital region of an extinct large lemur, *Pachylemur insignis*, with a conventional ^{14}C age of 1320 ± 40 yr BP, which calibrates at 2σ to 1283–1176 cal BP (70.1%) and 1166–1078 cal BP (25.3%).

Below 200 cm, down to ca. 240 cm, sediments are dominated by calcarenite cobbles in a matrix of coarse humic sand. This layer is damp, although above the water table at the date sampled (1 August). Anoxia is apparent, as the sediments at this level are gleyed blue, turning olive brown after brief exposure to the air. It is underlain (240–260 cm) by dark brown peaty sand. This layer contains highly abraded large bone fragments, including material identifiable as hippopotamus, giant tortoise, and crocodile. Plant fibers extracted from 250 cm were dated to 1580 ± 30 yr BP (1524–1356 cal yr BP at 2σ).

At this season (austral winter) the water table stood at 267 cm below the surface datum. From 260 cm down to 360 cm is a very dark brown sandy peat with well-preserved bones and many seeds. This unit is typical of shallow lake bottoms in other sites investigated in the southwest (Burney, 1993; Virah-Sawmy *et al.*, 2016). A fragment of tree bark from 290 cm yielded an age of 2470 ± 40 yr BP. This calibrates to 2545–2351 cal yr BP (60.6%), 2705–2629 cal yr BP (21.1%), and 2619–2555 cal yr BP (13.8%). At 330 cm, a wood fragment was dated to 2740 ± 40 yr BP, calibrated to 2882–2744 cal yr BP (93.5%) and 2920–2905 yr BP (1.9%). The base of this unit ends abruptly at 360 cm, with no transition to a unit of gray humic sand containing seeds and wood. Plant fibers from 415 cm dated to 3350 ± 30 yr BP, calibrated to 3594–3451 cal yr BP (88.3%), 3636–3600 (6%), and 3680–3671 cal yr BP (1.1%).

At its base (440 cm) the corer encountered an impenetrable layer of rock. About 1 cm of this material was recovered, consisting of dark gray humic sand and subrounded quartz pebbles.

Charcoal particles

Charcoal particles occur in all levels of the profile, but in highly varying amounts (Figure 3). Near the modern (10 cm) surface, micro charcoal is moderately high ($4.7 \times 10^7 \mu\text{m}^2 \text{cm}^{-3}$) but macro charcoal is absent. This is a pattern consistent with the present land-use situation: there is frequent use of fire by pastoralists in the region today, but the immediate vicinity is too dry and sparsely vegetated to support extensive local fires at this time. From 250 cm to the base of the profile at 440 cm (ca. 1500–3500 cal yr BP), however, micro charcoal values are much higher (up to $2.9 \times 10^8 \mu\text{m}^2 \text{cm}^{-3}$), including a significant component of macro (i.e., locally derived) charcoal, ca. 17,000 pcs cm^{-3} at this level and at 280 cm. Highest values are generally in the sediments from 270–340 cm, ca. 2000–3000 cal yr BP), although there is more charcoal even in the basal sediments (ca. 3500 cal yr BP) than near the modern surface. The preservation of charcoal throughout the record, despite oxidative conditions at some levels, is not surprising, as other studies (Burney *et al.*, 1994; Burney & Burney, 2003) have shown that charcoal

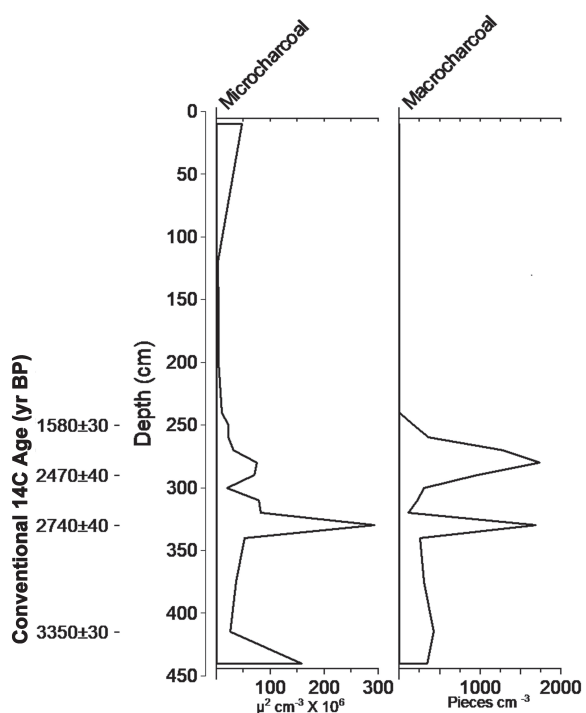


Figure 3. Diagram showing charcoal particle concentrations in TAO-1 profile. “Microcharcoal” values shown as $\mu\text{m}^2 \text{cm}^{-3} \times 10^6$. “Macrocharcoal” shown as pieces $>125 \mu\text{m} \text{cm}^{-3}$.

is more refractory than many other microfossils, and is often preserved in sediments with poor pollen preservation.

Pollen and spores

Thirty-four pollen types were identified to family or genus level. In addition, some levels contained unknown types, ranging from 0 to 13.4% per level. Pollen preservation was only suitable for analysis between 250–340 cm. All levels above and below this zone contained very few pollen grains, and these scarce palynomorphs showed signs of crumpling and oxidation typical of sediments that have at some point been subjected to drying and oxidative conditions unsuitable for preservation. Of identified terrestrial pollen and fern spores, 22 types occurred at 2% or more in at least one level (Figure 4). These were used for cluster analysis and pollen zonation. Constrained incremental sum-of-squares (CONISS; Grimm, 1987) showed moderately high to extreme difference between adjacent samples, probably reflecting vegetation change or variability at the centennial scale.

Pollen Zone 1 consists of two moderately dissimilar spectra, 330–340 cm, dominated by *Pentarrhopalopilina* (20.5% and 8.4%, Opiliaceae), Euphorbiaceae (36.4% and 7.6%), and Didiereaceae (8.0% and 4.6%). These are all indicators of presence of xeric spiny bush vegetation (Burney, 1993) typical today on the nearby dry forest parcel of the Bezà Mahafaly Special Reserve, such as *P. madagascariensis*, *Euphorbia stenoclada*, *E. tirucalli*, *Alluaudia humbertii*, and *A. procera*.

Zone 2, 290–320 cm, also contains xeric types, but shows a major increase in more mesic elements of the local flora, including Combretaceae (7.5%, 7.7%, 8.5%, 7.1%) and *Croton* (39.1%, 32.5%, 22.9%, 25.8%, Euphorbiaceae). The former is represented by *Combretum grandidieri* and four species of *Terminalia* in the Bezà Mahafaly parcels, both in riparian forest and dry woodland. Four species of the dry to mesic tree and shrub genus *Croton* occur locally today. The four pollen spectra in this zone show high similarity, suggesting a fairly stable dry-to-mesic vegetation over the centuries of the mid-first millennium BCE. This unit also shows an increase in *Medemia* (= *Bismarckia*, Arecaceae) a fire-adapted palm of dry woodlands and wooded savanna, *Salvadora* (Salvadoraceae), a dominant tree of the riparian forest of Bezà Mahafaly, and *Rhigozum* (Bignoniaceae), probably *R. madagascariensis*, a

dry-adapted shrub or small tree of wooded savanna and rocky areas.

Zone 3, 250–280 cm, comprises four highly dissimilar pollen spectra. Sub-zone 3A shows a stepwise return to a more arid signal comparable to Pollen Zone 1 at the base of the sequence. Sub-zone 3B is an outlier, a single pollen spectrum showing no strong similarity to the adjacent spectra. It contains the highest percent Didiereaceae pollen in the entire profile (11.8%), and also high values for *Acacia* (Fabaceae, 11.8%), Euphorbiaceae (29.4%), *Medemia*, (11.8%), cf. *Gymnosporia* (Celastraceae, 17.6%), and *Stereospermum* (Bignoniaceae, 5.9%). These types are dry adapted but also notably fire tolerant, persisting in arid to mesic areas subjected to frequent burning. This spectrum, the last well-preserved level for pollen and the most xeric pollen signal for more than a millennium at the site, dates to 1580 ± 30 yr BP (1524–1356 cal yr BP at 2σ , or 426–594 CE).

Coprophilous fungus spores

Sporormiella was the only coprophilous fungus spore type identified and tallied in this study. Like pollen, and unlike charcoal particles, it was only preserved in the organic segment of the profile from 250–340 cm. It is well-represented in every pollen spectrum except the two inferred to signal the driest conditions, 250 and 340 cm. Values in all other levels between ranged from 5.9 to 62.6% of the raw sum (total pollen and spores). Some of these are by an order of magnitude the highest values published from any site in Madagascar (cf. Burney *et al.*, 2003).

Discussion

Inferred paleoenvironments

This sediment profile and its microfossil contents can perhaps shed some light on the history of the site itself and on the previous evidence from paleontological surface surveys and excavations. After a dry period in southwestern Madagascar ending ca. 3500 yr BP (Faina *et al.*, 2021), it appears that slightly wetter conditions occurred, first scouring the basin and depositing quartz pebbles, then beginning to accumulate fine sand and humic debris in a seasonal marsh with grasses and sedges. By ca. 2700 yr BP (Pollen Zone 2, 290 to 320 cm) increasingly mesic conditions are indicated in the pollen evidence, with sufficient permanent water in the basin to accumulate sediment typical in this region for a shallow lake. On the surrounding uplands xeric spiny bush or thicket

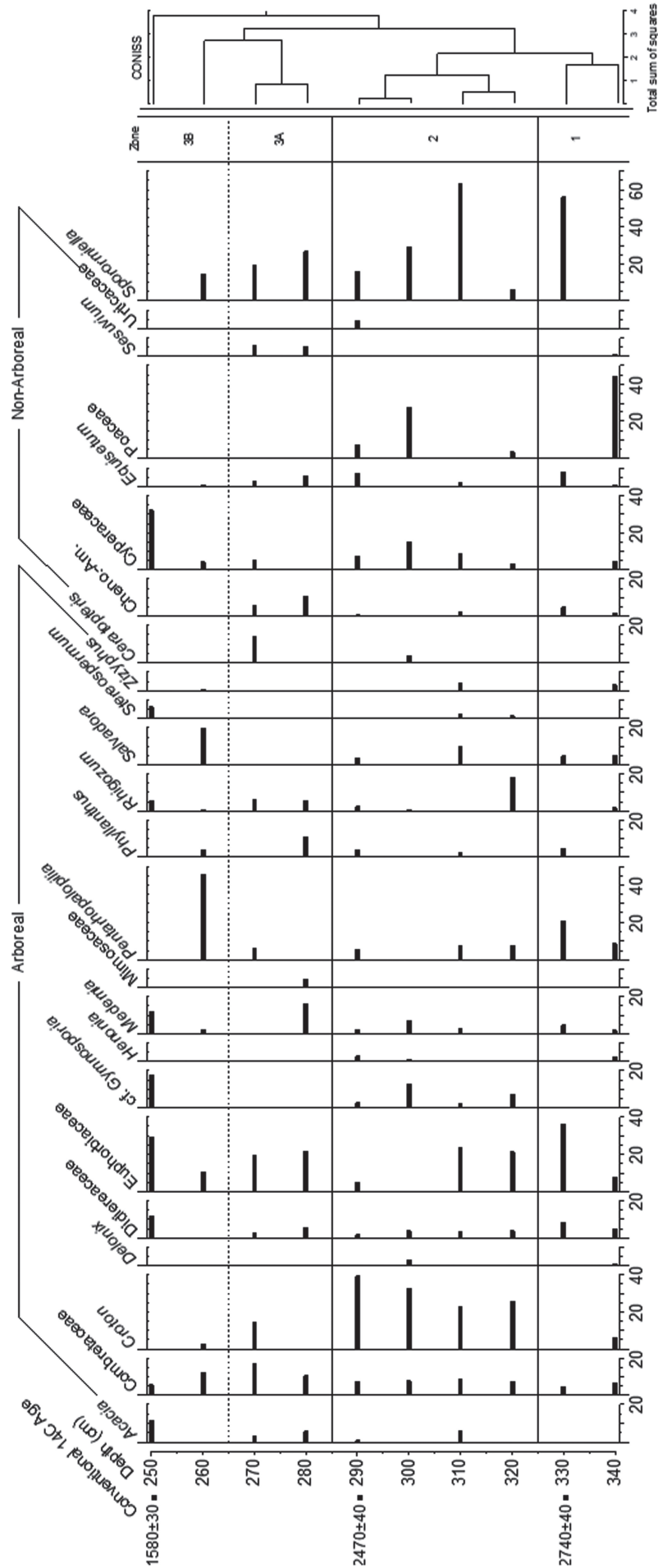


Figure 4. Diagram of percent pollen and spores for all types occurring at 2% or more for at least one level. Pollen preservation was suitable for analysis for the section from 250-340 cm below surface only. Constrained incremental sum-of-squares cluster analysis (CONISS) was performed on all terrestrial types shown, except aquatic and paludal types (Cyperaceae) and *Sporormiella* fungus.

largely gave way to more mesic, but still seasonally dry-adapted, trees. This water source must have been a magnet to the fauna, and the presence of crocodiles and hippos probably assured that the waters were a rich organic “soup” of animal bones, plant detritus, and large animal dung. During this entire wet period, fires increased on the site. Today, it is the gallery forest and riparian woodlands that are most vulnerable to fire, not the spiny bush. The latter typically have only scarce litter to support a fire; most plants are leafless succulents or evergreens with small leathery leaves; but dry woodlands with *Terminalia*, *Croton*, *Acacia*, and other dry-mesic trees in this area typically have a flammable understory of graminoids and forbs, making them quite vulnerable to fire and livestock grazing and generally scarce in this part of Madagascar today outside of protected areas (Ratsirarson *et al.*, 2001).

By ca. 1500 yr BP the climate was once again becoming arid, and dry-mesic woodlands had given way to xeric spiny bush and fire-adapted woody vegetation. The basin itself returned to seasonal marshland and eventually dried out almost completely and began to erode during extreme rainfall events. Studies of human-modified bones and latest occurrences of extinct megafauna from the site (Perez *et al.*, 2005; Anderson *et al.*, 2018) suggest that humans were at the site by the middle of the first millennium CE, or soon after, with disputed evidence for human activity a millennium earlier (Perez *et al.*, 2005). In either case, Taolambiby is a site that confirms a transformation of the system through aridification, notably accelerating around 1500 yr BP and perhaps not fully ameliorating until, according to the speleothem record at Asafora Cave (Faina *et al.*, 2021), the beginning of the second millennium CE.

Our sedimentary evidence, when compared to the published stratigraphic information from Raison and V  rin (1967) and Anderson *et al.* (2018), would indicate that their sequences may not penetrate as deeply as the TAO-1 profile. These investigators provide good details on the stratigraphic sequences of the last two millennia, we infer. The bone beds described by these investigators, and dated in the case of Anderson *et al.*, probably trace to the bone beds exposed by the central ravine. This deposit is probably the one from which other investigators (e.g., Walker, 1967) collected bones from an exposure. Both probably correspond to the humic layers described in TAO-1 between 90 and 240 cm below the surface. It is not clear where Methuen (reported in Godfrey *et al.*, 2001) and Lamberton (1933) found

their bones as only scant information is provided. At other sites, Lamberton dug large holes that were generally not backfilled, and piled the excavated sediments alongside, often without fine sifting (Burney, 1999). It is likely that the modern waterhole at the site, utilized for watering livestock, may in fact include Lamberton’s unfilled excavations, and may have contributed spoil to the top ca. 1 m of sediment in the TAO-1 profile. This would explain the turbated appearance of upper layers described in Figure 2. Alternatively, or in addition, these sediments may be the result of recent erosion of the land immediately uphill from the site, evidently the result of livestock trampling and subsequent erosion. Recent climate effects on the water table are also likely, as reflected in the drying cracks and root casts in upper layers. In August of 2004 the top of the water table was at 267 cm below surface in TAO-1, but the gleying evident in the overlying sand and cobbles at 200–240 cm would suggest the water table is higher seasonally, or has been higher in recent times. The abraded *Hippopotamus* bones that occur in the trench up to ca. 150 cm in the profile are not necessarily *in situ*, as they could have been redeposited during an erosion phase, or even be part of the unscreened spoil from past digging.

Regional climate change in the Late Holocene

The late Holocene climate trends inferred from the Taolambiby profile include: 1) a wet phase that initially created the basin at some time as yet undated; a dry period ending at ca. 3500 yr BP, with a return of mesic conditions before ca. 2700 yr BP; and 3) notably drier conditions beginning by ca. 1500 yr BP. These trends bear comparison to other sites in southwestern Madagascar. About 100 km to the northwest at Andolononby/Ambolisatra near Ifaty, Burney (1993) showed in a 5000-year record of pollen and charcoal particles evidence for a wetter climate prior to ca. 3000 yr BP, with increasing aridity until ca. 2000 yr BP. The record after this time contains microfossil evidence that suggests a human transformation of the environment, obscuring a climatic signal. In a pollen study from a core collected nearer to shore than the Burney (1993) site, and likely to contain a depositional hiatus, Virah-Sawmy *et al.* (2016) postulated a drying episode beginning at 1574 yr BP based on the decline in *Pandanus* (Pandanaaceae). Subsequent centuries showed declines in other dry to mesic species. At the endorheic Lake Ihotry, 120 km north of Andolononby on the west coast, Vallet-Coulomb *et al.* (2006) noted

paleolimnological evidence for open water conditions until ca. 2250 yr BP, followed by increasingly dry conditions culminating in saline water by ca. 1500 yr BP. Details from all these sites confirm the assessment from bird fossils in the southwest (Goodman & Rakotozafy, 1997; Rasolonjatovo *et al.*, 2021) that southwestern lakes and marshes likely became less suitable for waterbirds during the drying phase of the late Holocene.

The detailed high-resolution speleothem records that have been obtained from Anjohibe and other caves in northwestern Madagascar are not likely to be directly applicable for climate reconstructions much farther south on the island (Voarintsoa, 2021). Evidence suggests that, although the isotopic records show major climatic events in the late Holocene (Voarintsoa *et al.*, 2017; Wang *et al.*, 2019; Railsback *et al.*, 2020), they are generally not closely correlated or in some cases may even be anti-phased with southwestern Madagascar (Faina *et al.*, 2021; Voarintsoa, 2021). A study of stable isotopes in a speleothem from southwestern Madagascar bears close comparison to Taolambiby. Asafora Cave (Faina *et al.*, 2021) is a site ca. 120 km north of Toliara. Late Holocene correspondences with our climatic inferences from the present study are notable. The Asafora $\delta^{18}\text{O}$ record begins around 3500 yr BP under relatively wet conditions. Slow drying began around three millennia ago followed by a sharp decrease in rainfall between 1680–1550 yr BP, with drought conditions persisting until 880 yr BP. Evidence in the same stalagmite from $\delta^{13}\text{C}$ supports the conclusion, also shown in the Taolambiby pollen record, that surrounding vegetation at Asafora shifted ca. 1500 yr BP from predominantly dry-mesic C3 trees to CAM and C4 xeric plants.

Extirpation at Taolambiby

The evidence presented here, in combination with subsequent research at the site, (Anderson *et al.*, 2018) still cannot definitively confirm or refute any of the past and current hypotheses proposed for Madagascar's subfossil extinctions of the late Holocene. Aridity is shown from the pollen evidence to have caused major vegetation changes at ca. 1500 yr BP. The hydrological regime of this seepage site probably changed back to conditions similar to those inferred for the dry period prior to 2700 yr BP. There is an apparent coincidence of abundant evidence for human perimortem modification of bones of extant fauna at the site on or soon after the onset of climatic change ca. 1500 yr BP (Anderson *et al.*, 2018, but see

Perez *et al.*, 2005). By the time climate conditions in the southwest may have ameliorated around 880 yr BP (Faina *et al.*, 2021), megafauna has apparently disappeared from the site and dates on human-modified bones are all from extant species (Burney *et al.*, 2004; Perez *et al.*, 2005; Crowley, 2010; Anderson *et al.*, 2018). The most recent calibrated dates for extinct vertebrates at Taolambiby fall around 1100 cal yr BP (Table 2), when southwestern Madagascar was still very dry (Faina *et al.*, 2021).

These results are consistent with the expectations of the Aridity Hypothesis (Mahé & Sourdlat, 1972; Virah-Sawmy *et al.*, 2016), but also with combinatorial explanations for the extinctions, including the Synergy Hypothesis (Burney, 1999) and Subsistence Shift Hypothesis (Godfrey *et al.*, 2019). On a local scale, one can imagine a spring-fed source, such as the pond or marsh envisioned for Taolambiby two millennia ago, to have served as a “water magnet” for thirsty animals at a time when fresh surface water was scarce. The small local river (Sakamena) probably dried up, as indeed it is seasonally dry in its upper reaches today. Rainfed ponds and marshes probably salinized or disappeared altogether, and rainfall events were likely to have been infrequent. Such a place would have become a “predator pit” *sensu* Janzen (1983) whereby crocodiles, boas, euplerids, raptors, and *Homo sapiens* all could have contributed to the final decline of remaining megafauna in the vicinity of Taolambiby. Horton (1984) referred to this type of extinction dynamic as “waterhole tethering,” in describing the demise of the Australian megafauna. Under this scenario, climatic drying in effect teams up with human predation. Although not a compelling explanation for what happened everywhere in Madagascar, it is certainly plausible at Taolambiby.

Conclusion

Paleoeological evidence suggests that the ephemeral basin containing the rich subfossil deposits at Taolambiby has responded to climatic forcing in the late Holocene. After a dry period prior to ca. 3500 yr BP, wetter conditions developed, first scouring the basin and depositing quartz pebbles, then beginning to accumulate fine sand and humic debris in a seasonal marsh. By ca. 2700 yr BP increasingly mesic conditions are evident on the site, with sufficient permanent water in the basin to accumulate sediment typical in this region of a shallow lake, and with preservation of abundant bones and plant remains and high concentrations

of coprophilous fungus spores. On the surrounding uplands xeric spiny bush or thicket largely gave way to more mesic, but still seasonally dry-adapted, trees. During this wetter period, fires increased in the vicinity.

By ca. 1500 yr BP the climate was once again arid, so that dry-mesic woodlands gave way to xeric bush and fire-adapted woody vegetation. The basin itself returned to seasonal marshland and eventually dried out almost completely and began to erode. Human-modified bones confirm that people were at the site by the middle of the first millennium CE, and perhaps as much as a millennium before. Taolambiby shows evidence for a multiplicity of deleterious effects on the subfossil megafauna at the site, including several human impacts, probably exacerbated by increasing aridification.

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