Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: www.tandfonline.com/journals/ujvp20

New large species of *Cryptoprocta* (Carnivora, Eupleridae) and new specimens of *C. Spelea* from the Holocene of Tsimanampesotse National Park, southwest Madagascar

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To cite this article: Margaret E. Lewis, Zachary S. Klukkert, Nick Scroxton, Stephen J. Burns, Brooke E. Crowley, David McGee, Kathleen M. Muldoon, Matthew Borths, Lindsay R. Meador, Phillip Lehman , Patrick Widmann , Noromamy J. Rahantaharivao, Lovasoa Ranivoharimanana & Laurie R. Godfrey (24 Aug 2026): New large species of *Cryptoprocta* (Carnivora, Eupleridae) and new specimens of *C. Spelea* from the Holocene of Tsimanampesotse National Park, southwest Madagascar, Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2026.2698802

To link to this article: https://doi.org/10.1080/02724634.2026.2698802

Journal of Vertebrate Paleontology e2698802 (23 pages)
Published with license by the Society of Vertebrate Paleontology
DOI: 10.1080/02724634.2026.2698802

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ARTICLE

NEW LARGE SPECIES OF *CRYPTOPROCTA* (CARNIVORA, EUPLERIDAE) AND NEW SPECIMENS OF *C. SPELEA* FROM THE HOLOCENE OF TSIMANAMPESOTSE NATIONAL PARK, SOUTHWEST MADAGASCAR

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ABSTRACT—Among the extant endemic carnivorans of Madagascar (family Eupleridae), the largest species is the fosa, *Cryptoprocta ferox*. A larger species, *Cryptoprocta spelea*, survived into the Late Holocene. Here, we report the discovery of a morphologically distinct partial humerus from Mitoho in Tsimanampesotse National Park, southwestern Madagascar, belonging to a larger extinct form of *Cryptoprocta* that existed prior to 8.3 ka. We review the history of the genus, describe this new taxon, and briefly describe the flooded cave system where it was found. We reconstruct body size for *Cryptoprocta* subfossils from Mitoho and other sites and document geographic variation in *C. spelea* across Madagascar. While the Mitoho *C. spelea* specimens are larger than those found elsewhere, the newly described humerus is even larger and cannot be attributed to a male *C. spelea*. Functional analyses suggest all species of *Cryptoprocta*, irrespective of body size, had arboreal adaptations and that the new species had enhanced strength associated with climbing or prey capture. Subfossils of all three species were found on the same submerged ledge at Mitoho, raising the possibility of sympatry in southwestern Madagascar. Regional stable carbon isotope analyses indicate that *C. spelea* preyed upon larger lemurs than those typically targeted by extant *C. ferox*. Body size and morphology suggest the new species targeted even larger prey. Collectively, these findings suggest that the Holocene Malagasy carnivoran guild exploited substantially larger lemur prey than do living euplerids, consistent with carnivore damage documented on remains of some of Madagascar's largest extinct lemurs.

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SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Lewis, M. E., Klukkert, Z. S., Scroxton, N., Burns, S. J., Crowley, B. E., McGee, D., Muldoon, K. M., Borths, M., Meador, L. R., Lehman, P., Widmann, P., Rahantaharivao, N. J., Ranivoharimanana, L., & Godfrey, L. R. (2026) New large species of *Cryptoprocta* (Carnivora, Eupleridae) and new specimens of *C. spelea* from the Holocene of Tsimanampesotse National Park, southwest Madagascar. *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2026.2698802

Submitted: December 6, 2025
Revisions received: May 15, 2026
Accepted: June 5, 2026

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Published online 24 Aug 2026

INTRODUCTION

Madagascar is known for its diverse and intriguing endemic fauna. The carnivorans are no exception and include eight extant endemic species comprising the family Eupleridae (Veron et al., 2017), as well as introduced species, such as the small Indian civet (*Viverricula indica*) and feral dogs and cats (e.g., Farris et al., 2017; Hixon et al., 2021; Sauther et al., 2020; Veron et al., 2017). Euplerids arrived on Madagascar between 26 and 18 Ma and all derive from a single herpestid ancestor (Hassanin et al., 2021; Veron, 2010; Veron et al., 2004, 2022; Yoder & Flynn, 2003; Yoder et al., 2003; Zhou et al., 2017). Note that we will use 'carnivore' for any carnivorous vertebrate, while 'carnivoran' will be used for animals belonging to the mammalian order Carnivora. In addition, we will use the term 'Malagasy' as a word qualifier for the people and culture of Madagascar, as well as all living organisms and inanimate objects from Madagascar, as recommended by Voarintsoa et al. (2019) as opposed to the term 'Madagascan.'

While most extant euplerid species average less than a kilogram in mass, the largest extant Malagasy carnivoran, the fosa (*Cryptoprocta ferox*), ranges in body mass from 5–12 kg, with most individuals ranging from 5–10 kg (Hawkins, 1998; Köhncke & Leonhardt, 1986; Veron et al., 2018). At home both in the trees and on the ground, fosa are found across Madagascar and on the island of Saint-Marie off Madagascar's eastern coast (Köhncke & Leonhardt, 1986).

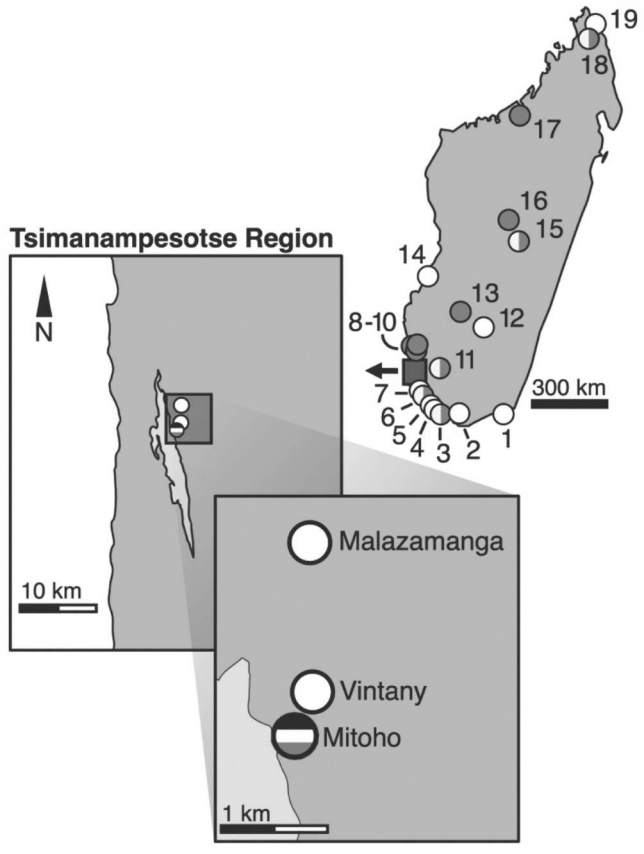

FIGURE 1. Location of Mitoho cave system within the Tsimanampesotse region of Madagascar and other locations where *Cryptoprocta* specimens used in this study were found. Gray for localities with *Cryptoprocta ferox*, white for *Cryptoprocta spelea*, and black for the new cryptoprocta species. **Site key**: **1**, Andrahomana; **2**, Anavoha; **3**, Beavoha; **4**, Bemafandry; **5**, Tsiandroina; **6**, Ankazoabo Grotte; **7**, Lelia; **8**, Manombo-Toliara; **9**, Andolonomby; **10**, Ankilitelo; **11**, Taolambiby; **12**, Christmas River; **13**, Tsirave; **14**, Belo-sur-Mer; **15**, Antsirabe; **16**, Ampasambazimba; **17**, Andranoboka; **18**, Ankarana; **19**, Lakaton'ny Akanga.

The first non-Malagasy mention of an even larger euplerid comes from Flacourt (1658), who recorded Malagasy accounts of an exceptionally powerful, giant fosa called the 'antamba' living in the mountainous regions of southeastern Madagascar near where Flacourt was stationed. In Malagasy oral histories, the antamba and fosa are distinct entities that interact with each other (e.g., Sibree, 1883). Flacourt accepted the antamba as extant, while later scientists did not (e.g., Jorgensen, 1884). The name 'antamba' appears again in the scientific literature when Jentink (1887) recorded extant lemur *Eulemur collaris* specimens from a southeastern locality called 'Antamba.' Malagasy villages are sometimes named for organisms that are (or were) common at that site (e.g., Marovoay, for 'many crocodiles' or Amparihingidro, for 'at the lemurs' lake').

Grandidier (1902) discovered the first subfossils of a possibly distinct form of *Cryptoprocta* from Andrahomana Cave in southeastern Madagascar near where Flacourt was once stationed. Grandidier called the form '*spelea*,' or cave fosa, and considered it to be a variety of the extant fosa, *C. ferox*. Subsequent finds of large *Cryptoprocta* subfossils convinced Petit (1935b) and Lamberton (1939) that the animal was its own species, *Cryptoprocta spelea*.

Lamberton (1939) erected a third species of *Cryptoprocta*, *Cryptoprocta antamba*, based on his discovery of damaged mandible with worn teeth from Tsiandroina in southwestern Madagascar. He knew that the Malagasy people spoke of multiple forms of *Cryptoprocta*: two named forms, the fosa and the antamba, and three color morphs, the red 'fosa mena,' the off-white 'fosa ondry,' and the black 'fosa mainty.' Although the type specimen is lost, Goodman et al. (2004) suggested this mandible was just an aberrant *C. spelea* based on Lamberton's (1939) photograph. Our review of this photograph reveals bone and enamel erosion of this mandible consistent with crocodile digestion rather than sedimentary transport. Passage through the crocodile digestive system causes erosion of teeth and cortical bone such that prey mandibles exhibit enamel loss and gaps between teeth (Meador et al., 2019, and references therein) and explains some of Lamberton's 'diagnostic' *C. antamba* traits. In short, despite Lamberton's (1939) claim for three species of *Cryptoprocta*, his monograph only describes two: *C. ferox* and *C. spelea*.

Since Lamberton's (1939) monograph, no researcher has supported the hypothesis that three species of *Cryptoprocta* existed and the presence of two has been debated. Köhncke and Leonhardt (1986) questioned the validity of *C. spelea* as a species on the grounds that differences from *C. ferox* could be explained by allometry. In contrast, Goodman et al. (2004) supported the hypothesis that there are two distinct species, with *C. spelea* being the larger, more robust form, and *C. ferox* the smaller, more gracile form. As the *C. spelea* type specimen is also lost, Goodman et al. (2004) designated a neotype for this species (MNHN 1977-755, a cranium from Ankazoabo Grotte, southwestern Madagascar). While Goodman et al. (2004) provided no specific characters distinguishing *C. spelea* from *C. ferox* other than size, Meador et al. (2019) demonstrated *C. spelea* differs from *C. ferox* in shape and proportions. For example, *C. spelea* has a significantly lower brachial index (i.e., the radius is shorter relative to the length of the humerus) and a significantly higher olecranon index (i.e., relatively greater leverage for the triceps surae muscle). Additional evidence that *C. ferox* and *C. spelea* are separate species comes from their size separation at single sites (Goodman et al., 2004; Hixon et al., 2021; Meador et al., 2019) that are obscured when individuals from different geographic areas or when subfossil and modern populations are combined.

With the discovery of more subfossils, *C. spelea* is now known to have had a geographic range from the northernmost (e.g.,

Ankarana) to the southernmost (e.g., Andrahomana, Beloha Anavoha) parts of the island (Fig. 1). Published radiocarbon dates for *C. spelea* range from 3284 ± 52 cal BP to 1756 ± 52 BP and they overlap with records of subfossil *C. ferox* (Crowley, 2010; Goodman & Jungers, 2014; Hixon et al., 2021; Meador et al., 2019; Michielsen et al., 2023). Researchers have turned to how these two predators partitioned their portions of the carnivore guild.

Today, *C. ferox* targets a wide range of prey, but prefers lemurs roughly 2 kg in body mass (e.g., ring-tailed lemurs, *Lemur catta*) or less, although species weighing up to 7 kg such as diademed sifakas (*Propithecus diadema*) are also consumed (Goodman & Ganzhorn, 2022). Within the Malagasy fossil record, canine punctures on subfossils of extant lemur taxa eaten by *C. ferox* today are consistent with the maxillary bi-canine breadth of *C. ferox* (Muldoon et al., 2017) suggesting that *C. ferox* diet has not changed.

Something larger than the extant fosa consumed giant lemurs in the past, as extinct, arboreal, large-bodied lemur species (30–85 kg; Jungers et al., 2008; Thompson et al, 2025) also show traces of carnivoran predation (Meador et al., 2019). Goodman and Jungers (2014) suggested *C. spelea* may have consumed prey that was larger, but more terrestrial, than that regularly targeted by *C. ferox*. They reconstructed the body size of *C. spelea* as being 10–15 kg, which made arboreal hunting difficult. In contrast, Meador et al. (2019) found numerous anatomical features of *C. spelea* consistent with a level of arboreality similar to *C. ferox*.

This paper provides the first anatomical evidence that a third arboreal species of *Cryptoprocta* did exist in Madagascar, one that was morphologically distinct from and larger than *C. spelea*. This new evidence is part of many new fossil discoveries from caves at Tsimanampesotse National Park (TNP; Godfrey et al., 2021).

This paper has five key objectives. First, we formally describe a new species of *Cryptoprocta*, describe associated *C. spelea* remains, and establish the chronological context for these findings. Second, we estimate the body masses of these extinct taxa. Third, we analyze geographic and morphological variation in *Cryptoprocta* humeri to reconstruct locomotor behavior, test for specific interspecific differences, and evaluate if the new humerus could be a male *C. spelea*. Fourth, we utilize stable carbon isotope ($\delta^{13}C$) analysis of subfossil teeth and bones of *Cryptoprocta* and potential prey species to evaluate dietary differentiation between *C. spelea* and the smaller *C. ferox*, predicting that *C. ferox* should resemble extant lemurs isotopically, while *C. spelea* should resemble the larger-bodied extinct lemurs. Finally, we synthesize these findings to examine the ecological niche partitioning of the Malagasy carnivore paleoguild.

GEOLOGICAL SETTING

All *Cryptoprocta* subfossil specimens described herein come from a site named Mitoho at TNP in southwestern Madagascar. The associated cave system is a flooded cave and fresh water spring located within the TNP. The cave sits 8 km from the Mozambique Channel (Fig. 1), with two entrances approximately 46 m above sea level (Fig. 2). These once-dry passages are now submerged by upwelling of fresh water from the local water table, which fluctuated with Quaternary sea level changes associated with glacial and interglacial cycles.

Local people use distinct names for the cave system's two entrances, which connect via a 396 m water-filled passage (Fig. 2). While the name 'Mitoho' refers to the overall locality (e.g., Godfrey et al., 2021; MacPhee, 1986), local people use it to refer to what we here call the 'Main' entrance (24°02'51.85"S, 43°45'11.74"E) for clarity. Fossils were recovered previously from dry deposits at this 'Main' entrance (MacPhee, 1986). In 2001, a team led by Karen Samonds (Godfrey et al., 2021) discovered fossils at the second entrance named 'Andranohilova' (24°02'45.06"S, 43°45'14.22"E), an entrance used primarily by bats today.

Most *Cryptoprocta* subfossils in the current study were found submerged on rock ledges within a narrow, somewhat vertical passageway or 'chimney,' located near the Andranohilova entrance (Fig. 2). A few were found just below the open-air pool near the Main entrance (Godfrey et al., 2021). Because subfossils found within the chimney were submerged in water for an extended period, they lacked collagen. Understanding their geological context is thus critical for inferring their age.

Bones retrieved from the chimney likely first accumulated closer to Andranohilova, where storm water periodically swept them onto the silt, debris, and guano mound below that entrance and then down over the rocks and ledges within the chimney. Today the chimney entrance is submerged (Fig. 2) 14 m below the modern water table surface and no longer acts as a natural funnel. A spring in the deep section of the cave forces water to ascend through the chimney, transporting disturbed silt from the *Cryptoprocta* fossil site upward and out of the chimney. Thus, once the passage was filled with water, the direction of the flow would have prevented the descent of falling debris through the chimney.

To estimate the minimum age of fossils in the chimney, we must know when floodwater first reached the chimney entrance. The history of the hydroclimate and cave flooding at Mitoho and related data has been published elsewhere (Godfrey et al., 2021; Scroxton et al., 2019) and will be summarized briefly here. During the Last Glacial Maximum (~21 Ka), global sea levels and the water table at TNP were significantly lower than today. Global records of postglacial sea level rise, beginning at ~20 Ka, suggest that sea level reached within 15 m of present-day levels by 8.2 Ka and 10 m no later than ~7.3 Ka (Camoin et al., 2004; Kopp et al., 2015; Lambeck et al., 2014; Stanford et al., 2011). This timing implies an age for the *Cryptoprocta* fossils in the chimney of greater than 7000 years, and possibly considerably more. However, local sea-level changes can be disconnected from global change via tectonic or isostatic effects, while the semi-freshwater lens that caps the saline groundwater incursion can vary in thickness with climate.

Since stalagmites do not grow when submerged, their growth phases indicate sub-aerial conditions, and therefore the top surface represents the earliest point at which the water table in the karst system reached the stalagmite growth surface. Analyses of stalagmite growth phases in TNP located below and at the same depth as the chimney entrance indicate that this system was likely still subaerial at 8.3 Ka or afterward (Godfrey et al., 2021; Scroxton et al., 2019). The date is broadly consistent with global sea level estimates and supports the hypothesis that local effects on sea-level and freshwater lens thickness were relatively small. As it is likely that fossils were washed into the chimney before that date, we infer that the cache of *Cryptoprocta* fossils found in the vertical passage at −22 m are certainly older than 7 Ka (based on global sea level) and probably older than 8.3 Ka (based on local stalagmite growth phases).

MATERIALS AND METHODS

Materials

This paper focuses on eight *Cryptoprocta* humeri (all adult) from Mitoho cave in southwestern Madagascar, including an enigmatic, exceptionally large (but fragmentary) individual that warrants separate species attribution. Two of these specimens, UABEC 0039 and UABEC 0014, were microCT-scanned at the Duke University Shared Materials Instrumentation Facility using a Nikon XTH 225 ST scanner. These scans are available at MorphoSource.org, as described at the end of this article.

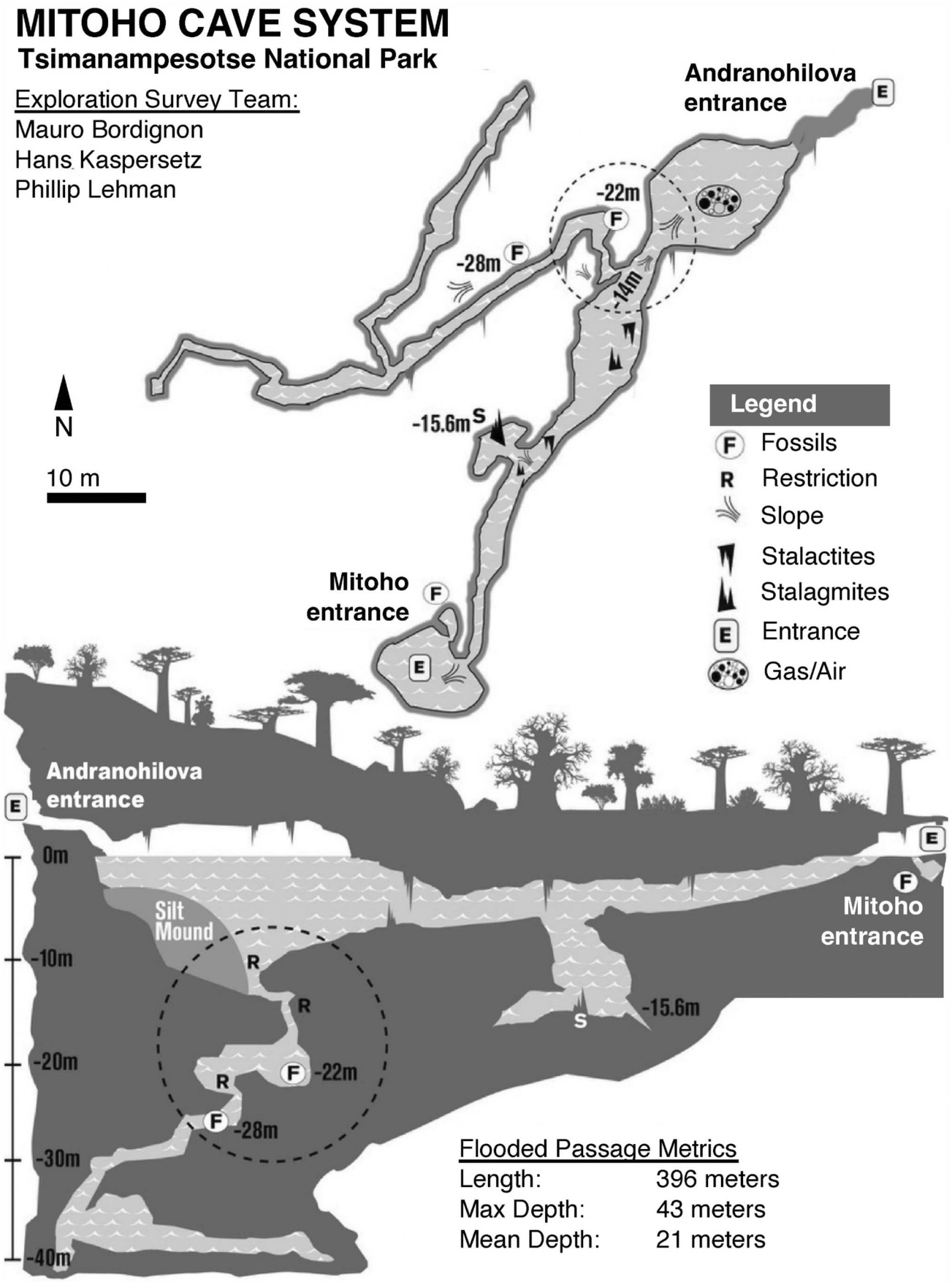

FIGURE 2. Map of Mitoho cave system showing aerial and cross-sectional views. *Cryptoprocta* fossils have been found at locations (marked F) below the Main and Andranohilova entrances. Below Andranohilova is a mound of silt, debris, and bat guano. Below this, a nearly vertical 'chimney' leads to a deep section of the cave; bone accumulation within the chimney is suggestive of regular inward-washing of debris from higher segments of the cave.

To explore taxonomic distinctions, reconstruct body size, intraspecific geographic variation, and locomotor function we compared our eight new *Cryptoprocta* humeri to 11 *C. spelea* and nine *C. ferox* humeri from other subfossil sites (Anavoha, Ankazoabo Grotte, Beavoha, and Belo-sur-Mer for *C. spelea*; Ankarana, Antsirabe, Beavoha, Belo-sur-Mer, and Tsirave for *C. ferox*) as well as 11 humeri belonging to modern *C. ferox* (Table 1).

We also compared these specimens to fully adult specimens of other extant carnivoran species (Table 2). Size classes in this paper follow those formulated by Lewis and Werdelin (2007) based on body mass, behavior, and ecology of extant members of the order Carnivora. Size classes are based on shifts in dietary and prey procurement abilities, among other features. Size Class 1 (<10 kg) includes all euplerids except *Cryptoprocta*. While Size Class 2 carnivorans (10–21.5 kg) tend to include mesopredators in other areas of the world (Lewis & Werdelin, 2007), in Madagascar the largest known carnivorans prior to this study fall into this group. Lewis and Werdelin (2007) based the cutoff between Size Class 2 and Size Class 3 on the discovery by Carbone et al. (1999) that only predators larger than 21.5 kg tended to capture prey near their own mass.

Specimens of extant and extinct *Cryptoprocta* are housed primarily in the UA with one extant specimen coming from the AMNH. Specimens of other carnivoran species are housed at the AMNH, BMNH, FMNH, KNM, NMNH, and NRM. All common names for Malagasy carnivorans follow Duckworth et al. (2014), including 'fosa' rather than 'fossa' for *C. ferox* for reasons stated therein. No live animals were studied. Table 3 lists vertebrate taxa reported at Mitoho by us and by prior researchers; it is not intended as a comprehensive subfossil species list for all caves within TNP.

TABLE 1. List of humeral specimens of *Cryptoprocta* used in this analysis. Geographic location is listed when known. Depth within the cave is reported for Mitoho specimens.

Specimen #	Location (depth)	Taxon	Status
AM280	–	*C. ferox*	modern
AM940	–	*C. ferox*	modern
AM942	–	*C. ferox*	modern
AM943	–	*C. ferox*	modern
AM944	–	*C. ferox*	modern
AM945	–	*C. ferox*	modern
AM946	–	*C. ferox*	modern
AM961	–	*C. ferox*	modern
AM963	–	*C. ferox*	modern
AM965	–	*C. ferox*	modern
AMNH 199544	Ampanihy, Toliara	*C. ferox*	modern
UA10521	Beavoha	*C. ferox*	subfossil
UA10522	Beavoha	*C. ferox*	subfossil
UA10569	Belo-sur-Mer	*C. ferox*	subfossil
UA10570	Tsirave	*C. ferox*	subfossil
UA10582	Antsirabe	*C. ferox*	subfossil
UA10586	Antsirabe	*C. ferox*	subfossil
UA10587	Antsirabe	*C. ferox*	subfossil
UA6127	Ankarana	*C. ferox*	subfossil
UA6128	Ankarana	*C. ferox*	subfossil
UA6129	Ankarana	*C. ferox*	subfossil
UA8443	Ankarana	*C. ferox*	subfossil
UA10477	Anavoha	*C. spelea*	subfossil
UA10478	Anavoha	*C. spelea*	subfossil
UA10479	Anavoha	*C. spelea*	subfossil
UA10480	Anavoha	*C. spelea*	subfossil
UA10481	Anavoha	*C. spelea*	subfossil
UA10496	Anavoha	*C. spelea*	subfossil
UA10497	Anavoha	*C. spelea*	subfossil
UA10526	Beavoha	*C. spelea*	subfossil
UA10528	Beavoha	*C. spelea*	subfossil
UA10563	Ankazoabo Grotte	*C. spelea*	subfossil
UA10567	Belo-sur-Mer	*C. spelea*	subfossil
UABEC 0014	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0015	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0016	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0036	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0037	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0038	Mitoho (66 ft.)	*C. spelea*	subfossil
UABEC 0039	Mitoho (66 ft.)	*Cryptoprocta*, n. sp.	subfossil
UABEC 0881b	Mitoho (92–94 ft.)	*C. spelea*	subfossil

Specimen Collection from Mitoho

We conducted five expeditions to caves at TNP and a nearby lacustrine site (Antsirafaly/Soalara), including two exploratory trips (2014 and 2015), and three longer expeditions (May–June 2016, 2018, and 2019). While prior researchers collected subfossils in dry deposits at the entrances to the caves (Godfrey et al., 2021; MacPhee, 1986; Perrier de la Bâthie, 1934; Petit, 1935a), our expeditions were the first to collect submerged fossils in three flooded caves: Vintany, Mitoho, and Malazamanga (Godfrey et al., 2021). All specimens are housed in the Mention Bassin sédimentaire, Evolution, Conservation in the Université d'Antananarivo (UABEC).

Specimens from Mitoho were collected from rocky horizontal crevices within a deep, water-filled chimney, located below a wide chamber bordering a dry entrance (Andranohilova). Only the top of this chamber is not submerged. Silt, debris, and bat guano cover much of the dry and flooded floors of this chamber and Andranohilova (Fig. 2). The chimney entrance is located 14 m below the pool's surface. Fossil collection is difficult as divers must enter the chimney with tanks positioned on either side of their bodies, using corkscrew maneuvers to get diving equipment through the restrictions (marked R on Fig. 2) in the chimney. At 22 m below today's water table, there is a larger, approximately 1 m square cavity in the wall (labeled 'F' for 'fossils' in Fig. 2). Almost all of the *Cryptoprocta* subfossils in the chimney, including the new species, were found at this depth.

Data Analysis

Measurements—Eleven linear measurements were made on the humeri of 31 extant carnivoran taxa (206 individuals). Of these measurements, only six (Fig. 3) could be taken on the large but fragmentary fossil specimen (UABEC 0039) herein described as a new species. The remaining five measurements were humeral maximum length (MXL), functional length (articular surface to articular surface; FNL), mediolateral midshaft width (MMLW), anteroposterior midshaft width (MAPW), and midshaft circumference (MCIRC). All measurements were taken with 500-172-20 Mitutoyo digital calipers accurate to 0.02 mm and are included in Supplementary File 1.

Humeral midshaft circumference was reconstructed for the large, incomplete specimen (UABEC 0039), by extending the broken medial portion of the shaft proximally using the lateral portion of the shaft as a guide and extending a few millimeters beyond with modeling clay. As the humerus narrows distally from the midshaft in other species of *Cryptoprocta* and our reconstruction was likely slightly distal to true midshaft, this estimate may underestimate the true midshaft width. This estimate was only used for body mass reconstructions involving midshaft measurements (i.e., not all body mass reconstructions) and not for shape analyses or behavioral reconstructions. Body mass reconstructions based on midshaft circumference, therefore, may underestimate true body mass.

Body Mass Reconstruction—As the large fossil specimen (UABEC 0039) is an incomplete humerus, our options for reconstructing body mass were limited. As a result, body mass reconstructions were derived from equations published by Anyonge (1993), Heinrich (1995), and Heinrich and Houde (2006), all of whom employed humeral measurements to reconstruct body

TABLE 2. Number of individuals by taxon measured for this study with body mass, size class, and assigned locomotor category for multivariate analyses. Body mass and behavioral data from Albignac (1972, 1974, 1976), Anderson et al. (1985), Köhncke and Leonhardt (1986), Poglayen-Neuwall and Toweill (1988), Kingdon (1997), Hawkins (1998), Nowak (2005), Lewis and Werdelin (2007), Jones et al. (2009), Prange and Prange (2009), Lührs et al. (2013), Nakashima et al. (2013), Veron et al. (2018), and Meador et al. (2019). Size classes following Lewis and Werdelin (2007). Behavioral categories follow Tarquini et al. (2017). Body mass for subfossil/extinct forms are from Goodman and Jungers (2014) and not the results of this study. **Abbreviations**: **Sc**, scansorial; **TCl**, terrestrial-climbing; **TCu**, terrestrial-cursorial; **TG**, terrestrial-generalist; **TrD**, tree-dwelling.

Taxon	Common name	N	Body mass (kg)	Size class	Mode
Eupleridae:					
Cryptoprocta ferox	Fosa	11	5–12	2	Sc
C. ferox (subfossil)	Fosa	9	5–12?	2	?
C. spelea	Extinct fosa	17	10–15?	2	?
Eupleres goudotii	Eastern falanouc	1	2–4	1	TG
Fossa fossana	Fanaloka	3	?–2	1	TG
Galidictis fasciata	Broad-striped vontsira	1	0.5–0.8	1	TG
Salanoia concolor	Brown-tailed vontsira	2	~0.7	1	Sc
Felidae:					
Acinonyx jubatus	Cheetah	13	35–72	3	TCu
Caracal caracal	Caracal	2	6–19	2	TG
Felis nigripes	Black-footed cat	2	1.5–2.75	1	TG
Neofelis nebulosa	Clouded leopard	2	16–23	3	Sc
Oncifelis geoffroyi	Geoffroy's cat	7	2–6	1	TCl
Panthera leo	Lion	22	120–250	4	TCl
Panthera onca	Jaguar	11	36–158	4	TCl
Panthera pardus	Leopard	19	28–90	3	TCl
Panthera uncia	Snow leopard	1	25–75	3	TCl
Herpestidae:					
Ichneumia albicauda	White-tailed mongoose	1	1.8–5.2	1	TG
Hyaenidae:					
Crocuta crocuta	Spotted hyena	9	40–90	3	TCu
Hyaena hyaena	Striped hyena	5	25–55	3	TCu
Parahyaena brunnea	Brown hyena	5	37–47.5	3	TCu
Proteles cristatus	Aardwolf	2	9–14	2	TCu
Mustelidae:					
Eira barbara	Tayra	5	4–5	1	Sc
Gulo gulo	Wolverine	3	7–32	3	TCl
Mellivora capensis	Honey badger	3	7–16	2	TCl
Nandiniidae:					
Nandinia binotata	African palm civet	7	1.7–4.7	1	TrD
Procyonidae:					
Bassaricyon medius	Western lowland olingo	2	~1	1	TrD
Bassariscus astutus	Ringtail	6	0.87–1.1	1	Sc
Potos flavus	Kinkajou	14	1.4–4.6	1	TrD
Procyon lotor	Raccoon	5	2–12	1	TCl
Viverridae:					
Arctictis binturong	Binturong	3	9–14	2	TrD
Arctogalidia trivirgata	Small-toothed palm civet	1	2–2.5	1	TrD
Paguma larvata	Masked palm civet	4	3.6–5.0	1	Sc
Paradoxurus hermaphroditus	Asian palm civet	8	1.7–2.5	1	Sc

mass in carnivorous mammals. In general, these studies found that features of the humeral shaft and/or articular surface were far superior to humeral length in estimating body mass. Humeral length is affected greatly by locomotor needs (e.g., cursorial species usually have elongated limbs to lengthen stride length), while the dimensions of the shaft and articular surface reflect the need to withstand body mass loading in addition to forces engendered via positional/locomotor behavior. Nevertheless, we included equations based on humeral length for individuals with complete humeri, as well as other humeral dimensions, for comparison. We used linear measurements in our study as cross-sectional data, although more useful (e.g., Anyonge, 1993; Egi, 2001; Heinrich, 1995), were not available for the fossils or euplerid comparative material.

Although none of the above studies included euplerids, Heinrich (1995) and Heinrich and Houde (2006) used species that are most comparable to *Cryptoprocta* based on both locomotor categories and relatively small body size. Anyonge's (1993) work is less applicable as it focuses on Size Class 3 and 4 carnivorans, but includes some commonly used regression equations.

In addition to reconstructing body mass for all of the *C. spelea* from Mitoho, we reconstructed body mass for subfossil *C. ferox* and *C. spelea* from other sites, as well as for modern *C. ferox*. Reconstructed body masses of extant *C. ferox* provided a means of determining how accurate a particular equation was likely to be for the extinct specimens. Although there is regional, environmental, and social variation in body mass in *C. ferox*, we used the known aggregate range of 5–12 kg to determine the appropriateness of a particular method for reconstructing body mass in this genus. (Note that none of our extant specimens had recorded body mass data.) Published reconstructed body masses for specimens of *C. spelea* allowed us to assess how closely our reconstructions replicate previous work.

Morphometric Variation—Bivariate plots and linear regressions (Reduced Major Axis) were employed to test differences between the Mitoho material and extant and previously published subfossil specimens of *Cryptoprocta*. To determine whether measurements taken on the distal humerus could be used to discriminate between locomotor and substrate categories and then to assign such categories to extinct species of *Cryptoprocta*, extant taxa were assigned to the locomotor and substrate

TABLE 3. Terrestrial vertebrate remains found underwater or at entrances in the Mitoho cave system. There are additional miscellaneous bones of Microchiroptera, fish, snakes, and other reptiles not listed here. Data from this paper and Godfrey et al. (2021), MacPhee (1986), Perrier de la Bâthie (1934), Petit (1935a), Rosenberger et al. (2015). See Godfrey et al. (2021), for additional information. **Abbreviations**: **Andra**, Andranohilova; **DE**, dry entrance; **CR**, critically endangered; **EN**, endangered; **EX**, extinct; **IN**, introduced; **UW**, underwater; **VU**, vulnerable.

Taxon	Status	Location found
Carnivora:		
Cryptoprocta sp. nov.	EX	Mitoho UW
C. ferox	VU	Mitoho UW
C. spelea	EX	Mitoho UW
Felis catus	IN	Andra DE
Primates:		
Lemur catta	EN	Main DE
Megaladapis edwardsi	EX	Main DE
Pachylemur insignis	EX	Vintany UW
Propithecus verreauxi	EN	Main DE
Rodentia:		
Hypogeomys antimena	EN	Main DE
Chiroptera		
Macronycteris sp.	EN	Mitoho UW
Artiodactyla:		
Bos taurus	IN	Main and Andra DEs
Potamochoerus larvatus	IN	Main DE
Crocodilia:		
Voay robustus	EX	Main DE
Testudines:		
Astrochelys radiata	CR	Main DE
Aldabrachelys sp.	EX	Main DE
Aepyornithiformes:		
Mullerornis modestus	EX	Main DE
Aepyornithid eggshell	EX	Main DE

categories of Tarquini et al. (2017) using behavioral data drawn from published literature (Table 2). Principal components analyses (PCA) and discriminant function analyses (DFA) were then performed on raw, logged, and shape-transformed measurements (i.e., measurements divided by the geometric mean). These shape-transformed measurements will be referred to as 'shape data.' Missing values were estimated via iterative imputation during PCA (Ilin & Raiko, 2010). DFA and PCA analyses of logged data, both without shape-transformation, were also used to test for geographic structure in *C. spelea* (i.e., to test whether specimens from different subfossil localities could be distinguished from one another).

Sexual Size Dimorphism—Euplerids are reported to have relatively low levels of sexual size dimorphism (SSD), and *Cryptoprocta* is no exception (Law, 2019). To test the hypothesis that UABEC 0039 is a male *C. spelea* we compared the geometric means of UABEC 0039 to those of all *C. spelea* included in this study. The geometric mean indicates the overall size of the specimen. If the UABEC 0039 geometric mean falls within the range of *C. spelea*, then the hypothesis cannot be rejected.

Dietary Preference and Niche Partitioning—We used $\delta^{13}C$ values to test the degree to which *C. spelea* and *C. ferox* may have overlapped in their preferred prey. Carbon isotopes in tooth and bone can distinguish herbivores that consumed primarily or exclusively C_3 plants (lower, more negative values) from those that consumed CAM succulents or C_4 plants such as grasses (higher, less negative values). Smaller-bodied extant lemurs favored by extant *C. ferox* have higher $\delta^{13}C$ values than the larger-bodied extinct lemurs, who tended to rely more on C_3 foods than extant species (Crowley et al., 2011).

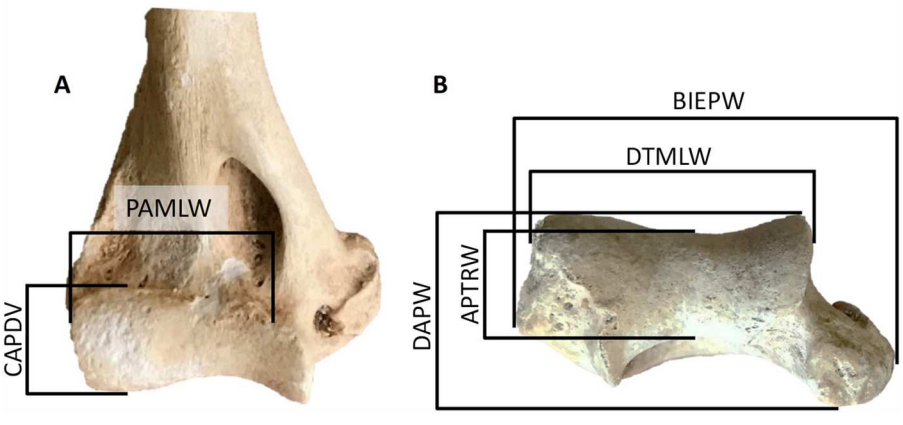

FIGURE 3. Distal right humerus of *Cryptoprocta ferox* (AMNH 199544) showing the measurements of the distal humerus taken on the new cryptoprocta species (UABEC 0039). **A**, anterior view; **B**, distal view with the anterior surface positioned superiorly. These measurements comprise the Distal Dataset (DDS) used in most multivariate analyses. **Abbreviations**: **APTRW**, minimum anteroposterior trochlear width; **BIEPW**, biepicondylar width; **CAPDV**, maximum dorsoventral height of capitulum; **DAPW**, maximum anteroposterior width of distal humerus; **DTMLW**, distal mediolateral trochlear width; **PAMLW**, proximal mediolateral width of anterior articular surface. Measurement abbreviations are for Supplementary File 1.

We compiled published collagen $\delta^{13}C$ values for subfossil *C. spelea,* extant *Lemur catta*, and *Microcebus griseorufus*, and larger-bodied extinct *Archaeolemur majori*, *Megaladapis edwardsi*, and *Megaladapis madagascariensis* from the coastal portion of the spiny thicket ecoregion, where the three species of *Cryptoprocta* have been found. We chose to focus on these particular six lemur taxa because they are known to have occurred at TNP caves or at nearby open-air sites (Godfrey et al., 2021). Modern *C. ferox* is known to prey on *Microcebus* species and *L. catta* (Goodman & Ganzhorn, 2022), and both of these species are common at TNP today. *Pachylemur insignis* is the most common lemur and *C. spelea* the most common euplerid recovered from flooded caves at TNP. If *C. spelea* targeted large arboreal lemurs, *Pachylemur* likely would have been primary among them. We excluded lemur species for which isotopic data are lacking in the coastal southwest (e.g., extant *Propithecus verreauxi*) or sample sizes are very small (e.g., extinct species *Mesopropithecus globiceps*, *Daubentonia robusta*, and *Hadropithecus stenognathus*).

We augmented published collagen $\delta^{13}C$ values with new collagen data from three subfossil *C. ferox*, two *L. catta,* and 10 *Microcebus griseofurus* from TNP, Andrahomana, and Ankazoabo Grotte, as well as enamel from two *C. spelea* and eight *Pa. insignis* from TNP. A breakdown of the total sample is provided in Table 4 and details for all individuals are provided in Supplementary File 3). We were unable to collect stable isotope data from the new cryptoprocta species.

We included data from tooth enamel in our comparisons because the sample size for subfossil *Cryptoprocta* collagen is very small. Collagen and enamel $\delta^{13}C$ values differ by 4–10‰ due to differences in how these tissues incorporate dietary macronutrients, as well as digestive physiology, and are therefore not directly comparable (reviewed in Hedges, 2003). Nevertheless, the enamel data are informative as they triple the sample size for *C. spelea* and help clarify the degree to which this species plausibly relied on *Pa. insignis* in the coastal southwest. Because all enamel came from specimens that were recovered from TNP, we can directly compare *C. spelea* and a potential prey species from the same site.

Samples were processed following standard methods for collagen and enamel (Cooke & Crowley, 2018; Crowley et al., 2012, 2017). Collagen was analyzed at the University of California, Santa Cruz (UCSC), or the University of Cincinnati (UC). At UCSC, ca. 0.7 mg of isolated collagen were analyzed on a Finnigan Thermo Electron DeltaXP continuous flow system connected to a Carlo Erba Elemental Analyzer. Data were calibrated to account for size and drift using homogenized gelatin (PUGEL), and analytical precision and accuracy were monitored using International Atomic Energy Agency (IAEA) acetanilide. Based on long-term lab performance, precision (± 1 SD) is estimated to have been <0.2‰.

At UC, ca. 0.4 mg of isolated collagen were analyzed on a Costech elemental analyzer connected to a Thermo Scientific Delta V IRMS via a Costech Conflo IV interface. Data were corrected for linearity, drift and scale following Skrzypek (2013). We used powdered caffeine to correct for linearity and drift, and scale using caffeine and U.S. Geological Survey (USGS) 41. Analytical accuracy was evaluated using two independent references: PUGEL and glycine, which were interspersed throughout each run. Precision was monitored using all four reference materials. Based on long-term performance in the lab, accuracy and precision are estimated to have been ca. 0.3‰ for carbon.

Enamel was analyzed at the Light Stable Isotope Mass Spec Lab in the Department of Geological Sciences at the University of Florida. Samples were dissolved in five drops of 100%

TABLE 4. Summary details for subfossil samples analyzed for stable carbon isotopes. For each species, the localities and types of samples are indicated along with the total number of samples. New data in this paper include bone collagen from three *Cryptoprocta ferox*, two *Lemur catta*, 10 *Microcebus griseorufus*, and all enamel samples. Published data compiled from Burney et al. (2004), Crowley et al. (2012), Crowley and Godfrey (2013), Anderson et al. (2018), Faina et al. (2021), Godfrey et al. (2021), Hixon et al. (2021), and Crowley et al. (2023). † = extinct.

Taxon	Anavoha	Andolomomby	Andrahomana	Ankazoabo Grotte	Antsirafaly/ Soalara	Manombo-Toliara	Tsimanampesotse	Bone collagen	Tooth enamel	Total N
Cryptoprocta ferox		x						3	0	3
†*C. spelea*				x				1	2	3
Lemur catta			x			x	x	17	0	17
Microcebus griseorufus			x				x	24	0	24
†*Archaeolemur majori*	x	x				x		18	0	18
†*Pachylemur insignis*			x			x	x	8	8	16
†*Megaladapis edwardsi*	x		x		x	x		17	0	17
†*M. madagascariensis*	x				x	x		8	0	8
Total								96	10	106

phosphoric acid at 70 C for 5 minutes in a Thermo Scientific Kiel III carbonate device, and the evolved CO_2 was analyzed on a Finnigan-MAT 252 isotope ratio mass spectrometer. Precision, based on 9 NBS-19 replicates, was 0.070‰.

All isotope data are reported relative to international standard Vienna Pee Dee Belemnite (VPDB). Most of the subfossil lemurs and all of the subfossil euplerids in our sample pre-date the Industrial Revolution (Crowley, 2010; Faina et al., 2021; Godfrey et al., 2021). We therefore corrected $\delta^{13}C$ values for all specimens for the Suess Effect (changes in atmospheric CO_2 following the Industrial Revolution) by subtracting 1.2‰ (see Crowley et al., 2012). There may also be small (on the order of 1–1.5‰) differences in $\delta^{13}C$ values between herbivores and the faunivores that consume them. However, we did not attempt to correct for this trophic level effect as it may vary among species and could be as small as 0‰ (see Clementz et al., 2009).

We used t-tests to compare collagen $\delta^{13}C$ values for subfossil *C. ferox* and *C. spelea* with each of the extant and extinct lemur species, and enamel $\delta^{13}C$ values for *C. spelea* and *Pa. insignis* from TNP. We also compared $\delta^{13}C$ values for *C. ferox* and *C. spelea* independently to a pooled sample of extinct lemurs and a pooled sample of extant lemurs, to test the importance of body size in prey selection for species of *Cryptoprocta*.

Software—All analyses were carried out using Past 4.03 (Hammer et al., 2001), Microsoft Excel 365 or earlier versions, or SPSS versions 28 or 29.

Institutional Abbreviations—**AM**, Académie Malgache, Université d'Antananarivo, Antananarivo, Madagascar; **AMNH**, Department of Mammalogy, American Museum of Natural History, New York City, U.S.A.; **BMNH**, Zoology Collection, Natural History Museum, London, U.K.; **FMNH**, Mammals Collection, Field Museum of Natural History, Chicago, IL, U.S.A.; **KNM**, Department of Osteology, Kenya National Museums, Nairobi, Kenya; **NMNH**, Division of Mammals, United States National Museum of Natural History, Washington, DC, U.S.A.; **NRM**, Vertebrate Zoology Collection, Swedish Museum of Natural History, Stockholm, Sweden; **TNP**, Tsimanampesotse National Parks, Antananarivo, Madagascar; **UA**, Laboratoire de Primatologie et Paléontologie des Vertébrés, Université d'Antananarivo, Antananarivo, Madagascar; **UABEC**, Mention Bassin sédimentaire, Evolution, Conservation, Université d'Antananarivo, Antananarivo, Madagascar.

Other Abbreviations—**CDS**, the 'complete data set' including all 11 humeral measurements taken on most specimens other than UABEC 0039; **DDS**, the 'distal data set' that were the only measurements that could be taken on humerus UABEC 0039; **DFA**, discriminant function analysis; **PCA**, principal components analysis; **SSD**, sexual size dimorphism. Measurement abbreviations are listed in Fig. 3 (DDS) and in the Measurements portion of the Material and Methods section (CDS) of this paper.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Family EUPLERIDAE Chenu, 1850
Genus *CRYPTOPROCTA* Bennett, 1833
CRYPTOPROCTA BEVATABE, sp. nov.
(Figs. 4, 5, and 6; Tables 5 and 6; Supplementary File 1)

Referred Specimens—UABEC 0039, distal third of right humerus (Figs. 4, 5, 6).

Etymology—The combination of two Malagasy words, 'bevata' meaning 'heavy' or 'big' and 'be' which means 'very' or 'a lot.' When used together, 'bevata be' means 'enormous.' Pronunciation: beh-VAH-tah-BEH.

Diagnosis—Larger than *C. ferox*, *C. spelea*, or any other known euplerid. Like *C. ferox* and *C. spelea*: capitulum is relatively round; medial epicondyle projects posteromedially from the trochlea; supratrochlear foramen is absent; large entepicondylar foramen is present. Differs from *C. ferox* and *C. spelea* by having greater distance between entepicondylar foramen and anterosuperior edge of the trochlea; more rounded capitulum projecting more posteriorly; lateral epicondylar crest larger and extends more proximally; olecranon fossa shallower; posterior lateral crest of olecranon fossa less distinct.

Locality, Horizon, and Age—Mitoho (24°02'51.85"S, 43°45'11.74"E) chimney, Holocene, older than 8.3 Ka (see below for geochronological analysis).

Description—The humerus of *C. bevatabe*, UABEC 0039, is clearly similar to known species of *Cryptoprocta* (Fig. 4) but larger than any known euplerid and morphologically distinct. UABEC 0039 is much more robust than the humerus of *C. ferox* and more robust in some features than that of *C. spelea*. In anterior view, *C. bevatabe* differs in its proportions from both *C. ferox* and *C. spelea*. There is a relatively greater span between the distal edge of the entepicondylar foramen and the anterosuperior edge of the trochlea than in previously known species. In anterior view, the capitulum is slightly more rounded, which makes the distal edge of the trochlea appear to be more curved. The medial edge of the trochlea extends further proximally, as well. The lateral epicondylar (= supracondylar) crest is larger and extends relatively more proximally than in extant *C. ferox* or extinct *C. spelea*. In posterior view (Fig. 5), the greater size and extent of the lateral epicondylar crest of *C. bevatabe* is even more obvious when compared with the lateral epicondylar crest of *C. ferox* and *C. spelea.* Unexpectedly, the lateral epicondyle itself is roughly the same size or even relatively smaller than in extant *Cryptoprocta*. The olecranon fossa is shallower and the posterior lateral crest bordering the olecranon fossa is less distinct and projecting than in other *Cryptoprocta*. No species of *Cryptoprocta* has a supratrochlear foramen, while all have an entepicondylar foramen. In all three species, the medial epicondyle projects posteromedially to roughly the same angle relative to the articular surface in contrast to other taxa (Fig. 6). The capitulum projects slightly more posteriorly in *C. bevatabe* and there is less distinction between the capitulum and the trochlea than there is in *C. ferox*.

CRYPTOPROCTA SPELEA Grandidier, 1902
(Figs. 4 and 5; Tables 5, 6, and 7; Supplementary File 1)

Cryptoprocta ferox spelea Grandidier 1902 (original description; raised to species status by Lamberton, 1939).

Cryptoprocta antamba Lamberton 1939 (juvenile specimen altered by crocodile ingestion).

Referred Specimens—UABEC 0014 (right), UABEC 0015 (left), UABEC 0016 (left), UABEC 0037 (right), UABEC 0038 (right), and UABEC 0881b (left), all complete humeri; UABEC 0036 (right), a distal half of a humerus.

Locality, Horizon, and Age—Mitoho (24°02'51.85"S, 43°45'11.4.74"E), chimney and deep section passage, Holocene, contemporaneous with *C. bevatabe*.

Comments—Our seven humeral specimens attributed to *C. spelea* (Figs. 4, 5) are slightly larger overall in length and other features than *C. spelea* humeri from other localities, yet they differ in that their mediolateral width at midshaft is marginally smaller relative to other portions of the bone, making them appear slightly more gracile than other *C. spelea* specimens. All specimens referred to herein as *C. spelea* are larger than *C. ferox* and smaller than *C. bevatabe*.

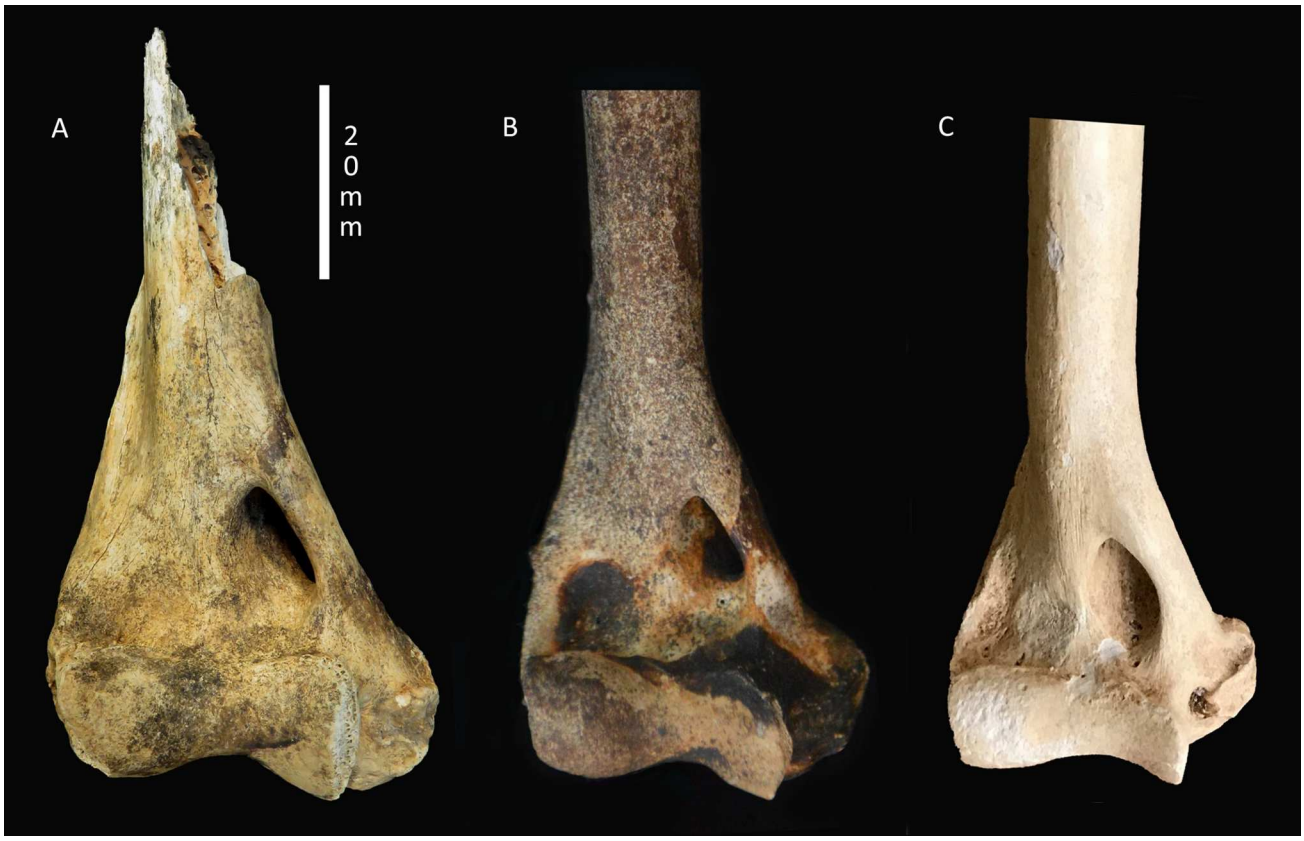

FIGURE 4. Comparison of distal humeri in anterior view. **A**, *Cryptoprocta bevatabe*, UABEC 0039; **B**, *Cryptoprocta spelea*, UABEC 0014; **C**, extant *Cryptoprocta ferox*, AMNH 199544. Both **A** and **B** are from Mitoho. Photographs by M. Lewis (**A**, **C**) and K. Muldoon (**B**). MicroCT scans of UABEC 0039 and UABEC 0014 are archived and available at www.morphosource.org.

RESULTS

Estimating Body Mass of Extinct Species of *Cryptoprocta*

All analyses presented here provided reasonable estimates of body mass for modern *C. ferox*, subfossil *C. ferox*, and previously published *C. spelea* (Table 5) as discussed in the Methods section. Estimates derived from regressions published by Heinrich (1995) and Heinrich and Houde (2006) returned lower sizes for all taxa than did estimates derived from regression equations published by Anyonge (1993). This result is not unexpected as Anyonge (1993) was estimating body mass for taxa in Size Classes 3 and 4, while the other studies were estimating body masses for Size Classes 1 and 2. When Anyonge's (1993) regressions were used, estimates for *C. ferox* were slightly (in modern individuals) or quite a bit (in subfossils) above the reported range for extants. Humeral length equations returned body sizes that were slightly lower than their equivalent equations drawn from midshaft size.

For all reconstructions, *C. spelea* was larger than all groups of *C. ferox*, with minimal overlap between the two species. Individuals of *C. spelea* from Mitoho overlapped in body mass with previously published specimens of *C. spelea* (Table 5). However, with every means of reconstruction used, the largest individuals in the Mitoho sample were larger than other known specimens of *C. spelea*. This size difference can also be seen in the linear measurements of these specimens; the Mitoho material is absolutely larger. With the Mitoho sample included, the estimated upper limit of body size for *C. spelea* increases dramatically even when the most conservative formulae are used. This species may have ranged in mass from 10–20 kg or more.

Cryptoprocta bevatabe was even larger (~29 kg or larger); our analyses confirm its likely Size Class 3 status. As the midshaft is not preserved in the only known humerus (and specimen) of this species, the reconstructed midshaft circumference for *C. bevatabe* (56 mm) was entered into Anyonge's (1993) circumference-based equations and also used to calculate average humeral diameter (= $56/\pi$) for use in Heinrich and Houde's (2006) equations. Reconstructed AP diameter was used in Heinrich's (1995) equations. Although our reconstructed midshaft measurements may underestimate body mass, all formulae yielded body mass estimates higher than the largest *C. spelea* (Table 5). Given the high body mass estimates for all groups of *C. ferox* and *C. spelea* when using Anyonge's (1993) equations, body mass estimates for *C. bevatabe* based on these equations are likely to also be overestimates.

We created two-dimensional representations of the three *Cryptoprocta* species (Fig. 7), based on the following body size estimates: 8.5 kg for *C. ferox*, 16 kg for *C. spelea*, and 29 kg for *C. bevatabe.* The first two estimates are the mean body mass estimates for these taxa in our study and the third estimate is the median to provide a conservative estimate for *C. bevatabe* (*C. bevatabe* mean = 32 kg). As there is only one known bone of *C. bevatabe*, we assumed geometric similarity in scaling to estimate proportions. While this hypothesis may not be correct, it can be tested when more specimens are found. We found the proportional linear increase in each extinct taxon by dividing the body size of the extinct taxon by the body size of *C. ferox* and then taking the cube root of the result. That cube root expressed as a percentage (i.e., multiplied by 100) is how much longer a body part should be in the extinct taxon relative to *C. ferox*. The results are in Table 6. Given that scaling patterns may vary even among closely related species and that extinct species may exhibit greater variability in size-related trends than

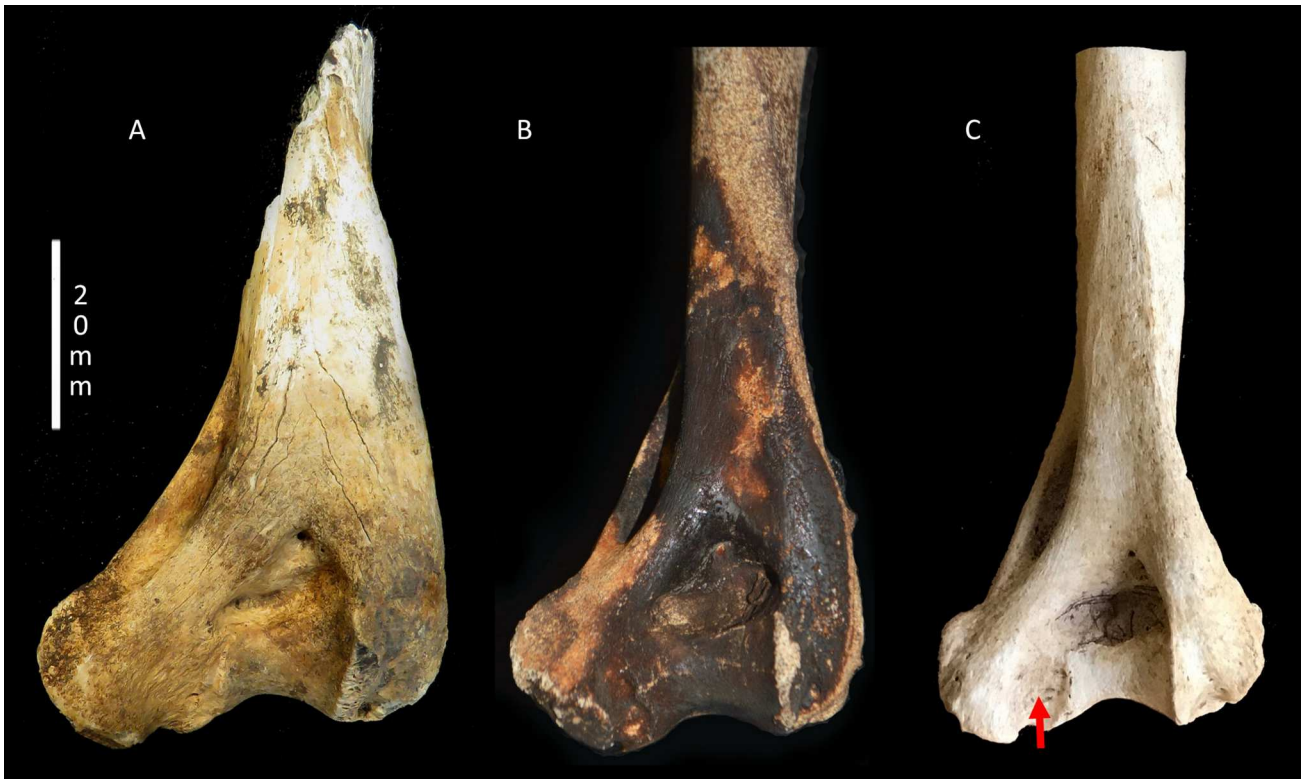

FIGURE 5. Comparison of distal humeri in posterior view. **A**, *Cryptoprocta bevatabe*, UABEC 0039; **B**, *Cryptoprocta spelea*, UABEC 0036; **C**, extant *Cryptoprocta ferox*, AMNH 199544. Both **A** and **B** are from Mitoho. Arrow indicates the attachment of the olecranon ligament as described by Heinrich and Houde (2006) for the arboreal kinkajou (*Potos*). Photographs by M. Lewis (**A**, **C**) and K. Muldoon (**B**). MicroCT scans of UABEC 0039 are archived and available at www.morphosource.org.

extant relatives (Lewis & Lague, 2010), we consider these estimates tentative, serving mostly to illustrate relative sizes of *Cryptoprocta* species (Fig. 7).

Morphometric Variation in *Cryptoprocta* Humeri

Geographic Variation in *Cryptoprocta spelea*—We used DFA to test whether specimens of *C. spelea* could be discriminated by locality based on logged data and by shape data. This DFA shows a clear separation of Mitoho specimens from specimens at all other sites (Fig. 8). Humeri of Mitoho *C. spelea* have a trochlea that is both mediolaterally wider and larger in anteroposterior width than those at other sites and are larger overall. While small sample sizes are a concern, PCA showed the same separation between the localities with the largest sample sizes (Mitoho, Anavoha, and Beavoha).

Mitoho *C. spelea* differ in humeral proportions from specimens of *C. spelea* from other sites based on logged data. For example, Mitoho specimens have an anteroposteriorly wider midshaft than would be predicted based on other *Cryptoprocta* and especially other *C. spelea* (Fig. 9A). This proportional difference is interesting given that most Mitoho *Cryptoprocta* are absolutely larger than most other *C. spelea* in many features. Both biepicondylar and distal anteroposterior widths are generally greater than in other known *C. spelea* humeri (Fig. 9B). However, in the Mitoho *C. spelea* specimens, only the anteroposterior dimension of the shaft is larger than expected.

Interspecific Variation in *Cryptoprocta* and Comparison to other Carnivorans—We performed both DFA and PCA using

FIGURE 6. Comparison of distal humeri in distal view. **A**, *Cryptoprocta bevatabe*, UABEC 0039; **B**, extant *Cryptoprocta ferox*, AMNH 199544; **C**, extant arboreal *Arctictis binturong*, USNM 589180. Note how the medial epicondyle in the two species of *Cryptoprocta* angles more posteromedially in comparison to *Arctictis*, where the medial epicondyle is closer to being in line with the mediolateral axis of the articular surface. Photographs by L. Godfrey (**A**) and M. Lewis (**B**, **C**). All elements scaled to the same size. Scale bars equal 10 mm.

TABLE 5. Body mass reconstructions (kg) based on *Cryptoprocta* humeral measurements. Ranges for all species studied and individual specimens of *Cryptoprocta bevatabe* (UABEC 0039) and *Cryptoprocta* spelea are included. Mitoho *C. spelea* is slightly larger than non-Mitoho *C. spelea* for all equations. For comparison to our data, modern *Cryptoprocta ferox* body mass has been reported to range from 5–12 kg (Hawkins, 1998; Köhncke & Leonhardt, 1986; Veron et al., 2018). Most previous reconstructions of *C. spelea* body mass range from 10–15 kg (Anderson et al., 1985; Goodman & Jungers, 2014; Meador et al., 2019). **Abbreviations**: **A**, Anyonge (1993); **AP**, anteroposterior, **avg**, average; **circum**, circumference; **diam**, diameter; **H**, Heinrich (1995); **HH**, Heinrich and Houde (2006).

	H: All taxa AP diam y = 2.47x-1.72	H: scansors AP diam y = 2.43x-1.71	HH: Non-cursors AP diam y = 2.48x-1.74	HH: Data set II avg diam y = 2.389x-1.544	A: total circum y = 2.47x-2.72	A: canid circum y = 1.86x-1.75	A: felid circum y = 2.65x-3	A: ursid circum y = 3.04x-3.89	HH: Data set II length y = 2.152x -3.63	A: total length y = 2.93x-5.11	A: felid length y = 3.13x-5.53
Extant *C. ferox*	5–10	5–10	5–10	5–10	6–14	8–14	6–14	3–7	5–8	7–11	7–11
Subfossil *C. ferox*	7–9	7–9	7–9	7–12	10–17	11–17	9–17	5–9	7	9–10	9–10
Mitoho *C. spelea*	15–27	14–25	15–26	13–21	18–30	17–26	18–32	10–19	9–12	13–19	14–20
Other *C. spelea*	11–24	10–22	12–23	11–19	16–27	12–15	16–29	9–17	8–11	12–17	12–17
C. bevatabe	29.81	27.62	29.03	27.88	39.63	31.74	42.92	26.58			
Individual Mitoho *C. spelea* specimens:											
UABEC 0014	22.66	21.09	22.05	21.27	29.95	25.71	31.79	18.83	10.96	17.7	18.28
UABEC 0015	16.37	15.31	15.91	17.42	24.38	22.02	25.49	14.61	8.96	13.46	13.64
UABEC 0016	24.86	23.1	24.2	21.27	29.95	25.71	31.79	18.83	10.85	17.46	18.01
UABEC 0036	27.01	25.06	26.3	19.97	28.07	24.48	29.65	17.38			
UABEC 0037	15.39	14.41	14.95	12.78	17.69	17.29	18.07	9.85	11.18	18.19	18.82
UABEC 0038	25.13	23.35	24.46	18.16	25.44	22.73	26.68	15.4	11.53	18.97	19.68
UABEC 0881b	18.44	17.22	17.93	15.83	22.08	20.43	22.91	12.94	10.92	17.61	18.18

TABLE 6. Estimated linear dimensions in the three species of *Cryptoprocta*. We assumed geometric similarity in scaling using estimated body sizes as described in the text. Linear measurements of *Cryptoprocta ferox* are from Nomenjanahary et al. (2021). **Abbreviations**: **PVI**, proportional volumetric increase relative to *C. ferox*; **PLI**, proportional linear increase relative to *C. ferox*.

	Body size (kg)	PVI	PLI	Head and body length (cm)	Tail length (cm)
C. ferox	8.5	–	–	75	69
C. spelea	16	188%	123%	92.25	84.87
C. bevatabe	29	341%	151%	113	104

our distal humeral data set (DDS) to determine which carnivoran species is most similar in distal humeral shape to extinct *Cryptoprocta* (Fig. 10). The results for both analyses are similar, so only the DFA will be discussed here. All euplerids except the new species, *C. bevatabe*, cluster with carnivoran species that share similar locomotor behavior and substrate preferences. In contrast, *C. bevatabe* not only falls outside the range of its congeners in both DFA and PCA analyses of distal humeral shape data, but also outside the convex hulls of other carnivoran families. The new species falls between its congeners on one side and other scansorial and arboreal taxa on the other in multivariate space (Fig. 10). *Cryptoprocta bevatabe* shares a greater relative biepicondylar width and mediolateral articular surface width and a relatively smaller distal anteroposterior width with *Arctictis binturong*. In other relative proportions, it is more similar to other *Cryptoprocta* species. DFA assigns UABEC 00039 to the scansorial *C. ferox* (DDS; Fig. 10). Despite the fact that the distributions of shape data reveal good discrimination for other species in our analysis (Fig. 10), the distal humeri of *C. spelea* and *C. ferox* are difficult to distinguish when the effect of size is minimized. However, analyses presented here include only one skeletal element.

Sexual Dimorphism—The geometric mean of the DDS of UABEC 0039 falls entirely outside the range of the *C. spelea* sample, not just those from Mitoho (Fig. 11). Given that nearly all measurements of UABEC 0039 fall outside the *C. spelea* range, this is not surprising. Notably, only the anteroposterior width of the trochlea is small, falling within the range of *C. spelea*, which highlights distinct shape differences between *C. bevatabe* and *C. spelea*.

Predicting Locomotor Behavior and Substrate Use—When DFA is used to predict locomotor/substrate use category on the basis of the distal humeral measurements used in this study, it can discriminate these behavioral categories reasonably well (Fig. 12). *Cryptoprocta spelea* was assigned to the scansorial group. In contrast, *C. bevatabe* was assigned to 'tree dweller,' a group that includes binturongs (*A. binturong*), African palm civets (*Nandinia binotata*), and kinkajous (*Potos flavus*).

Dietary Preferences and Niche Partitioning within *Cryptoprocta*

Subfossil *C. ferox* from the coastal spiny thicket has Suess-corrected collagen $\delta^{13}C$ values that are higher (less negative) than *C. spelea* from the same region (Fig. 13). Similarly, the two extant lemurs have higher Suess-corrected collagen $\delta^{13}C$ values than the four extinct lemur species that we analyzed from the coastal spiny thicket (Fig. 13; Supplementary File 3). Collagen $\delta^{13}C$ values for *C. ferox* are statistically indistinguishable from those of extant lemurs but significantly different from those of extinct lemurs, while the opposite is true for *C. spelea* (Table 7). Tooth enamel $\delta^{13}C$ values for *C. spelea* and *Pa. insignis* are also indistinguishable (Fig. 13). The mean and standard deviation for *C. spelea* is -12.0 ± 1.0‰ while that for *Pa. insignis* is -12.3 ± 0.6‰ ($t = 0.51$, $df = 8$, $p = 0.63$).

DISCUSSION

New Species or Male *Cryptoprocta spelea*?

Distal humerus UABEC 0039 is unlikely to be a male *C. spelea*. The specimen's geometric mean, which indicates overall size, falls entirely outside the range of the *C. spelea* sample, not just those from Mitoho (Fig. 11). Given that nearly all measurements of UABEC 0039 fall outside the *C. spelea* range, this is not surprising. Notably, only the anteroposterior width of the trochlea is small, falling within the range of *C. spelea*, which highlights distinct shape differences between *C. bevatabe* and *C. spelea*. If the new humerus were a male and the other specimens from Mitoho were female, that would require not only a difference in size, but distal humeral shape change (and an implied functional difference) between sexes, as well.

Functional Significance

Our analyses support the inference that *C. bevatabe* was at least as proficient at locomoting in trees as were the other species of *Cryptoprocta*, despite its larger size. Several

TABLE 7. T-tests comparing Suess-corrected bone collagen $\delta^{13}C$ values (in ‰) for sympatric *Cryptoprocta* and extinct (†) or extant lemurs from TNP and other sites in coastal southwestern Madagascar.

Comparisons of single taxa with means and standard deviations	t	df	p
Cryptoprocta ferox (-19.0 ± 0.9) vs. *Lemur catta* (-19.9 ± 1.0)	1.33	18	0.2
C. ferox (-19.0 ± 0.9) vs. *Microcebus griseorufus* (-19.5 ± 0.9)	0.8	26	0.43
C. ferox (-19.0 ± 0.9) vs. †*Pachylemur insignis* (-22.1 ± 0.8)	5.87	9	< 0.001
C. ferox (-19.0 ± 0.9) vs. †*Megaladapis madagascariensis* (-22.0 ± 1.2)	3.91	9	0.004
C. ferox (-19.0 ± 0.9) vs. †*Megaladapis edwardsi* (-22.2 ± 0.5)	9.53	18	< 0.001
C. ferox (-19.0 ± 0.9) vs. †*Archaeolemur majori* (-20.7 ± 1.2)	2.24	19	0.04
†*Cryptoprocta spelea* (-22.2) vs. *L. catta* (-19.9 ± 1.0)	−2.2	16	0.04
†*C. spelea* (-22.2) vs. *M. griseorufus* (-19.0 ± 0.9)	−3.0	24	0.006
†*C. spelea* (-22.2) vs. †*P. insignis* (-22.0 ± 0.7)	−0.1	7	0.91
†*C. spelea* (-22.2) vs. †*Me. madagascariensis* (-22.0 ± 1.2)	−0.2	7	0.87
†*C. spelea* (-22.2) vs. †*Me. edwardsi* (-22.2 ± 0.5)	−0	16	0.98
†*C. spelea* (-22.2) vs. †*A. majori* (-20.8 ± 1.2)	−1.2	16	0.26
Comparisons of extant and extinct *Cryptoprocta* with pooled samples of sympatric extinct or extant lemurs	t	df	p
C. ferox (-19.0 ± 0.9) vs. extant lemurs pooled (-19.6 ± 1.0)	0.99	43	0.33
C. spelea (22.2) vs. extinct lemurs pooled (-21.7 ± 1.1)	−0.5	49	0.63
C. ferox (-19.0 ± 0.9) vs. extinct lemurs pooled (-21.7 ± 1.1)	3.97	51	< 0.001
C. spelea (-22.2) vs. extant lemurs pooled (-19.6 ± 1.0)	−2.7	41	0.01

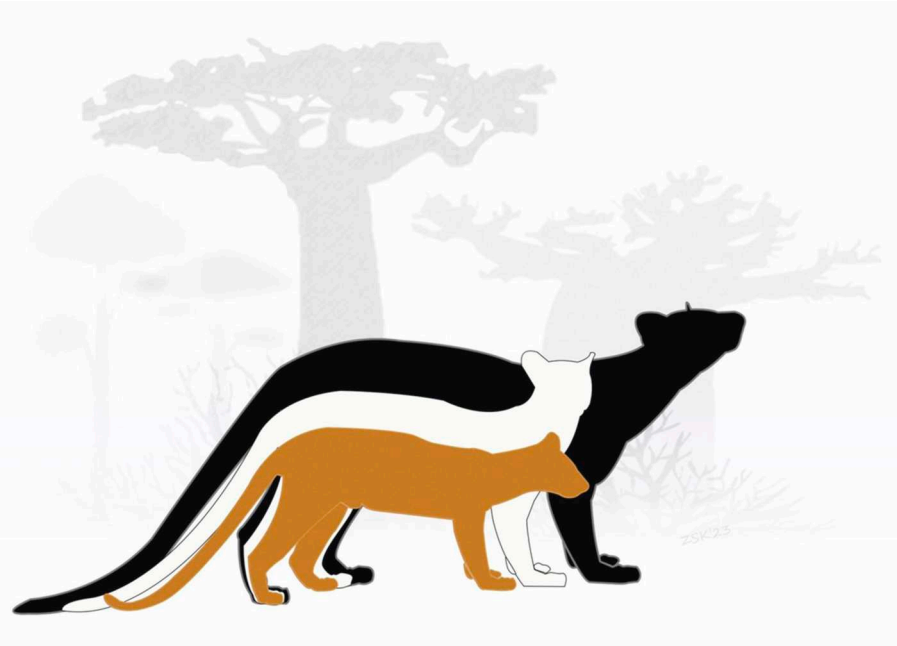

FIGURE 7. Relative body size reconstruction of extinct *Cryptoprocta*. Body mass estimates follow data in Tables 5 and 6 whereby the mean mass of *Cryptoprocta ferox* (foreground) is 8.5 kg, the mean mass of *Cryptoprocta spelea* (middle) is 16 kg, and the median mass of *Cryptoprocta bevatabe* is 29 kg (rear). As noted in the text, the median for *C. bevatabe* is a more conservative (i.e., lower) estimate than the mean. Ethnohistoric data refer to three color morphs for *Cryptoprocta*—the 'fosa mena' (red), 'fosa ondry' (off-white, or colored like sheep), and 'fosa mainty' (black). The 'fosa mena' is clearly the extant species, but the identities (and indeed, existence) of the black and the off-white forms are unclear. Here we have followed the ethnohistoric data and made each species a different color. Drawing by Z. Klukkert.

anatomical features support greater arboreality in *C. bevatabe*, or at least the ability to maintain functional equivalence with other species of *Cryptoprocta*. Most importantly, the well-developed medial epicondyle in UABEC 0039 indicates strong wrist and digital flexors; the medial epicondyle is relatively larger than that of any previously known species of *Cryptoprocta*. Relatively large digital flexors and a concomitant large medial epicondyle are associated with arboreality in mammals (e.g., Argot, 2001; Szalay & Sargis, 2001).

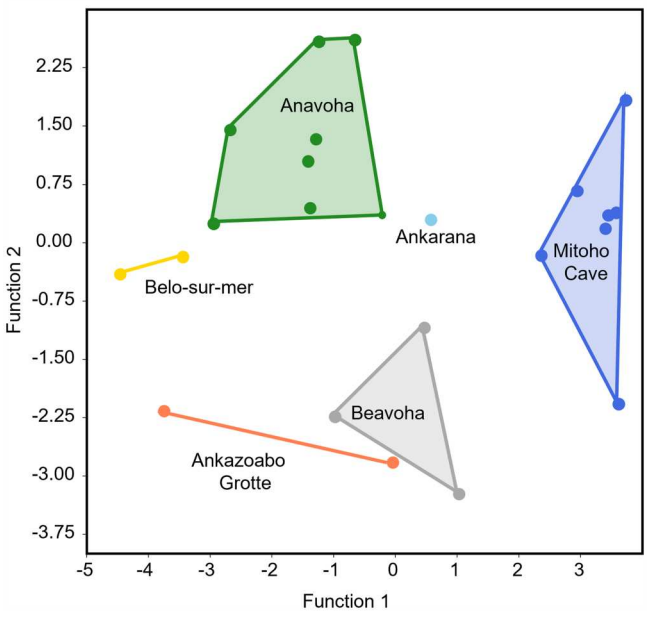

FIGURE 8. DFA of humeri of *Cryptoprocta spelea* by site using the logged CDS (except functional length and midshaft circumference). Mitoho specimens are easily distinguished from specimens from other localities. There is 100% correct classification of Mitoho specimens. Cross validation generates 100% accuracy despite the small sample sizes. See Supplementary File 2 for confusion matrices.

As noted by Heinrich and Houde (2006), cursorial carnivorans, like herpestids, tend to have a deep olecranon fossa that is often perforated by a supratrochlear foramen resulting in a relatively stable humeroulnar joint. In contrast, *C. bevatabe* has a relatively shallow olecranon fossa, as in African palm civets (*Nandinia*) and other truly arboreal carnivorans. The morphology of the posterior lateral crest bordering the olecranon fossa can also indicate general locomotor category (Szalay & Sargis, 2001). In *C. bevatabe*, this crest is less distinct and projects less than in *C. ferox*, which is associated with arboreal locomotion (Szalay & Sargis, 2001). The humeral trochlea in *C. bevatabe* is slightly deeper than in extant *C. ferox*, giving the capitulum a slightly rounder appearance. This depth provides a more stable humeroulnar joint and a humeroradial joint with greater supinatory abilities (Lewis, 1995).

In *C. bevatabe*, the region between the medial epicondyle and trochlea provides slightly more space for the olecranon ligament (and the area of attachment is slightly larger) than in other extant and subfossil specimens of *Cryptoprocta* (arrow in Fig. 5). This ligament connects the distal humerus and olecranon process of the ulna and holds the ulna against the humerus (Heinrich & Houde, 2006). An expansive attachment area for this ligament is seen in arboreal kinkajous (*Potos*) and the Viverravidae (an extinct relative of carnivorans), but not in most other extant carnivorans (Heinrich & Houde, 2006). Presumably, the olecranon ligament aids in stabilizing the joint during arboreal locomotion as the joint surfaces themselves do not provide as much stability as they do in cursorial carnivorans.

The lateral epicondylar crest or ridge in *C. bevatabe* is much wider and more flaring than in *C. spelea* (Fig. 5). It extends much further proximally than in *C. ferox* and provides a

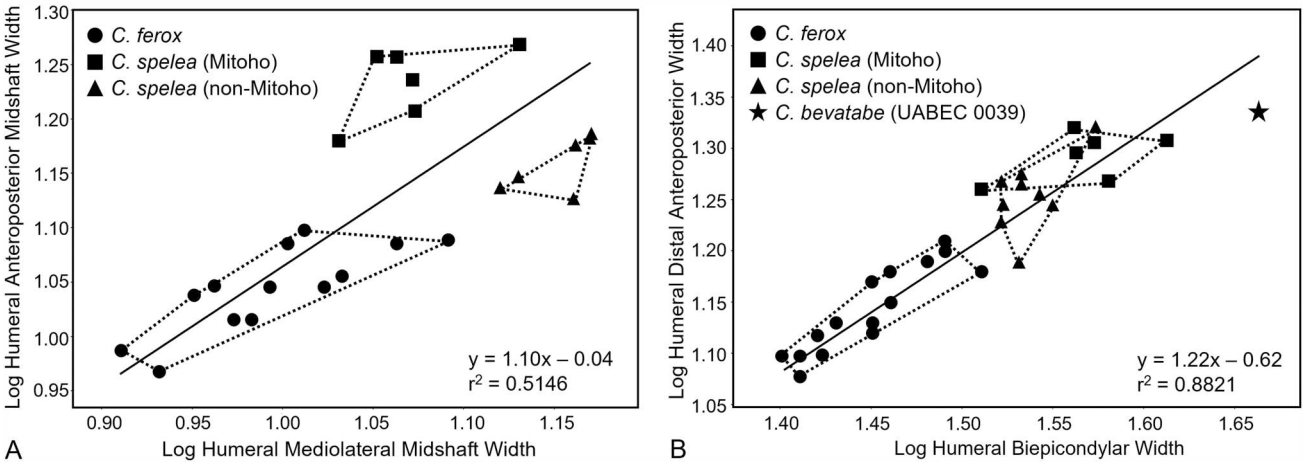

FIGURE 9. Bivariate plots of *Cryptoprocta* log-transformed humeral measurements. **A**, RMA regression of log humeral mediolateral midshaft width versus log humeral anteroposterior midshaft width in *Cryptoprocta*. Note that Mitoho *Cryptoprocta spelea* has a much wider anteroposterior width than non-Mitoho *C. spelea*. *Cryptoprocta ferox* falls roughly between the two in proportion (and is similar in proportions to other euplerids, not shown). Midshaft is not fully preserved in *Cryptoprocta bevatabe.* **B**, RMA regression of log humeral biepicondylar width versus log humeral distal anteroposterior width in *Cryptoprocta*. Note that Mitoho *C. spelea* is generally larger but is otherwise similar in its proportions to *C. ferox* and non-Mitoho *C. spelea*. *Cryptoprocta bevatabe* has a slightly smaller anteroposterior width than expected, but it is only slightly different in proportions from other taxa.

greater area of muscle attachment, particularly along the sweeping anterior surface. An extended lateral epicondylar crest, as in *C. bevatabe*, has been identified as indicative of arboreality (e.g., Argot, 2001), while a proportionally larger epicondylar breadth is associated with taking larger-bodied prey among felids (Meachen-Samuels & Van Valkenburgh, 2009). Numerous muscles arise from the anterior and posterior faces and edge of this crest. The brachioradialis, an important forearm flexor and supinator, is perhaps the most important muscle originating on this crest. The short head of brachialis, when present in Carnivora, originates on the anterior side of this ridge (Davis, 1964) and is also a forearm flexor. The anconeus arises on the posterior side of the region of the lateral epicondylar crest (Davis, 1964) and aids in extension and stabilization of the elbow. The extensor carpi radialis brevis and longus arise from the distal and anterior faces respectively of the lateral epicondylar crest. These two muscles adduct (i.e., radially flex) and extend the manus in quadrupedal mammals. The extensor digitorum communis also originates from the distal portions of the ridge and onto the lateral epicondyle. A large brachioradialis muscle has also been suggested to indicate the ability to place the palms on either side of a tree branch (e.g., Chester et al., 2010; McEvoy, 1982). *Cryptoprocta ferox* do place their forepaws on either side of a trunk, at least when descending down an oblique trunk (Laborde, 1986), so this is further evidence of behavior similar to extant fosa. The fact that the area for brachioradialis attachment is even larger in *C. bevatabe* than in extant fosa indicates at a minimum a change related to maintaining functional equivalence or, possibly, that this behavior could have been even more important (or done with greater strength) within the locomotor repertoire of *C. bevatabe*. Extant fosa hold and capture prey with their paws. Increased strength and supinatory abilities would enhance (or maintain functional equivalence of) prey capture and manipulatory abilities in *C. bevatabe*. This enhancement would be particularly important if *C. bevatabe* regularly captured relatively large-bodied, extinct lemurs. In striking contrast to *C. bevatabe*, the distal humerus of *C. spelea* is remarkably similar to that of *C. ferox*, despite its larger size.

Extant fosa are known for their remarkable climbing skills and use vertical and horizontal supports and even lianas as a substrate. Climbing is facilitated by their short limbs and retractile claws. These features in combination with a rotating ankle allow fosa to descend head-first down trees (Albignac, 1970; Laborde, 1986). While ascending, the forelimbs are placed on either side of the trunk to grip it, while the hind limbs propel the animal upward (Laborde, 1986). During vertical descent, the hind limbs are wrapped around the trunk to control descent, while the flexed forelimbs are held near one another against the trunk (Albignac, 1970). This allows fosa to use vertical looping (Laborde, 1986), as described for some viverrids (Taylor, 1970). While descending along an oblique trunk, the forelimbs may encircle the trunk and the plantar and palmar pads and retractile claws aid in gripping the trunk (Laborde, 1986). The tail is used for balance while in the trees. Although the tail may wind partially around a branch for use as a break during head-first descent, it is not prehensile (Albignac, 1970; Laborde, 1986; Youlatos, 2003). Fosa have been observed leaping one to two meters between vertical supports (Crompton & Sellers, 2007). The hind limb is longer than the forelimb and it is this elongated hind limb that provides the force for the leap even though fosa may land first on their forelimbs. Although fosa are usually digitigrade on the ground, they switch to plantigrady while in the trees on horizontal branches (Albignac, 1970).

Goodman and Jungers (2014) suggested that *C. spelea*, as an animal larger than the extant fosa, may have been less agile than the extant fosa. In contrast, Meador et al. (2019) found little evidence that *C. spelea* was less arboreal than *C. ferox*; they discussed numerous morphological features in support of arboreality. These include (1) the general similarity of *C. spelea* to *C. ferox* in humeral morphology (which our study confirms), (2) shortened distal elements, and (3) a low brachial index. In fact, Meador et al. (2019) reported a lower brachial index in *C. spelea* than in *C. ferox*, which we suggest here could be due to the need to maintain functional equivalence during locomotion by keeping what would otherwise have been a higher center of gravity closer to the trunk while balancing a larger

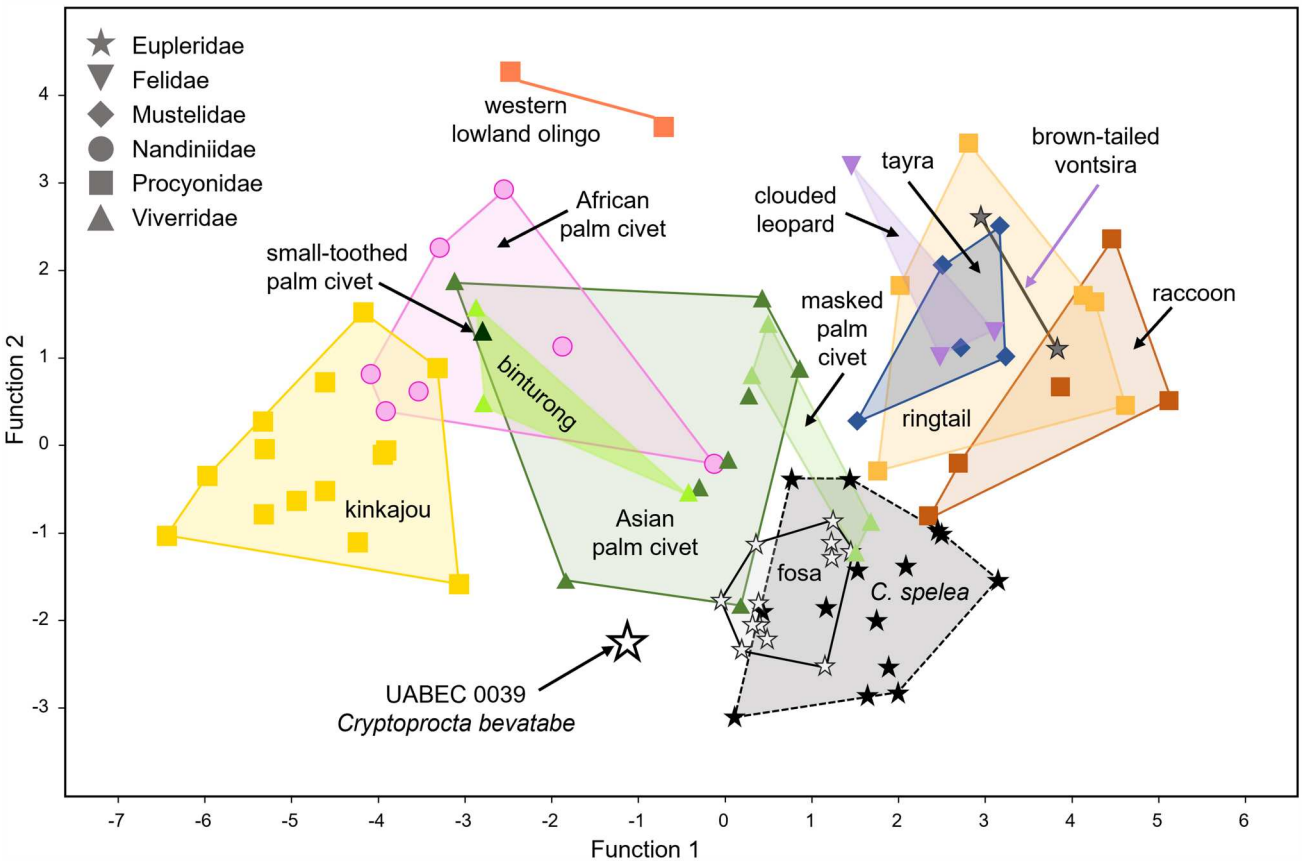

FIGURE 10. DFA by species using distal humeral shape data (DDS) for scansorial, tree-dwellers, and smaller terrestrial-climbers. UABEC 0039 (*Cryptoprocta bevatabe*) is denoted by a large star. Data included all measurements depicted in Fig. 3 (DDS). Taxa sort from the more dedicated tree dwellers (e.g., kinkajou) at the lower end of Function 1 to more scansorial taxa at the higher end (e.g., ringtail and raccoon). UABEC 0039 was classified as *Cryptoprocta ferox*, although it falls outside of the range of that species in multivariate space. Only 62.8% of specimens were correctly classified to taxon. See Table 2 for scientific names of each taxon and Supplementary File 2 for confusion matrices.

mass on arboreal supports. We note that clouded leopards (*Neofelis nebulosa*) are similar in body mass to *C. spelea* (including our large specimens from Mitoho; Table 2); yet, they have no difficulty in engaging in many arboreal behaviors similar to *C. ferox* such as climbing head-first down trees and what might now be described as vertical looping (see descriptions and figures, especially Abb. 1–6, in Hemmer, 1968).

Dietary Preferences and Niche Differentiation

Our results support niche differentiation in terms of the dietary preferences of *C. ferox* and *C. spelea*. Sample sizes are small for both *C. ferox* and *C. spelea*, so the isotopic data should be interpreted with caution. Nevertheless, the patterns are consistent with *C. ferox* targeting smaller-bodied extant lemurs and *C. spelea* targeting the larger-bodied, relatively arboreal extinct lemurs (Table 7). We presume that *C. bevatabe* also hunted arboreal lemurs, although at present, this cannot be directly tested as we were not able to collect isotope data from this new species.

The isotopic evidence is also consistent with previous taphonomic work. Meador et al. (2019) studied predator traces on giant lemur bones from six subfossil sites in Madagascar and confirmed that while giant lemurs fell victim to predators of all types, some have traces that can only have been made by a mammalian carnivore, such as extinct species of *Cryptoprocta*. This taphonomic evidence bolsters the ecomorphological argument that one or both of the large-bodied, extinct species of *Cryptoprocta* were skilled predators in arboreal settings.

Could introduced dogs have been responsible for these taphonomic traces? Isotopic evidence indicates that dogs and *Cryptoprocta* spp. have little overlap in their diets, with dogs relying more on domesticated livestock and other human foods (Hixon et al., 2021). Although it is difficult to distinguish *Cryptoprocta* marks from those of introduced dogs, it is reasonable to attribute nearly all carnivoran traces on extinct Malagasy vertebrates to euplerids given the isotopic evidence.

Cooperative Hunting, Prey Size, and the Significance of Body Mass Variation

We must also consider the possibility of cooperative hunting by species of *Cryptoprocta*. Extant male fosa are known to engage in cooperative hunting, which impacts the size of their preferred prey (Lührs et al., 2013). Behavioral studies of extant fosa indicate that the most commonly eaten vertebrates tend to weigh 1–2 kg (e.g., tenrecs, shrews, other euplerids, small nocturnal lemurs), while the largest primates eaten with any regularity, *Eulemur* and *Propithecus*, range from 2–7 kg, depending on the species taken (Dollar, 2006; Dollar et al., 2007; Gerber & Hawkins, 2022; Goodman & Ganzhorn, 2022; Hawkins, 1998; Hawkins & Racey, 2008; Irwin et al., 2009; Rasoloarison et al., 1995; Wright et al., 1997). The degree to which extant fosa prey on *Propithecus* and *Eulemur* is not correlated with the local relative abundance of these lemur species

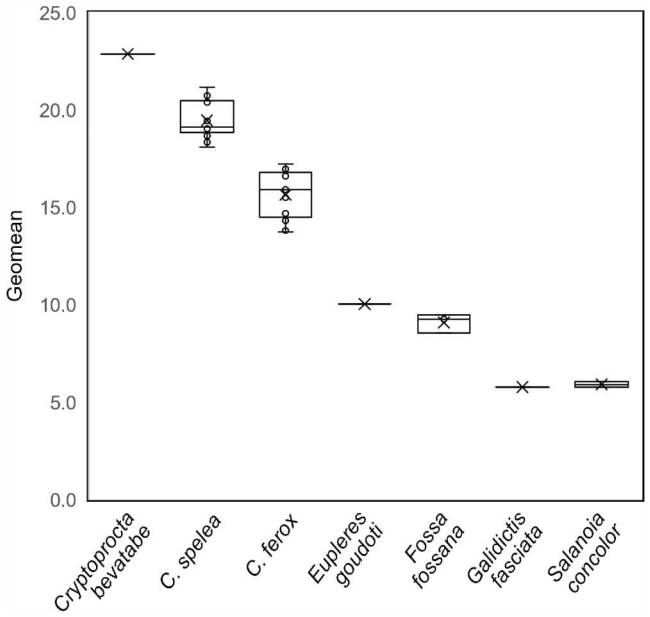

FIGURE 11. Box plot of distal humeral geometric mean (DDS) of all *Cryptoprocta* specimens in study. Note how *Cryptoprocta bevatabe* is outside of the range of all other species. *Cryptoprocta spelea* is outside the range for *Cryptoprocta ferox*. Subfossil and extant specimens of *C. ferox* are not substantially different from one another in size and are included together.

(Dollar, 2006). Instead, cooperative hunting among male fosa leads to having higher proportions of the largest lemurs (e.g., *Propithecus*) in the diet than is seen among solitary males (Lührs et al., 2013). Thus, extant fosa can consume prey species that are known to weigh more than half of a particular individual's own body mass (Hawkins & Racey, 2008) or even rival them in size (e.g., *P. diadema*; Irwin et al., 2009). This behavior is especially remarkable because *C. ferox* is smaller than 21.5 kg, the threshold above which mammalian predators tend to consume prey near their own body mass (Carbone et al., 1999).

Males that hunt cooperatively grow larger than males that do not (Lührs et al., 2013). Cooperative hunting, if it occurred in any of the species of *Cryptoprocta* of the past, would have allowed a shift to slightly larger prey than that of solitary individuals of the same species. In fact, Lührs and Dammhahn (2010) suggest that cooperative hunting in extant fosa may have evolved precisely for this purpose, i.e., to allow them to capture large lemurs, including species that became extinct in Madagascar during the Late Holocene. Trace evidence of carnivory is most common on the remains of smaller extinct lemurs (i.e., *Pachylemur*; ca. 10 kg) particularly at sites such as Tsirave (Fig. 1) where only subfossil *C. ferox* (and no *C. spelea*) has been found (Meador, 2018). Thus *C. ferox* may have been capturing animals that were roughly their own size (and slightly larger than their current largest prey), presumably via cooperative hunting.

Geographic variation in the size of *C. spelea* may have signaled differences in cooperative behavior and thus prey preference. As noted above, *C. spelea* at Mitoho are larger than members of the same species at other sites, and they differ slightly in humeral morphology (e.g., Figs. 8, 9). Extant fosa that hunt cooperatively grow larger than solitary males and females (Lührs et al., 2013). If this relationship between larger body mass and cooperative hunting held for *C. spelea*, then the large-bodied Mitoho individuals may have included more cooperative hunters and smaller *C. spelea* from other geographic areas may have hunted more often alone. Prey near the body mass of Mitoho *C. spelea* or slightly below would have included both mid-sized lemurs (*Archaeolemur*) and possibly some of the larger extinct lemurs with carnivoran predator traces identified by Meador et al.

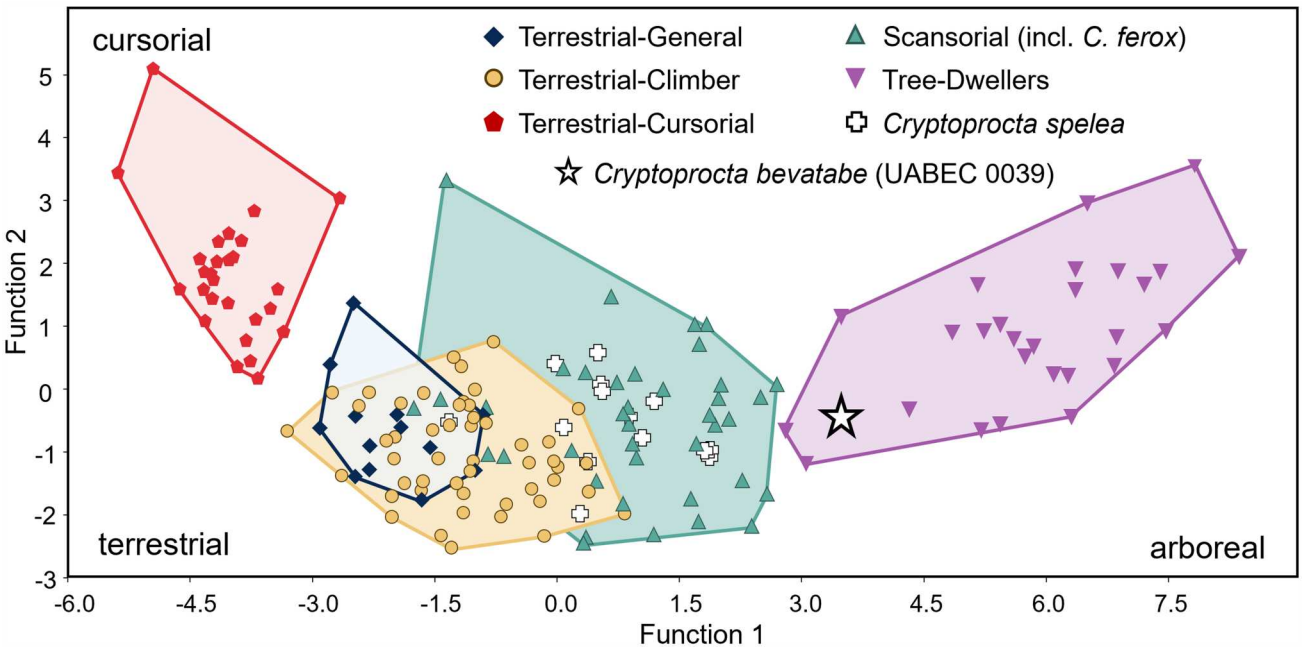

FIGURE 12. Predicted locomotor category of *Cryptoprocta bevatabe* and *Cryptoprocta spelea* from Mitoho based on DFA of distal humeral shape data (DDS) of all taxa using locomotor and substrate categories of Tarquini et al. (2017). 87.2% of specimens were correctly classified. *Cryptoprocta bevatabe* (UABEC 0039) was assigned to the tree-dweller category and *C. spelea* to the scansorial category. Taxa and behavioral categories as in Table 2. UABEC 0039 (*C. bevatabe*) is denoted by a star. See Supplementary File 2 for confusion matrices.

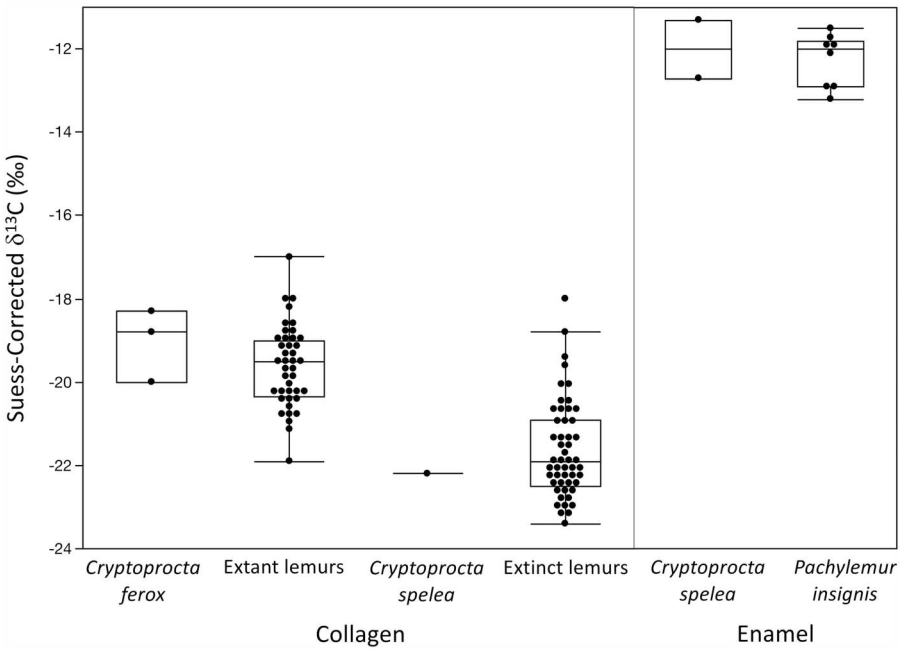

FIGURE 13. Box plots of collagen and enamel carbon isotope ($\delta^{13}C$) values for subfossil *Cryptoprocta ferox*, *Cryptoprocta spelea*, extant lemurs, and extinct large-bodied lemurs from coastal subfossil sites in southern Madagascar, corrected for the Suess Effect. See Supplementary File 3 for details about the included specimens.

(2019). However, it is certainly possible that differences in prey availability and habitat account for the size difference between Tsimanampesotse *C. spelea* and its conspecifics, with or without the presence of cooperative hunting.

At anywhere from 27–43 kg (the lower end of Size Class 3), *C. bevatabe* was the largest known Malagasy carnivoran and yet was still relatively small in comparison to the largest carnivorans in the various African continental carnivore guilds. Nonetheless, their larger body size would have meant that they could capture larger prey than their congeners. If they hunted cooperatively, that would push their potential prey size higher. Meador et al. (2019) identified a group of large-bodied lemur prey (e.g., *Hadropithecus*, *Palaeopropithecus*, and *Megaladapis*) with predatory traces attributable to mammalian carnivores. They made the reasonable assumption that *C. spelea* had made those marks, as this was the largest mammalian predator then known. We now posit that *C. bevatabe* was preying on those large-bodied, extinct lemurs (with *C. spelea* preying on some of the smaller large-bodied lemurs). While previous studies estimated these large-bodied lemurs with carnivoran traces to be 42–85 kg (Jungers et al., 2008), new lower estimates place these taxa at 30–65 kg (*Hadropithecus* was not included; Thompson et al., 2025). Since carnivorans greater than 21.5 kg tend to prey on species similar to them in mass (Carbone et al., 1999) and *C. bevatabe* is greater than 21.5 kg, we predict that this species should have been able to prey upon species roughly similar in size to itself. This prediction would put many of the large-bodied, extinct lemurs identified by Meador et al. (2019) within the range of *C. bevatabe.* We do not know if UABEC 0039 is on the larger or smaller end of variation within *C. bevatabe* and exactly where the upper cut off for *C. bevatabe* prey size would be. We also cannot rule out the possibility that the largest lemurs were scavenged, although Meador et al. (2019) discounted this possibility. No direct observations of extant fosa scavenging carcasses in the wild have been made despite numerous behavioral studies of fosa.

Could three species of *Cryptoprocta* have existed sympatrically in the past?

We believe that it is possible that in the past all three species of *Cryptoprocta* were sympatric, at least in the southwest. While *C. bevatabe* and many specimens of *C. spelea* are present at Mitoho, only one possible *C. ferox* fossil (UABEC 0013, a femur) has been found. All three species were found on the same ledge within the chimney at Mitoho, although they may have accumulated over a period of time. Nonetheless, remains of both *C. ferox* and *C. spelea* have been found together at other subfossil sites in the southwest (e.g., Taolambiby, Beavoha, and Anavoha; Meador et al., 2019). No other locality yet shows signs of the new species *C. bevatabe* being present. While *C. ferox* does not exist in the immediate area around the cave today, this species does occur in TNP alongside *Galidictis grandidieri* and feral introduced cats (Goodman et al., 2002; Sauther et al., 2020).

Could TNP have supported three species of *Cryptoprocta* in the past? Increased energy availability promotes the ability of closely related species to live sympatrically and thus supports higher species richness in a given area (Pigot et al., 2016). Prey biomass specifically is correlated with carnivoran biomass (Carbone & Gittleman, 2002). Thus, the presence of many more primate species, and especially larger-bodied primate species, in the past would have supported a greater predator biomass and likely a greater diversity of predators, even those that are closely related like the three species of *Cryptoprocta*.

Other regions of the world have supported closely related carnivorans today and in the past. The cat family Felidae are probably most similar to *Cryptoprocta* species in behavior, as this hypercarnivorous family includes arboreal and semi-arboreal taxa. Extant sympatric South American felids have been shown to partition their niches by consuming prey that differ in body mass (see Metz et al., 2024, and references therein), not unlike what we are suggesting for the three species of *Cryptoprocta* at Mitoho. The extant felid genus *Leopardus*, for example, has

multiple Size Class 1 and 2 species that are often sympatric with each other and with other felids in a given region. These taxa often differ in daily activity patterns such that species may be strictly diurnal, strictly nocturnal, or cathemeral, which may be a means of reducing the impact of intraguild competition or killing (Di Bitetti et al., 2010). In some instances, the smaller species are less common, which may reflect the threat of intraguild predation (Oliveira et al., 2010). Likewise, the smallest *Cryptoprocta*, *C. ferox* may have only been present in low numbers in areas where the largest two species were present.

Like Mitoho, the eastern African Pliocene likely had multiple individuals of the same carnivoran genus in a given region (e.g., Hadar, Koobi Fora). These sites commonly have more than one species of *Crocuta* and more than one species of the sabertoothed felid *Dinofelis* (e.g., Lewis & Werdelin, 2022; Werdelin & Lewis, 2001, 2013). While isotope analyses indicate that species of *Crocuta*, for example, overlap in diet, they differ in morphology and somewhat in body size (Lewis & Werdelin, 2022; Robinson et al., 2025). Like the Holocene of Madagascar, the African Pliocene had an increased number and greater diversity of large-bodied prey species (Bibi & Cantalapiedra, 2023) that supported a greater number of carnivoran taxa.

Thus, the two large, extinct species of *Cryptoprocta* may have competed directly for giant lemur prey, particularly in the coastal southwest where we know that they were likely sympatric. However, their preferred prey may have differed in body size (as we have demonstrated for *C. ferox* and *C. spelea*), allowing all three species to coexist in the same area. Reduction in prey abundance results in a five- to sixfold larger decline in the largest carnivorans compared to the smallest species (Carbone et al., 2011). The disappearance of giant lemurs would have had a much greater impact on the largest euplerids (i.e., *C. bevatabe* and *C. spelea*) in comparison to the smaller euplerids. *Cryptoprocta ferox* may have survived simply because its preferred lemur prey survived and the majority of its food items are relatively small vertebrates. The loss of *C. spelea* and *C. bevatabe* removed the top mammalian predators in Madagascar. The influence that this may have had on the extant fosa and other smaller predators is unknown, particularly as any mesopredator release would eventually have been affected by the increasing number of humans and their impact.

CONCLUSION

Our analyses show that prior to 8.3 Ka there were likely three *Cryptoprocta* species (*C. ferox*, *C. spelea*, and *C. bevatabe*) inhabiting coastal southwestern Madagascar. *Cryptoprocta bevatabe* was clearly larger than *C. spelea* and morphologically distinct from its congeners. This new species also had greater strength in flexion and somewhat greater supinatory abilities. Given the manner in which extant fosa wrap their limbs around tree trunks as they climb, this increased strength and supination would have been important to at least maintain, if not increase, the level of scansorial behavior and/or arboreality in the much larger *C. bevatabe*. Increased strength and flexibility in the forelimbs would have also facilitated the ability of this taxon to capture relatively larger prey than its congeners. These differences appear to be more than size-related shape change.

Likewise, *C. spelea* was larger and more robust than the extant *C. ferox*, yet morphological analyses confirm that it maintained a similar arboreal lifestyle. There is a strong geographic signal in its variation in body mass and morphology. Carbon isotope data indicate that *C. spelea* likely targeted lemur prey larger than those targeted by *C. ferox*. The latter likely preferred smaller primate species such as *L. catta*, while *C. spelea* preferred larger species such as the now-extinct *Pachylemur*.

All species of *Cryptoprocta* likely preyed on lemurs in the past, with *C. spelea* targeting moderately large extinct lemurs and *C. bevatabe* able to capture some of the largest species of both semiterrestrial and arboreal extinct lemurs (e.g., *Hadropithecus*, *Palaeopropithecus*, and *Megaladapis*). The ability to capture large-bodied prey by both extinct species of *Cryptoprocta* is even more likely if either or both of the two larger-bodied species hunted cooperatively like extant *C. ferox*. *Cryptoprocta bevatabe* has arboreal features and belongs to a genus where extant forms can hunt cooperatively to take down prey up to roughly their body size even though their body size would suggest that they should not be able to do so. At ~30 kg, *C. bevatabe* was larger and more robust than the large Mitoho *C. spelea*, although its body size was smaller than the largest predators found in continental carnivore guilds. Even though at least two, and possibly all three species of *Cryptoprocta* were sympatric at various times in the past, we believe that *C. bevatabe* is the best current candidate for the predator that left marks assignable to a mammalian predator on the bones of the largest extinct lemurs.

ACKNOWLEDGMENTS

This research could not have been completed without the support of Madagascar National Parks (MNP); our collaborative research embraces and promotes their mission to conserve the remaining biota and to advance the education of local people as well as tourists through visits to the national parks. In particular, we thank former directors of MNP, G.S. Ramangason and M. Rakotoarijaona (both now deceased), for facilitating our research. We thank our dive team which comprised (in addition to co-authors ZSK, PL, and PW) members of the Dominican Republic Speleological Society and Madagascar Cave Diving Association and others: R. Dart, V. Alexandrova, H. Kaspersetz, K. Davidson, M. Bordignon, B. Coleman, C. Pittaro, P. Donaggio Bitner, A. Coffield-Feith, J. De La Puerta Salazar, J. Bulman, and E. Smith. All fossil specimens from Mitoho were collected in 2016, 2018, and 2019 under a convention with Madagascar National Parks and collaborative accord between the UM and the UABEC. The fossils collected during this mission are housed at the UABEC. We thank the curators and collections managers in the mammalogy and zoology departments of the following institutions for access to osteological specimens: AMNH, BMNH, FMNH, KNM, NMNH, NRM, and UA. We also thank M.R. Lague for comments on the manuscript, C. Borgerson and P. Faina for help with the Malagasy language, and Z. Lague for German translation services. We thank the anonymous reviewers and the editors handling this manuscript. This is Duke Lemur Center 1663.

Field research in Madagascar was supported by NSF RAPID grants (BCS 1446959 and BCS 1548223 to Alfred L. Rosenberger), a grant from the National Geographic Society (9571-14, awarded to Alfred L. Rosenberger, KMM, LRG, and the late Gregg F. Gunnell), NSF BCS 1750598 awarded to LRG and SJB, NSF AGS 1702891 awarded to SJB, and NSF EAR-1439559 awarded to DM. Data collection on extant comparative material was supported by NSF (DBS-9222721), Sigma Xi, and Stockton University Distinguished Faculty Fellowships to MEL. Additional analytical work (including isotope analysis and taphonomic research) was supported by grants NSF BCS 1749676 to BEC, NSF BCS 1749211 to KMM, and the Paleontological Association, the University of Massachusetts (UM) Department of Anthropology and Natural History Collections Committee to LRM.

AUTHOR CONTRIBUTIONS

MEL and LRG designed the project. MEL, LRG, NS, ZSK, and BEC drafted the manuscript. LRG, ZSS, SJB, NS, LR, NJR, and PL conducted the fieldwork at Tsimanampesotse National Park. ZSK, PL, and PW (with help from other divers)

collected underwater fossils and stalagmites and prepared an underwater map. NS and SJB reconstructed the local history of cave flooding conducted and DM conducted U-Th dating from stalagmite samples. LRG, KMM, NJR, LR, ZSK, and MB identified and catalogued fossils. MEL and LRG collected morphometric data and performed the morphometric analyses, with commentary by MB. MEL performed body mass analyses. BEC collected new isotope data and MEL and LRG ran statistical analyses of morphometric and isotope data. ZSK created a scale reconstruction of the three *Cryptoprocta* species. KMM and LRM identified and analyzed *Cryptoprocta* predation traces on lemur bones. ZSK and NJR examined the distribution of fossils in the cave and, with LRG, conducted the analysis of taphonomic processes. MB performed the CT scanning. All authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Previously unpublished morphometric and isotopic data can be found in supplementary files. MicroCT scan data and 3D model is available online at MorphoSource (https://www.morphosource.org) using ID: 000084645 and 00084647. DOI:10.17602/M2/M84645 and DOI:10.17602/M2/M84647.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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SUPPLEMENTARY FILES

Supplementary File 1.xlsx: Data set of raw humeral measurements of *Cryptoprocta*.

Supplementary File 2.xlsx: Confusion matrices for DFAs.

Supplementary File 3.xlsx: Raw and Suess-corrected collagen $\delta^{13}C$ values for bone collagen from *Cryptoprocta* and extant and extinct lemurs from subfossil sites along the southern and southwestern coasts of Madagascar. Suess correction follows Crowley et al. (2012).

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Handling Editor: Anthony Friscia.