

On the specific identification of subfossil *Cryptoprocta* (Mammalia, Carnivora) from Madagascar

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ABSTRACT

Grandidier (1902) described a large form of *Cryptoprocta ferox* Bennett, 1833, a genus of Carnivora endemic to Madagascar, from subfossil material dating from the presumed Holocene that he referred to the variety *spelea*. Subsequently there has been varying opinion on the validity of this taxon. In this paper 159 subfossil and 32 modern osteological specimens of *Cryptoprocta* are examined and analyzed to determine if indeed two separate forms can be morphologically distinguished within the sample. On the basis of these tests we conclude that *C. spelea* Grandidier, 1902 is a valid species that existed on the island in the recent geological past. It was presumably a formidable predator that may well have feed on a variety of large lemur species that are now extinct.

KEY WORDS

Mammalia,
Carnivora,
Cryptoprocta,
subfossil,
Holocene,
Madagascar.

RÉSUMÉ

Identification spécifique de Cryptocarpa subfossiles (Mammalia, Carnivora) de Madagascar.

À partir de matériel subfossile datant probablement de l'Holocène, Grandidier (1902) a décrit une forme de *Cryptoprocta ferox* Bennett, 1833 de grande taille, carnivore endémique de Madagascar, qu'il a nommé « variété » *spelea*. Par la suite, il y eut des opinions variées quant à la validité de ce taxon. Dans le présent article, des spécimens ostéologiques subfossiles (n = 159) et modernes (n = 32) de *Cryptoprocta* sont examinés et analysés afin de déterminer si deux formes séparées peuvent vraiment être distinguées à partir de l'échantillon. Sur la base de ces tests, la conclusion est que *C. spelea* Grandidier, 1902 est une espèce valide ayant existé sur l'île au cours d'un passé géologique récent. C'était probablement un redoutable prédateur qui se nourrissait d'une variété d'espèces de lémuriniens de grande taille, éteintes actuellement.

MOTS CLÉS

Mammalia,
Carnivora,
Cryptoprocta,
subfossile,
Holocène,
Madagascar.

INTRODUCTION

The modern native Carnivora fauna of Madagascar is composed of eight species, the largest of which is *Cryptoprocta ferox* Bennett, 1833. This animal shows sexual dimorphism in body mass with adult males reaching between 6.2-8.6 kg and adult females between 5.5-6.7 kg; average body mass across adults is 6.8 kg (Hawkins 1998, 2003). *C. ferox* occurs in a variety of natural and human modified habitats. Its diet is largely composed of vertebrates, particularly mammals, although a wide assortment of other items are taken (Albignac 1973; Rasolonandrasana 1994; Rasoloarison *et al.* 1995; Goodman *et al.* 1997; Rasamison 1997; Goodman 2003). It is a very proficient hunter, being to pursue prey both on the ground and in trees (Laborde 1986). The systematic position of *Cryptoprocta* Bennett, 1833 (e.g., Veron & Catzeflis 1993; Veron 1995) and Malagasy Carnivora in general have been the subject of numerous studies that have reached very different conclusions about the familial and inter-familial relationships of these animals. However, recent molecular studies indicate that all native Malagasy Carnivora form a monophyletic group (Yoder *et al.* 2003).

Bones referable to the genus *Cryptoprocta* have been recovered from a wide variety of Holocene paleontological sites on Madagascar, particularly in the west and extreme south; none of these specimens show signs of mineralization and are hence referred to as "subfossils". Grandidier (1902, 1905) studied osteological material of *Cryptoprocta* from the subfossil sites of Ambolisatra (23°03'S, 43°24'E) to the north of Toliara in the southwest and the cave of Andrahomana (25°50'S, 46°40'E) to the west of Tolagnaro in the extreme southeast and concluded that the material represented a form larger than extant *C. ferox* and he proposed to name it as a distinct "variété" *C. ferox* var. *spelea*. He did not designate a holotype specimen. Petit (1935) subsequently concluded that specimens housed in the Muséum national d'Histoire naturelle, Paris, and presumably part of the Grandidier collection, and redescribed the form *spelea* as a distinct species. This latter author mentioned no holotype.

Lamberton (1939) conducted a detailed osteological and morphometric analysis of *Cryptoprocta* bones collected at a variety of paleontological sites on the island, all presumably dating from the Holocene. He concluded that indeed subfos-

sil *Cryptoprocta* were for the most part larger than the living species of this genus and concurred with Petit (1935) in considering Grandidier's form *spelea* to be a full species. Material referred to *C. spelea* by Lamberton was excavated from the sites of Beavoaha (25°04'S, 44°19'E), grotte d'Ankazoabo (north of Itampolo), Beloha (25°10'S, 45°03'E), Belo-sur-Mer (20°44'S, 44°00'E), Bemafandry (25°07'S, 44°16'E), and Tsiandroina (24°59'S, 44°07'E). Lamberton also noted that at some sites certain subfossils were closer in measurements to extant *C. ferox* than the extinct *C. spelea*, particularly material from Antsirabe, Beloha, and Beavoaha – indicating the possibility that at some sites the two species lived in temporal sympatry. However, given the lack of stratigraphic control associated with the material studied by Lamberton and that no corroborative radiocarbon dates are available, it cannot be substantiated if the two species actually lived at the same time and in the same area.

The work on Malagasy subfossils conducted by Lamberton has been of paramount importance in subsequent work in Quaternary paleontology (e.g., Godfrey & Jungers 2003). However, one of the weak points of his monograph on *Cryptoprocta* was the lack of modern comparative material to assess intraspecific variation in *C. ferox*. On the basis of comparisons he made, it appears that a maximum of three skeletons of recent *C. ferox* were available to him. Given the range of sexual dimorphism in this species (Hawkins 1998) and the possibility of geographic variation associated with the island's dramatic bioclimatic zonation (Ljungquist 1930), this number of specimens was insufficient to capture the possible range of variation in this species. Subsequently certain authors have considered *C. spelea* to be a synonym of *C. ferox* (Savage 1978; Köhncke & Leonhardt 1986).

Finally, amongst the subfossils studied by Lamberton was a mandible from Tsiandroina that had a form distinctly different from other species of *Cryptoprocta*, which he named as a distinct species, *C. antamba*. The name *antamba* was derived from a reputed animal living in southern Madagascar and described by Flacourt

in 1658 (reprinted edition 1995: 221): « C'est une bête grande comme un grand chien qui la tête ronde et au rapport des Nègres, elle a la ressemblance d'un léopard, elle dévore les hommes et les veaux. Elle est rare et ne demeure que dans les lieux des montagnes les moins fréquentés. »

Since Lamberton's study of *Cryptoprocta* more modern and subfossil osteological specimens have become available. The purpose of this paper is to reevaluate these subfossil specimens and specifically to assess morphological variation in extant *C. ferox*, then to compare this range of variation to subfossil material, in order to examine if at last some of these bones can be separated from extant members of this genus.

SPECIMENS AND MEASUREMENTS

In 1989 a substantial portion of the paleontological collections from the Académie malgache were transferred to the Laboratoire de Primatologie et Paléontologie des Vertébrés, Université d'Antananarivo. This included a considerable number of the *Cryptoprocta* specimens described by Lamberton (1939) in the collections of the Académie malgache. A number of recent paleontological field studies have resulted in new material of subfossil *Cryptoprocta* and we have had access to these collections (e.g., the sites of Ankarana and Lakaton'ny akanga). Further, we have been able to measure subfossil and modern material of *Cryptoprocta* in several other museums (see below).

A series of measurements were taken by the first author with a dial calipers to an accuracy of 0.05 mm. The measurements include:

Cranial measurements

Condylbasal length: from the anterior edge of the premaxillae to the posteriormost projection of the occipital condyles.

Skull width: greatest skull width perpendicular to the greatest skull length, above bullae.

Interorbital width: minimum width between the orbits.

Nasal length: greatest length of nasal bone (rostral end to fusion with frontal).

Zygomatic breadth: greatest breadth across the zygomatic process, perpendicular to skull length at the junction of the zygomatic-orbital suture.

Palatal length: from anterior edge of premaxillae to anteriormost point on posterior edge of palate.

Incisive foramen: the inside length of one of the foramen.

Upper molar row: length across the occlusal surface of the maxillary molar series.

Width rostrum: least breadth of rostrum of maxilla above the nasal constriction of the premaxilla.

P²: length of the upper second premolar at greatest width of cusp.

P³: length of the upper third premolar at greatest width of cusp.

P⁴: length of the upper fourth premolar at greatest width of cusp.

M¹: length of the upper first molar at greatest width of cusp.

Lower molar row: length across the occlusal surface of the mandible molar series.

P₂: length of the lower second premolar at greatest width of cusp.

P₃: length of the lower third premolar at greatest width of cusp.

P₄: length of the lower fourth premolar at greatest width of cusp.

M₁: length of the lower first molar at greatest width of cusp.

Post-cranial measurements

Humerus length: greatest length of humerus.

Humerus width distal: greatest width of the distal portion of the humerus, from the medial epicondyle to the lateral epicondyle.

Humerus width proximal: greatest dimension across the humerus head.

Humerus minimum shaft width: smallest width across the humerus shaft.

Ulna length: greatest length of ulna.

Ulna width proximal: greatest dimension across the ulna base.

Radius length: greatest length of radius.

Radius width distal: greatest dimension across the radius head.

Radius width proximal: greatest dimension across the radius base.

Femur length: greatest length of femur.

Femur width distal: greatest width of distal part of femur, from median condyle to lateral epicondyle.

Femur width proximal: greatest width of distal portion of femur, from medial condyle to the greater trochanter.

Femur minimum shaft width: smallest width across femur shaft.

Tibia length: greatest length of tibia.

Tibia width proximal: greatest width of tibia proximally from the lateral condyle to medial condyle.

Tibia width distal: greatest distal width of tibia.

Modern and subfossil material was examined from the following collections (Appendices 1 and 2)

AMNH American Museum of Natural History, New York;

FMNH Field Museum of Natural History, Chicago;

MCZ Museum of Comparative Zoology, Harvard University;

MNHN Muséum national d'Histoire naturelle, Zoologie (Mammifères et Oiseaux) and Anatomie comparée, Paris;

UA Département de Paléontologie et d'Anthropologie biologique, Université d'Antananarivo;

USNM National Museum of Natural History (formerly United States National Museum), Washington, D.C.

Both modern and subfossil specimens were divided into two age classes: sub-adult and adult. For cranium post-canine tooth eruption patterns were used to classify age groups – individuals retaining aspects of sub-adult dentitions or with non-fully-erupted molars were considered sub-adult and those with fully erupted molars were noted as adults. In a few cases this system could not be used (e.g., cranial fragments lacking molars) and suture development was used to separate the two age classes. For long bones evidence of non- or partial-ossification of sutures was used to classify sub-adults and completely ossified bones for adults. Designation of the sex of modern material was obtained directly from specimen labels, and numerous individuals lacked this information.

On the basis of descriptions of excavated *Cryptoprocta* subfossils (Grandidier 1902; Lambertson 1939; Petit 1935), there is no evidence that any of this material was found articulated and thus at a given site it is not possible to determine how many unique individuals are involved in each sample. Given this situation and the fact that the number of elements available for any given measurement was often limited, we decided to consider the right and left elements of any given long bone as independent data points. A considerable number of missing measurements imposed notable restrictions on the types of statistical analyses that could be conducted, particularly with regards to multivariate tests (e.g., discriminant function and principal components). Visual examination of the data and statistical tests indicate that at least some of the subfossil samples

belong to a different population of larger size than the modern samples of *Cryptoprocta ferox*. The subfossil sample could be composed of *C. ferox*, of another form of *Cryptoprocta* or of both. Since bones recovered from the collections did not allow comprehensive measurements for the same bones (in case of skull fragments) and/or could not be assigned to specific individuals (post-cranium) it was impossible to run any meaningful multivariate ordination analyses or multivariate tests for the significance of differences. Therefore we had to restrict the statistical analyses to univariate tests. In order to distinguish forms in the subfossil sample that could not be assigned to *C. ferox*, we used the measurements for modern adults to calculate normal distributions for the various characters. These normal curves are characterized by the mean and standard deviations of the modern *C. ferox*. We then used these statistics to calculate z-values for the subfossil samples.

Analyses performed to evaluate species differences were based on the pooled sample of specimen belonging to both sexes. As modern *Cryptoprocta ferox* males are larger than females, pooling sexes does blur possible size differences between modern and subfossil animals, the latter of which might have belonged to a different, larger species. However, we do not think that this procedure affects our conclusions for several reasons. First, there is no evidence that the representation of the two sexes differs between the modern and the subfossil samples. Second, in the modern sample of known sex there are more males ($n = 3$ or 4) than females ($n = 2$; Table 2). If we used these specimens for a balanced sample of sexed individuals to characterize the modern form (based on equal numbers of males and females) the mean values of morphological measurements listed for the pooled sample of the modern form would be lower than the actual means listed in Table 1. This would increase the difference between the modern and the subfossil sample and more of the subfossil specimens would have been assigned to the larger subfossil form. By including all specimens we are likely to make a conservative error.

RESULTS

AGE VARIATION IN MODERN *CRYPTOPROCTA FEROX*

For several of the osteological measurements statistical differences were found between adult and subadult *Cryptoprocta ferox* (Table 1). As a result only adult specimens are used in the subsequent comparisons made in this paper. In a few cases individuals classified as sub-adults fell within the measurement range of adults, but in order to maintain a rigid separation of the age classes it was decided not to include these individuals in the analysis – this had the consequence of reducing sample sizes.

SEXUAL DIMORPHISM IN MODERN *CRYPTOPROCTA FEROX*

Hawkins (1998) has already established that adult male *C. ferox* is larger on average than adult females based on a series of external morphological measurements. For most of her linear measurements males tended to be less than 10% larger than females. Here we examine the existence of the same pattern in cranial, dental, and post-cranial characters. The number of complete and sexed skeletons of this species available in museums is rather limited. In total a maximum of four adult male and two adult female skulls and mandibles were measured and only two adult male and one adult female post-cranial skeletons. Adult males were larger than females with respect to the condylobasal length, braincase width, palatal length, width rostrum, and lower molar row (Table 2). These differences were statistically significant with probability values at least at the 0.05 level. For those variables that showed statistically significant differences males were 5.2-17.6% larger than females. The same general pattern held for the dental measurements, with males being larger than females, but in this case none of these differences were statistically significant. This degree of sexual dimorphism is within the range of that found in similar sized sympatrically occurring felids (Felidae; Dayan *et al.* 1990) and mongooses (Herpestidae; Simberloff *et al.* 2000) in the Middle East and Asia. The ratio of the condylobasal length of the skulls of males to females varies between 1.075 and 1.110 for three species of felids and

Table 1. — Cranial and post-cranial measurements of extant *Cryptoprocta ferox* Bennett, 1833 and subfossil *Cryptoprocta* Bennett, 1833. Measurements are presented as mean \pm standard deviation, number of specimens, minimum and maximum measurements. For samples of two or less no descriptive statistics are presented. Abbreviations: ¹, in several cases specimens recovered during paleontological excavations, particularly in upper strata of sites such as caves, may represent individuals that were alive during historical times. However, given the lack of stratigraphic control for much of the material analyzed herein it is not possible to separate the “modern” from the “subfossil” bones based on external appearance. Hence, all of this material is combined into a single category. Statistically significant t-values between adult modern specimens of *Cryptoprocta ferox* and adult subfossil specimens of *Cryptoprocta*: *, $0.05 \geq P < 0.01$; **, $P \leq 0.01$; ***, $P \leq 0.001$; ², see text for the procedure for assigning specimens of the subfossil sample to *Cryptoprocta spelea* Grandidier, 1902; ³, statistically significant t-values between adult and sub-adult modern specimens of *Cryptoprocta ferox*: *, $0.05 \geq P < 0.01$; **, $P \leq 0.01$.

	Modern <i>Cryptoprocta</i> <i>ferox</i> (adult)	Modern <i>Cryptoprocta</i> <i>ferox</i> (sub-adult)	Subfossil <i>Cryptoprocta</i> ¹ (adult)	Subfossil <i>Cryptoprocta</i> <i>spelea</i> ² (adult)	Ratio of <i>C. spelea</i> / <i>C. ferox</i>
Condylbasal length	124.7 \pm 5.88 ^{3*} 12, 114.5-133.3	117.3 \pm 7.88 5, 107.3-128.6	141.5 \pm 10.61 ^{**} 3, 133.1-153.4	153.4	1.23
Braincase width	43.5 \pm 0.97* 14, 42.0-45.0	41.9 \pm 1.96 5, 39.0-44.2	45.7 \pm 1.68 ^{**} 3, 43.8-47.0	46.7 2, 46.3-47.0	1.07
Nasal length	22.7 \pm 1.70* 14, 20.3-25.0	20.8 \pm 2.10 6, 17.5-23.3	26.2 \pm 3.47* 3, 23.2-30.0	30.0	1.32
Zygomatic breadth	76.3 \pm 4.74 13, 67.8-85.0	72.0 \pm 7.58 6, 61.2-81.8	2, 84.7-92.4 ^{**}	92.4	1.21
Interorbital width	25.0 \pm 1.56 16, 22.3-28.5	24.0 \pm 1.38 6, 21.9-25.8	2, 24.2-27.0	27.0	1.08
Palatal length	60.4 \pm 3.93 16, 52.6-66.2	56.9 \pm 4.04 6, 51.6-62.0	70.0 \pm 7.17 ^{**} 3, 65.1-78.2	78.2	1.29
Upper molar row length	32.6 \pm 1.41 16, 30.4-35.6	31.9 \pm 1.56 6, 30.1-34.6	36.0 \pm 1.60 ^{***} 5, 34.4-38.4	37.6 2, 36.8-38.4	1.15
Width rostrum	28.2 \pm 2.09 16, 23.3-30.7	27.0 \pm 2.08 6, 23.6-30.1	32.3 \pm 4.26* 3, 28.2-36.7	36.7	1.30
p²	5.8 \pm 0.40 16, 5.1-6.3	5.7 \pm 0.36 6, 5.2-6.1	6.4 \pm 0.32 ^{**} 6, 6.0-6.9	6.7 2, 6.5-6.9	1.15
p³	9.6 \pm 0.55 16, 8.5-10.4	9.7 \pm 0.72 6, 8.6-10.8	10.4 \pm 0.69* 7, 9.5-11.3	11.2 2, 11.1-11.3	1.17
p⁴	15.3 \pm 0.60 16, 13.9-16.2	15.1 \pm 0.79 6, 14.1-16.1	16.0 \pm 0.90* 9, 15.1-17.7	17.1 2, 16.4-17.7	1.12
M¹	7.4 \pm 0.72 13, 5.4-8.2	7.3 \pm 0.43 6, 6.7-7.8	8.2 \pm 0.64 4, 7.7-9.1	9.1	1.23
Lower molar row length	34.6 \pm 2.17 15, 29.2-37.0	33.3 \pm 1.53 6, 31.4-35.9	36.9 \pm 2.34* 10, 32.1-40.1	39.3 \pm 0.69 3, 38.9-40.1	1.14
P₂	5.5 \pm 0.51 11, 4.5-6.1	5.3 \pm 0.36 6, 4.9-5.9	2, 6.1-6.8*	6.8	1.24
P₃	7.9 \pm 0.32* 13, 7.3-8.3	7.5 \pm 0.48 6, 6.7-7.8	8.5 \pm 0.76 3, 7.7-9.2*	9.2	1.16
P₄	9.6 \pm 0.51 13, 8.9-10.6	9.3 \pm 0.43 6, 8.9-10.0	10.3 \pm 1.06 3, 9.1-11.7	11.7	1.22
M₁	12.4 \pm 0.53* 13, 11.6-13.1	11.8 \pm 0.53 6, 11.1-12.6	12.8 \pm 0.51 3, 12.4-13.4	13.4	1.08
Humerus length	116.1 \pm 5.25* 9, 108.5-127.5	108.9 \pm 5.30 4, 101.8-114.0	134.4 \pm 9.9 ^{***} 9, 121.9-146.8	137.9 \pm 8.24 7, 122.7-146.8	1.19
Humerus width distal	27.9 \pm 1.40 ^{**} 12, 26.0-30.0	25.7 \pm 1.14 5, 24.1-27.2	32.1 \pm 2.61 ^{***} 27, 26.2-36.5	33.7 \pm 1.67 16, 30.7-36.5	1.21
Humerus width proximal	22.5 \pm 1.50* 9, 20.8-25.0	20.5 \pm 0.94 4, 19.1-21.2	27.7 \pm 2.58 ^{***} 12, 23.5-32.0	28.6 \pm 1.89 10, 26.5-32.0	1.27
Humerus minimum shaft width	8.4 \pm 0.56* 12, 7.7-9.5	7.6 \pm 0.64 5, 6.9-8.3	10.0 \pm 0.98 ^{***} 27, 8.6-11.9	10.7 \pm 0.69 16, 9.6-11.9	1.27
Ulna length	112.9 \pm 5.47 13, 104.1-123.2	107.8 \pm 8.20 4, 97.3-116.6	134.7 \pm 6.65 ^{***} 9, 122.3-143.2	136.3 \pm 5.07 8, 126.6-143.2	1.21
Ulna width proximal	13.3 \pm 1.21 12, 11.4-15.2	13.4 \pm 1.58 4, 11.1-14.6	17.7 \pm 1.81 ^{***} 16, 14.0-20.5	18.2 \pm 1.44 14, 16.0-20.5	1.37

	Modern <i>Cryptoprocta</i> <i>ferox</i> (adult)	Modern <i>Cryptoprocta</i> <i>ferox</i> (sub-adult)	Subfossil <i>Cryptoprocta</i> ¹ (adult)	Subfossil <i>Cryptoprocta</i> <i>spelea</i> ² (adult)	Ratio of <i>C. spelea</i> / <i>C. ferox</i>
Radius length	88.6 ± 4.14* 10, 83.6-97.4	82.9 ± 4.62 4, 76.9-88.0	106.2 ± 4.24*** 12, 96.5-111.6	106.5 ± 4.19 11, 97.4-111.6	1.20
Radius width distal	15.8 ± 1.06 10, 14.4-18.0	14.7 ± 0.60 4, 13.9-15.2	19.9 ± 1.61*** 12, 16.6-21.8	20.1 ± 1.42 11, 17.8-21.8	1.27
Radius width proximal	12.0 ± 0.70* 10, 11.1-13.4	10.9 ± 0.46 4, 10.5-11.5	14.2 ± 1.21*** 12, 12.0-16.0	14.4 ± 0.98 11, 13.4-16.0	1.20
Femur length	139.2 ± 7.51 11, 129.1-152.4	132.4 ± 8.53 5, 119.8-141.0	158.0 ± 11.08*** 18, 138.0-170.6	167.0 ± 2.89 10, 161.6-170.6	1.20
Femur width distal	26.3 ± 3.50 10, 23.1-35.3	24.3 ± 1.11 5, 23.2-26.0	30.0 ± 2.48** 17, 26.2-33.6	32.1 ± 0.96 9, 30.0-33.6	1.22
Femur width proximal	28.4 ± 1.67 10, 25.5-30.5	26.7 ± 1.75 5, 23.9-28.6	33.4 ± 2.62*** 23, 28.5-37.8	35.0 ± 1.29 15, 33.3-37.8	1.23
Femur minimum shaft width	10.0 ± 0.72 11, 8.6-11.0	9.2 ± 0.94 5, 7.7-10.1	12.6 ± 1.23*** 21, 10.5-14.9	13.2 ± 0.86 14, 11.9-14.9	1.32
Tibia length	129.1 ± 6.88 11, 119.1-142.1	124.8 ± 6.37 5, 115.0-130.7	142.1 ± 8.69*** 14, 127.0-155.6	150.3 2, 149.9-150.6	1.16
Tibia width proximal	27.0 ± 3.12 11, 24.0-34.8	25.4 ± 1.44 5, 23.3-26.7	29.5 ± 3.50 15, 22.3-36.0	34.8 2, 33.5-36.0	1.29
Tibia width distal	18.3 ± 1.60 11, 16.3-20.8	17.7 ± 1.13 5, 16.1-19.0	20.0 ± 1.09** 17, 18.9-22.2	22.2 2, 22.2-22.2	1.21

TABLE 2. — Sexual dimorphism in skull dimensions of adult modern *Cryptoprocta ferox* Bennett, 1833. Only characters are listed for which there was a significant difference between sexes with $P \leq 0.05$ according to t-tests. Measurements are presented as in Table 1. Dimorphism is expressed as the average size of male trait divided by the size of female trait.

	Female	Male	Dimorphism
Braincase width	42.4 ± 0.49 2, 42.0-42.7	44.6 ± 0.59 3, 43.9-45.0	1.052
Palatal length	55.2 ± 3.61 2, 52.6-57.7	63.4 ± 3.36 4, 58.5-66.2	1.149
Width rostrum	24.7 ± 1.91 2, 23.3-26.0	28.9 ± 1.26 4, 27.9-30.7	1.170
Lower molar row length	30.6 ± 1.98 2, 29.2-32.0	36.0 ± 1.00 4, 35.0-37.0	1.176

between 1.033 and 1.072 for three species of mongooses. This ratio is 1.077 for modern *Cryptoprocta ferox*. The number of sexed post-cranial specimens was insufficient for statistical comparisons, but males tended to be larger than females.

DIFFERENCES BETWEEN MODERN AND SUBFOSSIL *CRYPTOPROCTA*

Given the problem of often highly fragmentary subfossil material and missing values for numerous measurements, it was not possible to conduct

multivariate analyses to examine differences between extant and subfossil *Cryptoprocta* specimens. To further examine these distributions, measurements for the two dental characters, with largest sample size in the subfossil samples were plotted as frequency histograms (Fig. 1). In both of these cases the subfossil specimens for the most part are notably larger than the modern material. Further, bivariate plots of humerus and tibia measurements (Fig. 2) show the same pattern of the subfossil being larger than the modern

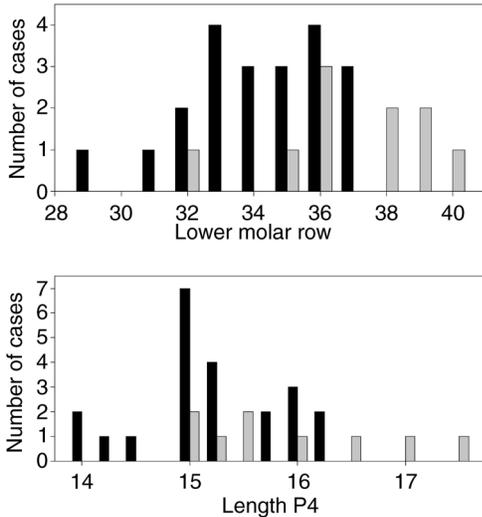


FIG. 1. — Frequency distributions of dental measurements of modern (black) and subfossil (gray) specimens of *Cryptoprocta* Bennett, 1833.

specimens. Our interpretation of these results is that there are two different species represented in the samples. However, for both the groups of tooth and long bone variables there is overlap between a subset of the subfossil and recently collected specimens. This can be best explained by the presence of two different species in the subfossil deposits: a larger subfossil species of *Cryptoprocta*, which is the more common taxon, mixed with some individuals of *C. ferox*.

In order to distinguish specimens in the subfossil sample that should not be assigned to *C. ferox* we used the measurements for modern adult *C. ferox* to calculate normal distributions for the various characters. These normal curves are characterized by the mean and standard deviations of the modern *C. ferox*. We then used these statistics to calculate z-values for the subfossil samples. Z-values above 1.96 indicate that the individual in question did not belong to the form *C. ferox* with $P \leq 0.05$. These samples were then assumed to represent a different form than *C. ferox*. If multiple measurements were available per specimen, it was assigned to *C. ferox* if the majority of z-values were below 1.96. If the majority of z-values were above 1.96 the specimen was classified as the larger sub-

fossil form. Z-values were remarkably consistent for multiple measurements per post-cranial bone and the skull. On the basis of these samples we then calculated size characteristics for *C. spelea* (Table 1). Using these criteria one or two specimens were assigned to larger subfossil *Cryptoprocta* based on skull measurement. The size ratio of morphometric measurements (size of the larger subfossil *Cryptoprocta* to the size of *C. ferox*) ranges between 1.07 and 1.32 for skull measurements (mean and standard deviation: 1.19 ± 0.08 ; $n = 17$ measurements). For post-cranial measurements, up to 16 specimens were assigned to the larger subfossil form. Here the size ratio varied between 1.19 and 1.37 (mean = 1.24 ± 0.06 ; $n = 16$ measurements; Table 1).

One of the few intact subfossil skulls and associated mandibles available for this study of *Cryptoprocta spelea* is illustrated in Figures 3-5. This individual, which is designated as the neotype of this species (see below), is compared in these photographs to one of the largest individuals of modern *C. ferox* examined by us. In general, *C. spelea* is notably more robust and with more massive teeth than extant *C. ferox*.

TAXONOMIC CONCLUSIONS

On the basis of the analyses presented herein we consider that there is evidence to recognize a larger species of subfossil *Cryptoprocta* that can be separated from extant *C. ferox*. No type material associated with the name *spelea* was designated by Grandidier (1902), and to our knowledge any other researcher addressing *Cryptoprocta* taxonomy has allocated the type material (Grandidier 1905; Petit 1935). Further, in the collections of the MNHN examined no type material was found. In the interest of taxonomic stability we prefer to maintain the name *C. spelea* for this larger form and designate a neotype.

NEOTYPE

We have not located the subfossil material from Andrahomana that was originally associated with

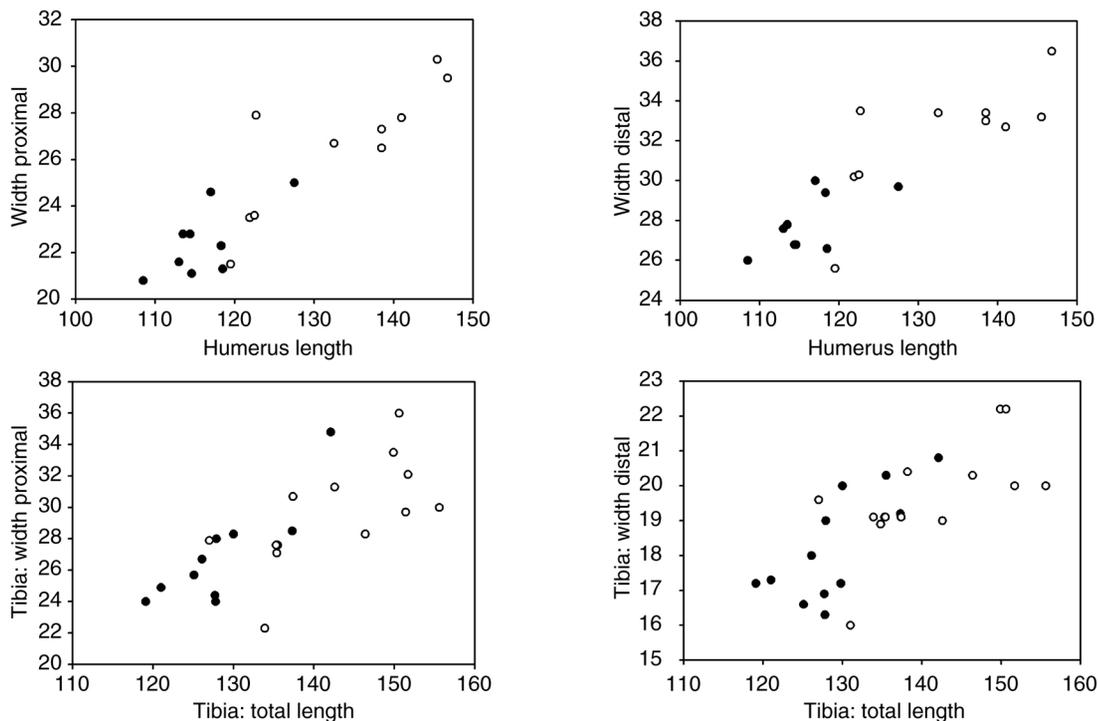


FIG. 2. — Bivariate plots of humerus and tibia measurements of modern (black) and subfossil (white) specimens of *Cryptoprocta* Bennett, 1833. The two bones were chosen for illustration because they represent cases of good separation (humerus) and the bone with the smallest differences (tibia) between modern and the subfossil sample.

the name *spelea*. One of the specimens of *C. spelea* illustrated in Lambertson's (1939) monograph was a skull and mandible collected in the grotte d'Ankazoabo (his plate I), that has a distinctive anomaly to the lower right tooth row of the mandible. This specimen was subsequently cataloged as MNHN CG 1977.755 and we designate it as the neotype of *C. spelea*. Although this specimen is not from the same subfossil deposits associated with the original utilization of the name *spelea*, it is in an excellent state of preservation and serves the purpose of characterizing this species.

Lamberton (1939) also named the species *Cryptoprocta antamba* based on an oddly shaped mandible found at Tsiandroina. We have not relocated this specimen in any museum collection, but it may be a slightly teratological individual of *C. spelea*.

DISCUSSION

Over the course of the past few thousand years a large number of land vertebrates have gone extinct on Madagascar. These extinctions have presumably had a notable influence on various ecological processes on the island, such as seed dispersal, predator-prey relations, etc. Amongst these vanished animals are at least 17 species of lemurs – the vast majority of which were larger than extant forms (Godfrey & Jungers 2001). On the basis of dental structure and long bone morphology inference can be drawn about certain aspects of the feeding ecology and locomotion of these extinct primates (Godfrey *et al.* 1997). However, nothing is known about other factors associated with their life history, such as predation pressure. Recently a subfossil eagle, *Stephanoaetus mahery* Goodman, 1994, has been described from the Quaternary of



FIG. 3. — Dorsal views of the cranium of a recently collected *Cryptoprocta ferox* Bennett, 1833 (above) and the neotype subfossil *C. spelea* Grandidier, 1902 (MNHN 1977.755). The specimen of *C. ferox* (AMNH 188213) collected at Manakara in 1931 is amongst some of the larger modern individuals of this species measured during the course of this study. Scale bar: 10 cm.

Madagascar that may have been able to feed on lemurs of considerable size (Goodman 1994). However, this raptor would not have been able to predate on the adults of the larger extinct lemur

species, several of which weighed more than 30 kg. Given the size of *Cryptoprocta spelea*, its massive jaws, and large carnassial teeth, it must have been a formidable predator and certainly



FIG. 4. — Ventral views of the cranium of a recently collected *Cryptoprocta ferox* Bennett, 1833 (above) and the neotype subfossil *C. spelea* Grandidier, 1902 (MNHN 1977.755). The specimen of *C. ferox* (AMNH 188213) collected at Manakara in 1931 is amongst some of the larger modern individuals of this species measured during the course of this study. Scale bar: 10 cm.

capable of taking larger prey than the extant *C. ferox*. This later species is known to physically take animals up to slightly more than 6 kg. Larger prey, such as the bush-pig (*Potamochoerus larvatus*

(F. Cuvier, 1822)), which weigh up to 70 kg, have been identified from food remains of this carnivore (Rasoloarison *et al.* 1995). However, it is unclear if these animals were physically taken by



FIG. 5. — Lateral views of the cranium of a recently collected *Cryptoprocta ferox* Bennett, 1833 (above) and the neotype subfossil *C. spelea* Grandidier, 1902 (MNHN 1977.755). The specimen of *C. ferox* (AMNH 188213) collected at Manakara in 1931 is amongst some of the larger modern individuals of this species measured during the course of this study. Scale bar: 10 cm.

C. ferox or their carcasses scavenged. Adults of many of the subfossil lemurs would presumably have been in the range of prey size of the more massive predator *C. spelea* and since its presumed extinction there may have been considerable changes in predator pressures on the island's larger land vertebrates.

On the basis of current subfossil evidence *Cryptoprocta spelea* occurred at a variety of sites from Lakaton'ny akanga in the far north near Antsiranana, along the western portion of Madagascar, south to numerous sites at the southern end of the island; it is also recorded on the central highlands at Antsirabe (Table 3). At sev-

eral of these sites both species of *Cryptoprocta*, *C. ferox* and *C. spelea*, are represented. As mentioned above, due to a lack of stratigraphic control at most of the sites we have analyzed bone remains from, it is impossible to verify if the two species co-occurred in the same horizon. Radiocarbon dating is needed to assess if these animals were temporally sympatric.

According to community ecology theory coexisting species with similar food requirements have to differ in size to avoid competition over food resources (Hutchinson 1959). Condylbasal length (CBL) does not seem to be the best measurement in support of this hypothesis. Nevertheless modern sympatric mongooses (Simberloff *et al.* 2000) and felids (Dayan *et al.* 1990) of similar size show size ratios of the CBL between pairs of sympatric species of descending sizes between 0.98 and 1.35 with a median of 1.16 ($n = 6$ pairwise comparisons; based on mean values per species without considering sexual dimorphism). The value of 1.25 calculated for the ratio of CBL of *C. spelea* to *C. ferox* is within this range. Size ratios of other cranial or post-cranial measurements were also within the size ratios found between sympatric carnivores (Table 1). This indicates that the two forms of *Cryptoprocta* might have been separated well enough in size to be able to coexist.

Throughout different areas of Madagascar local people describe two forms of *Cryptoprocta*, or *fosa* in Malagasy, to be living today – *fosa mainty* or “black *Cryptoprocta*” and *fosa mena* or “reddish *Cryptoprocta*”; the latter form is said to be smaller than the former. Further, there are reports from the southwest of a whitish morphotype (Decary 1950). It remains unclear if the differentiation of these forms is associated with sexual or age dimorphism or general variation in extant *C. ferox* or if indeed at least two species of this genus are amongst the extant fauna on the island. We quickly add to this point that all the modern specimens we have examined correspond to *C. ferox*. However, there are stories of extremely large *fosa* occurring in certain regions of the island. Louvel (1954: 45) reported « à Morondava l’agent forestier d’une compagnie nous a déclaré avoir capturé

TABLE 3. — Specific identity of *Cryptoprocta* Bennett, 1833 subfossils recovered from various paleontological sites based on the analyses presented in the text and measurement ranges in Table 1. Abbreviations: +, present at site; –, not present at site.

Site	<i>C. ferox</i> Bennett, 1833	<i>C. spelea</i> Grandidier, 1902
Ampasambazimba	+	–
Ankarana	+	+
Ankazoabo	–	+
Antsirabe	+	+
Bevoha	+	+
Beloha	+	+
Belo-sur-Mer	+	+
Bemafandry	–	+
Betioky	–	+
Lakaton’ny akanga	–	+
Lelia	+	–
Manombo	+	+
Tsiandroina	–	+
Tsiravé	+	–

dans son poulailler un *fosa* de deux mètres de longueur, pesant trente kilogrammes ! » However, this is the region that Hawkins (1998) captured nearly 30 individuals of *Cryptoprocta* and all of which fell within the morphological range of *C. ferox*. Genetic research involving samples gathered from various areas of the island and including material of subfossil *C. spelea*, might reveal the existence of a second extant species of this genus.

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APPENDIX 1

Modern comparative material of *Cryptoprocta ferox* examined. Abbreviations: CFPF, Centre de Formation Professionnelle Forestière; see text for museum acronyms.

AMNH: Betroka, 170 km E Toliara (100463); Manakara (188213).

FMNH: Kirindy (CFPF) (161707); Sakaramy (Antsiranana) (161793).

MCZ: Forêt entre Vondrozo et Ifanadiana (45969); no locality (45970); near Diego (45971).

MNHN: no locality (1-12.808); "Madagascar" (1880.2544); "Madagascar" (1880.2545); no locality (1927.227); "Madagascar" (1927.2366); 20 km à l'ouest de Vondrozo (1932.3553); no locality (1933.31); captive (1940.1211); Sakaraha (1952.93); Morondava (1960.3841); "Madagascar" (1962.364); "Madagascar" (1962.1601); "Madagascar" (1962.2088); Morondava (1962.3842); "Madagascar" (1963.348); no locality (1974.148); no locality (1977.544); no locality (1977.555); no locality (1977.556); "Madagascar" (1992.1667); Périnet (1992.1668); "Madagascar" (1992.1669).

UA: no locality (240); Kirindy (CFPF) (280).

USNM: "Ambohitratrimo" (112841).

APPENDIX 2

Subfossil specimens of *Cryptoprocta* spp. examined (see text for museum acronyms).

Ampasambazimba: tibia (UA three uncatalogued specimens).

Ankarana: cranium (UA 6121, 6122, 8446, 8447, 8453, 6125); humerus (UA 6127, 6128, 6129, 6808, 8443); radius (UA 6132); ulna (UA 6130); femur (UA 6168, 6169, 7270); tibia (UA 6170); fibia (UA 6171).

Antsirabe: cranium (UA two uncatalogued specimens); humerus (UA seven uncatalogued specimens); ulna (UA one uncatalogued specimen); femur (UA eight uncatalogued specimens).

Bevoha: cranium (UA four uncatalogued specimens); humerus (UA nine uncatalogued specimens); radius (UA four uncatalogued specimens); ulna (UA seven uncatalogued specimens); femur (UA 1232 and five uncatalogued specimens); tibia (UA nine uncatalogued specimens); fibia (UA one uncatalogued specimen).

Beloaha: cranium (UA three uncatalogued specimens); humerus (UA eight uncatalogued specimens); radius (UA four uncatalogued specimens); ulna (UA eight uncatalogued specimens); femur (UA 11 uncatalogued specimens); tibia (UA nine uncatalogued specimens).

Belo-sur-Mer: humerus (UA three uncatalogued specimens).

Bemafandry: humerus (UA one uncatalogued specimen); radius (UA one uncatalogued specimen); ulna (UA one uncatalogued specimen); femur (UA one uncatalogued specimen).

Betioky: humerus (UA one uncatalogued specimen); femur (UA one uncatalogued specimen).

Grotte d'Ankazoabo: humerus (UA four uncatalogued specimens); radius (UA one uncatalogued specimen); ulna (UA two uncatalogued specimens); femur (UA two uncatalogued specimens); fibia (UA two uncatalogued specimens); fibia (UA one uncatalogued specimen).

Lakaton'ny akanga: femur (UA two uncatalogued specimens).

Lelia: cranium (AMNH 199544).

Manombo: humerus (UA one uncatalogued specimen); radius (UA one uncatalogued specimen); femur (UA two uncatalogued specimens); tibia (UA one uncatalogued specimen); fibia (UA one uncatalogued specimen).

Tsiandroina: radius (UA one uncatalogued specimen); femur (UA one uncatalogued specimen); fibia (UA one uncatalogued specimen).

Tsirave: humerus (UA two uncatalogued specimens); ulna (UA one uncatalogued specimen); femur (UA one uncatalogued specimen).