



## See how they ran: morphological and functional aspects of skeletons from ancient Egyptian shrew mummies (Eulipotyphla: Soricidae: Crocidurinae)

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Animals served important roles in the religious cults that proliferated during the Late (ca. 747–332 BCE) and Greco-Roman Periods (332 BCE–CE 337) of ancient Egypt. One result was the interment of animal mummies in specialized necropolises distributed throughout the country. Excavation of a rock-tomb that was re-used during the Ptolemaic Period (ca. 309–30 BCE) for the interment of animal mummies at the Djehuty Site (TT 11–12) near Luxor, Egypt, was carried out in early 2018 by a Spanish–Egyptian team sponsored by the Consejo Superior de Investigaciones Científicas, Madrid. The tomb burned sometime after deposition of the mummies, leaving behind abundant disassociated skeletal remains, primarily of avians, but also including two species of shrews (Soricidae): *Crocidura olivieri* and *C. religiosa*. To investigate possible intraspecific variation in morphology and locomotor function in these two species during the last two millennia, we measured morphological features of individual postcranial bones from the two archaeological samples and calculated indices that have been used to assess locomotor function. We compared the measurements to those from modern *C. olivieri*, *C. religiosa*, and *C. suaveolens* using principal components analysis, and we compared locomotor indices to those we calculated for the three modern species of *Crocidura* and to those from nine species of myosoricine shrews. Osteological features of the postcranial skeleton of conspecific Ptolemaic and modern samples of *C. olivieri* and *C. religiosa* are generally similar in character and proportion, and, skeletally, these shrews and modern *C. suaveolens* are consistent with soricids having a primarily ambulatory locomotor mode. One exception is the deltopectoral crest of the humerus, which appears to be longer in modern *C. religiosa*. Despite general conservation of form and function, Ptolemaic *C. olivieri* had larger body size than modern Egyptian populations and were more similar in size to modern *C. olivieri nyansae* from Kenya than to modern *C. olivieri olivieri* from Egypt.

Key words: anatomy, body size variation, *Crocidura fulvastra*, geographic variation, Insectivora, Myosoricinae, Ptolemaic, Soricomorpha, substrate use

Animals served important roles in the religion of the ancient Egyptians, particularly during the Late (ca. 747–332 BCE) and Greco-Roman Periods (332 BCE–CE 337), when animal cults proliferated. Millions of animals were eventually mummified and ceremonially interred in specialized necropolises distributed throughout the country (Ikram 2005a, 2015; Kessler and Nur el-Din 2005; von den Driesch et al. 2005). Animal mummies and animal statues may have served as votive offerings to specific Egyptian deities (Ikram 2005a, 2005b, 2015), or their ritualized burial may have been part of a complex ceremonial

cycle that insured their eternal rebirth and participation in the annual transformation of the Egyptian chief god (or king) as part of the first creation myth (von den Driesch et al. 2005). Among the lesser-known mammals mummified and ceremonially interred in sacred cemeteries were shrews (Eulipotyphla: Soricidae) that, together with diurnal raptors, may have represented dark (night) and light (day) aspects, respectively, of the god Horus. Alternatively, shrews and other animals more commonly associated with nighttime and, therefore, with “darkness” (e.g., snakes, catfish, and worms) may have been forms

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of the “hidden” sun god Atum, who represented the setting sun that was believed to travel through the underworld each night. Other religious associations also have been suggested, but in each case, preservation by mummification was essential to ensure continuity of the cycle (Wilkinson 1847; Brunner-Traut 1965, 1984; Lurker 1980; Kessler 1989, 2007; Houlihan 1996; Osborn and Osbornová 1998; Ikram 2005a, 2005b, 2005c, 2015; Kessler and Nur el-Din 2005; von den Driesch et al. 2005).

The Djehuty Project, a long-term excavation sponsored by the Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain, is concerned with the study of the rock tombs of Djehuty and Hery, two Eighteenth Dynasty (ca. 1550–1290 BCE) court officials who were interred in the hillside of Dra Abu el-Naga near Luxor, Egypt (Galán 2018). Some of the many ceremonial and burial chambers in the immediate vicinity of these tombs were subsequently re-used as necropolises for sacred animal mummies. Demotic (ancient Egyptian script used ca. 650 BCE–5th century CE) writings painted on the tomb walls indicate deposition of animal mummies occurred mostly during the Ptolemaic Period (ca. 309–30 BCE). One aspect of the Djehuty Project’s 2018 field season focused on Excavation Unit (EU) 194, a burial chamber of a secondary tomb-chapel that overlaps the innermost room of Djehuty’s tomb-chapel. The soot-blackened roof and walls of EU 194 attest to the subsequent fire that burned most animal mummies deposited therein. As destruction of these mummies was antithetical to ancient Egyptian religious practices (several other tombs in the area contain undisturbed deposits of animal mummies) the fire in EU 194 was probably accidental, and it may have occurred long after the mummies were deposited. Although the wrappings and soft tissues of the mummies were destroyed, processing of sediments from these chambers provided abundant intact, but disassociated, skeletal remains that can be examined directly. The remains are predominantly from avians, but also include lesser numbers of bones from mammals, reptiles, and fishes (Ikram and Spitzer 2019). Among the mammalian remains, by far the most abundant are those of two species of soricids: *Crocidura olivieri* and *C. religiosa*.

At least seven species of soricids were embalmed by the ancient Egyptians. One species is now extinct and two do not occur in modern Egypt (Hutterer 1994; Woodman et al. 2017). We know little about how continuing regional desertification affected local populations of these animals in the Nile Valley (Brookfield 2010). We also do not know how large numbers of these animals were procured for religious practices (Woodman et al. 2017). Shrews may have been obtained locally, or, as documented for some other animals, they may have been raised in captivity or semi-captivity or captured and transported from elsewhere (Kessler 2003; Kessler and Nur el-Din 2005; von den Driesch et al. 2005; Woodman et al. 2017). The remains from the Djehuty Site provide the opportunity to compare directly osteological characteristics between archaeological and modern samples that may provide clues regarding past environmental conditions for these animals and possibly their source.

We measured morphological characters of individual postcranial bones of *C. olivieri* and *C. religiosa* and used the resulting variables to compare modern and archaeological samples of these species. We further used these variables to calculate morphological indices that have been used elsewhere to assess locomotor function. To provide context for understanding the relatively conservative morphology of *Crocidura*, we compared our indices to indices previously documented for myosoricine shrews, the sister group to the crocidurines and a clade with a range of locomotor morphologies (Woodman and Stabile 2015). The indices provide a guide for understanding possible intraspecific variation in the postcranial skeletons of *C. olivieri* and *C. religiosa*, as well as a gauge of whether locomotor efficiency of these two species has changed during the last two millennia.

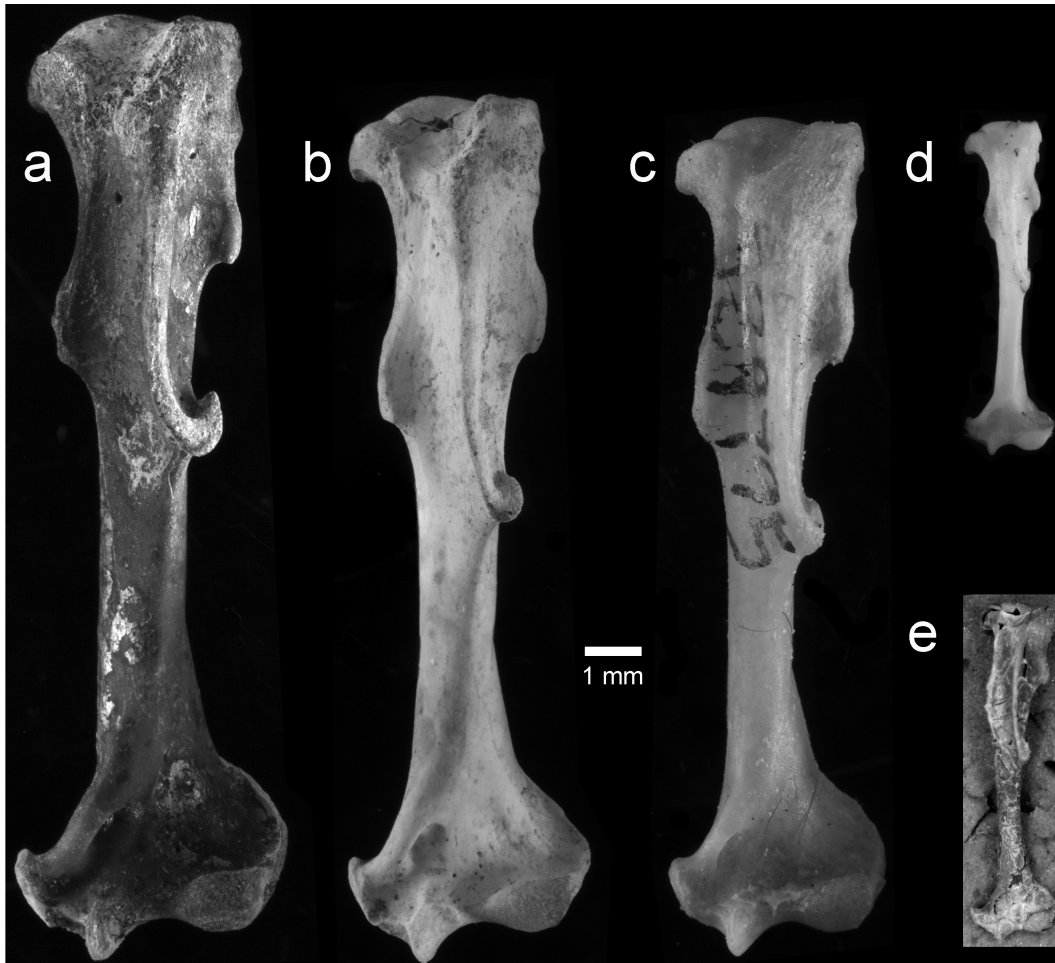
## MATERIALS AND METHODS

The Djehuty Site (ca. 25°44′11″N, 32°37′24″E) is located on the eastern side of Dra Abu el-Naga, a hill arising along the west bank of the Nile River floodplain and near the northern edge of the necropolis associated with the ancient Egyptian city of Waset (ancient Egyptian) or Thebes (ancient Greek) and the modern city of Luxor. Excavation of the fire-blackened burial chamber EU 194 in January 2018 by the Spanish–Egyptian Mission to Dra Abu el-Naga (TT 11–12) under the direction of José Manuel Galán, CSIC, yielded abundant skeletal remains resulting from the burning of animal mummies in the chamber. This material was sieved through screens with 1–5 mm steel mesh to concentrate remains, which were then handpicked and separated into taxonomic categories.

On the basis of preserved crania and dentaries from EU 194, we identified three species of soricids representing three distinct size classes (Table 1). Remains of large-sized *C. olivieri* were represented most abundantly, followed by those of small-sized *C. religiosa* (Fig. 1). Middle-sized *C. fulvastra* was represented by a single left dentary. Because no recovered postcranial remains could be associated with this last species, it is not addressed further herein. Hereafter, we refer collectively to the material recovered from the Djehuty Site as the “Ptolemaic” samples of *C. olivieri* and *C. religiosa* in order to clearly contrast them with our modern samples of these and other species.

**Table 1.**—Summary of numbers of shrew remains from Excavation Unit 194 at the Djehuty Site. “Skull remains” refers to the total number of identifiable elements of the cranium and dentaries; “postcranial remains” is the total number of identifiable postcranial bones; “MNI” is the minimum number of individuals based on the largest number of identifiable left or right dentaries.

Taxon	Skull remains	Postcranial remains	MNI
<i>Crocidura olivieri</i>	307	24	110
<i>Crocidura religiosa</i>	85	4	30
<i>Crocidura fulvastra</i>	1	0	1
Totals	393	28	141



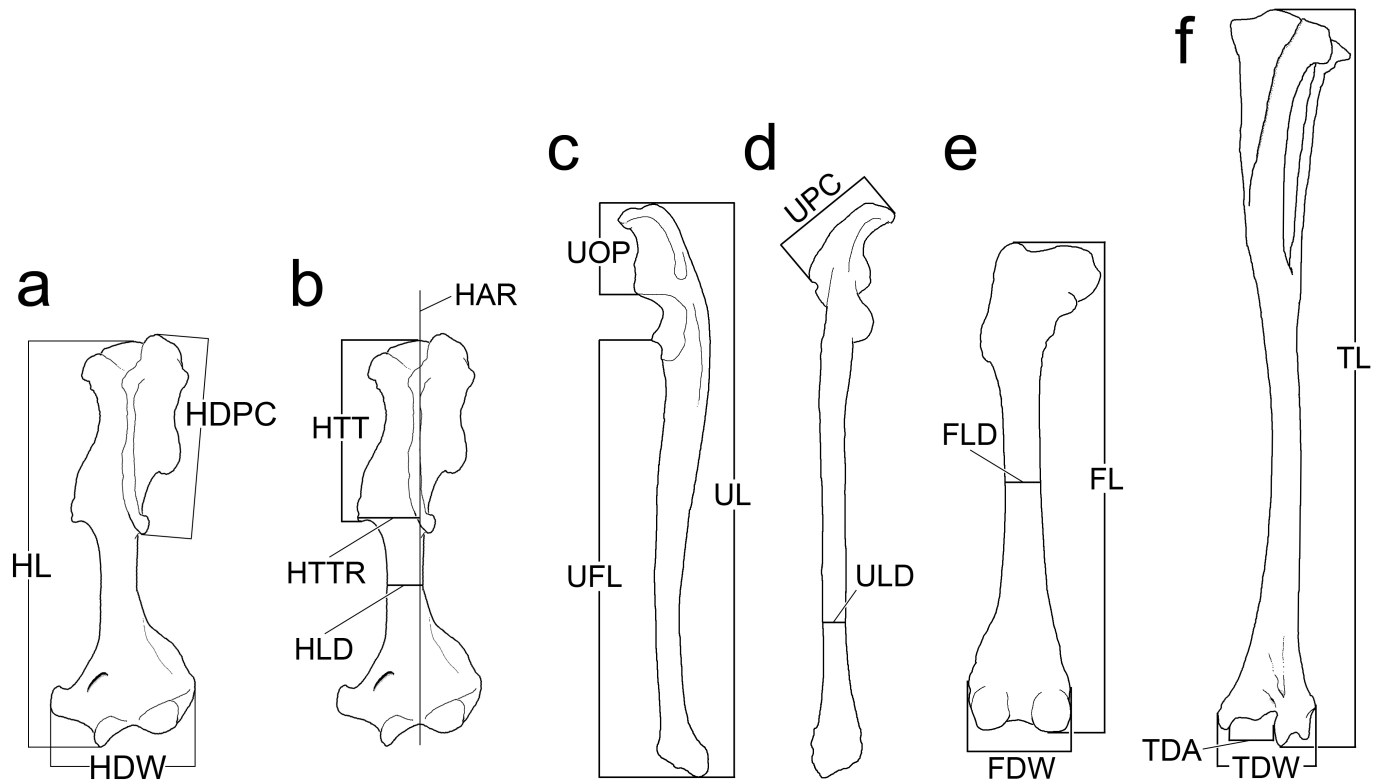
**Fig. 1.**—Anterior aspect of humeri from: a) Ptolemaic *Crocidura olivieri* (UE194 IV-2); b) Ptolemaic *C. olivieri* (UE194 IV-1); c) modern *C. olivieri* (USNM 589795); d) modern *C. religiosa* (USNM 341933); e) Ptolemaic *C. religiosa* (UE194 I.2–25). All are left humeri, except e, which is the inverted image of a right humerus. All images are to the same scale.

Because removal of remains from the Djehuty Site is prohibited, postcranial bones of mammals were digitally imaged with a Reflecta DigiMicroscope USB 200 digital microscope (Eutingen, Germany). Following procedures detailed by Woodman and Gaffney (2014) and Woodman and Stabile (2015), images of complete sorcid postcranial bones with fused epiphyses (humerus, ulna, femur, tibiofibula) were transferred to Adobe Photoshop CS3 Extended version 10.0.1 (Adobe Systems, Inc., San Jose, California) and measured using the custom Measurement Scale in the Analysis menu. Measurements were rounded to the nearest 0.01 mm. We obtained 18 measurements (Fig. 2; Table 2) from 24 individual postcranial bones (11 left, 7 right humeri; 2 left, 1 right tibiofibulae; 1 left, 1 right ulnae; 1 left femur) of *C. olivieri* and 4 bones (1 left, 2 right humeri; 1 left tibiofibula) of *C. religiosa* excavated from EU 194. Because the likelihood of having both right and left elements from the same individual was extremely low (humerus: 3.6% for *C. olivieri*; 2.4% for *C. religiosa*), we used both right and left elements in our analyses. For comparison with the archeological materials, we measured modern skeletons of seven *C. olivieri* and one *C. religiosa* (Appendix I). Sample sizes of modern species were limited by the availability

and completeness of skeletons (e.g., Bell and Mead 2014). To augment the modern sample, we also measured 13 *Crocidura suaveolens*. All measurements reported herein are in mm.

We used principal components analysis (PCA) to examine the overall similarity of Ptolemaic and modern humeri of the same species. Six log<sub>10</sub>-transformed humerus variables (Fig. 2: HL, HDW, HLD, HTTR, HAR, HTT) of 15 Ptolemaic and two modern *C. olivieri*, two Ptolemaic and one modern *C. religiosa*, and 13 modern *C. suaveolens* were analyzed using Systat 11 (Cranes Software, Bangalore, India).

To evaluate morphological variation and assess locomotor function, we used our measurements to calculate 12 osteological indices (Tables 3 and 4) that have been used elsewhere to characterize locomotor mode and adaptations for substrate use among sorcids (Woodman and Gaffney 2014; Woodman and Stabile 2015), rodents (Price 1993; Samuels and Van Valkenburgh 2008; Elissamburu and De Santis 2011), and other mammals (Sargis 2002; Hopkins and Davis 2009). To overcome the problem of missing data, we calculated indices from mean values of variables for each species (Table 2). As a test of indices thus calculated from variable means, we also calculated indices for individuals of modern *C. olivieri* and of modern *C.*



**Fig. 2.**—Postcranial measurements. a) Humerus: HL, length of humerus; HDW, distal width of humerus; HDPC, length of deltopectoral crest. b) Humerus: HAR, axis of rotation of the humerus; HLD, least mediolateral diameter of humerus; HTT, length from head of humerus to distal edge of teres tubercle; HTTR, length of the teres tubercle input lever for rotation. c) Ulna: UL, total length; UFL, functional length; UOP, length of olecranon process. d) Ulna: UPC, width of proximal crest; ULD, least mediolateral diameter. e) Femur: FL, length; FDW, distal width; FLD, least mediolateral diameter. f) Tibiofibula: TL, length; TDA, width of distal articular surface; TDW, distal width.

**Table 2.**—Mean measurements in mm for two Ptolemaic (<sup>P</sup>) and three modern (<sup>M</sup>) species of crocidurine shrews. Abbreviations of measurements are explained in Fig. 2.

Taxa	HL	HDW	HDPC	HLD	HTTR	HAL	HTT	UL	UFL
<i>C. religiosa</i> <sup>M</sup>	5.77	1.59	3.00	0.41	0.35	5.70	2.03	—	—
<i>C. religiosa</i> <sup>P</sup>	6.23	1.60	2.81	0.44	0.51	6.02	2.30	—	—
<i>C. suaveolens</i> <sup>M</sup>	7.91	2.43	3.74	0.62	0.88	7.73	2.73	7.58	5.94
<i>C. olivieri</i> <sup>M</sup>	14.12	3.87	7.05	1.21	1.09	13.89	5.10	—	—
<i>C. olivieri</i> <sup>P</sup>	14.20	4.14	6.79	1.26	1.17	13.92	5.44	16.07	12.28
Taxa	UOP	UPC	ULD	FL	FDW	FLD	TL	TDA	TDW
<i>C. religiosa</i> <sup>M</sup>	—	—	—	6.33	1.31	0.57	—	—	—
<i>C. religiosa</i> <sup>P</sup>	—	—	—	—	—	—	9.44	0.59	1.23
<i>C. suaveolens</i> <sup>M</sup>	1.04	1.18	0.38	9.07	1.90	0.74	11.25	0.43	1.47
<i>C. olivieri</i> <sup>M</sup>	—	—	—	13.87	2.95	1.42	—	—	—
<i>C. olivieri</i> <sup>P</sup>	2.42	2.69	0.74	17.09	3.85	1.71	22.09	1.58	3.18

*suaveolens* and calculated mean indices for the species from the individual indices. Comparison of the mean values provided by the two methods yielded only one difference between the means (CI for *C. suaveolens*; Table 5), verifying our original method for use with the present data sets.

All indices are expressed as whole number percentages (Table 4). For most of these indices, higher values are associated with more fossorial morphologies and lower values with more ambulatory morphologies. One exception is the crural index (CI), for which the opposite is true (Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014; Woodman and Stabile 2015). For our purposes, we employ “ambulatory”

to refer to terrestrial shrews that move and forage primarily on the surface of the ground and lack morphological traits clearly associated with specialized aquatic, fossorial, or scansorial behavior.

In the absence of measured locomotor data from other crocidurine shrews, we compared the indices we calculated for Ptolemaic and modern *Crocidura* with those previously calculated by Woodman and Stabile (2015) for nine species of mysoricine shrews that represent a range of ambulatory and fossorial morphologies (Table 4): *Congosorex phillipsorum*; *Myosorex blarina*; *M. cafer*; *M. geata*; *M. kihaulei*; *M. varius*; *M. zinki*; *Surdisorex norae*; and *S. polulus*. We used mysoricines

rather than soricines for this analysis because Myosoricinae and Crocidurinae are sister taxa (e.g., Dubey et al. 2007, 2008; Willows-Munro and Matthee 2011).

The indices were incorporated into two overlapping data sets for testing. The first included all 12 functional indices. The second data set contained five indices (Fig. 2: SMI, HRI, HTI, TTP, HEB) associated with functioning of the humerus, the postcranial structure that exhibits the most obvious modifications related to ambulatory–fossorial locomotor behavior in eulipotyphlans (Reed 1951; Woodman and Gaffney 2014; Woodman and Stabile 2015) and other quadrupedal vertebrates (Samuels and Van Valkenburgh 2008; Hildebrand 1985b). For each of these data sets, we computed percentile ranks for each of the morphological indices for each of the Ptolemaic and modern samples of *Crocidura* and the nine myosoricines. We then averaged the percentile ranks to obtain a mean percentile rank (MPR) for each sample. Together, these summary scores provide an overview of interspecific morphological variation, and they permit us to define relative adaptation of individuals in each sample for ambulatory versus

fossorial locomotion on a possible scale from 0 (most ambulatory) to 100 (most fossorial) (Woodman and Gaffney 2014).

## RESULTS

*PCA of the humerus.*—All variables contributed strongly and positively to the first principal component of the PCA, which corresponds to overall size of the humerus (Table 6). This axis separates the three crocidurine species *C. religiosa* (smallest humerus), *C. suaveolens*, and *C. olivieri* (largest humerus) by size (Fig. 3). The single specimen of modern *C. religiosa* is somewhat smaller than either of the Ptolemaic specimens of that species. Among *C. olivieri*, Ptolemaic and modern individuals overlap considerably in size, although all of the largest specimens are in the Ptolemaic sample. The second principal component is mostly heavily influenced by the negatively weighted variable HTTR, which is a measure of the length of the teres tubercle. This process of the eulipotyphlan humerus serves as the insertion for the latissimus dorsi and teres major muscles that retract and rotate the humerus (Reed 1951; Woodman and Gaffney 2014). A longer process is generally interpreted as providing greater surface area for larger, more powerful muscles. This second axis separates *C. religiosa* (shorter teres tubercle) from *C. suaveolens* (longer teres tubercle). *Crocidura olivieri* exhibits a broad range on the second axis, overlapping most of the individuals of the other two species. The single modern *C. religiosa* has a somewhat shorter teres tubercle than either of the Ptolemaic individuals of that species.

*12-index MPR model.*—The nine myosoricines are functionally diverse, exhibiting a range of MPRs from 28 (*M. cafer*) to 86 (*S. polulus*) within the hypothetical range of 0 (most ambulatory) to 100 (most fossorial). Half of the species rank below the theoretical midpoint of the scale, and half above this value (Table 7: MPR<sup>12</sup>). A large gap separates more ambulatory myosoricines from the more fossorial species (Fig. 4). These shrews provide a background scale for understanding

**Table 3.**—List of indices used in this study and their abbreviations. All indices are expressed as whole number percentages. See Woodman and Gaffney (2014) and Woodman and Stabile (2015) for additional information on the significance of these measures. Abbreviations of measurements are explained in Fig. 2.



**Table 4.**—Mean functional indices calculated for two Ptolemaic (P) and three modern (M) populations of crocidurine shrews from variables in Table 3. Data for myosoricine shrews are from Woodman and Stabile (2015). Species are listed in order within each subfamily by MPR<sup>12</sup> from Table 7. All indices are expressed as whole number percentages. Abbreviations of indices are explained in Table 3.

Taxa	SMI	HRI	HTI	TTP	HEB	OLI	OCI	URI	CI	FRI	FEB	DTA
<b>Crocidurines:</b>												
<i>C. suaveolens</i> <sup>M</sup>	47	8	11	35	31	18	22	6	147	8	21	32
<i>C. religiosa</i> <sup>M</sup>	52	7	6	36	28	—	—	—	—	9	21	—
<i>C. religiosa</i> <sup>P</sup>	45	7	9	38	26	—	—	—	—	—	—	48
<i>C. olivieri</i> <sup>M</sup>	50	9	8	37	27	—	—	—	—	10	21	—
<i>C. olivieri</i> <sup>P</sup>	48	9	8	39	29	20	22	6	129	10	23	50
<b>Myosoricines:</b>												
<i>M. cafer</i>	46	10	15	36	32	—	—	—	—	8	21	—
<i>M. varius</i>	48	10	18	43	35	19	30	5	149	9	22	45
<i>M. kahaulei</i>	46	9	16	40	35	—	—	—	—	10	23	—
<i>M. geata</i>	47	9	16	39	35	—	—	—	—	10	23	—
<i>M. blarina</i>	50	9	19	41	39	24	31	8	142	10	24	46
<i>C. phillipsorum</i>	50	11	20	39	42	—	—	—	—	10	24	—
<i>M. zinki</i>	47	13	18	42	47	—	—	—	—	11	25	—
<i>S. norae</i>	62	17	35	51	60	31	40	9	135	11	25	44
<i>S. polulus</i>	62	17	39	55	58	—	—	—	—	10	24	—

**Table 5.**—Comparison of mean locomotor indices calculated for modern *C. olivieri* and *C. suaveolens* from mean values of variables for each species (mean<sup>A</sup>) and from indices calculated for individuals of each species (mean<sup>B</sup>). The latter includes the mean  $\pm$  SD, range, and sample size. The only difference is for index CI for *C. suaveolens*. Abbreviations of indices are explained in Table 3.

	SMI	HRI	HTI	TTP	HEB	OLI
<i>C. olivieri</i>						
Mean <sup>A</sup>	50	9	8	37	27	—
Mean <sup>B</sup>	50 $\pm$ 2	9 $\pm$ 1	8 $\pm$ 2	37 $\pm$ 2	27 $\pm$ 1	—
	47–53	8–10	6–10	35–39	26–29	—
	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	—
<i>C. suaveolens</i>						
Mean <sup>A</sup>	47	8	11	35	31	18
Mean <sup>B</sup>	47 $\pm$ 2	8 $\pm$ 1	11 $\pm$ 1	35 $\pm$ 2	31 $\pm$ 1	18 $\pm$ 1
	44–50	7–9	9–13	29–38	29–32	16–19
	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 10
	OCI	URI	CI	FRI	FEB	DTA
<i>C. olivieri</i>						
Mean <sup>A</sup>	—	—	—	10	21	—
Mean <sup>B</sup>	—	—	—	10 $\pm$ 1	21 $\pm$ 1	—
	—	—	—	9–11	20–22	—
	—	—	—	<i>n</i> = 5	<i>n</i> = 5	—
<i>C. suaveolens</i>						
Mean <sup>A</sup>	22	6	147	8	21	32
Mean <sup>B</sup>	22 $\pm$ 1	6 $\pm$ 1	146 $\pm$ 4	8 $\pm$ 1	21 $\pm$ 1	32 $\pm$ 6
	21–23	5–7	139–154	7–9	20–22	21–39
	<i>n</i> = 9	<i>n</i> = 10	<i>n</i> = 11	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 10

**Table 6.**—Component loadings on the first two principal components from PCA of six variables from the humerus (see Fig. 3). Abbreviations of variables are explained in Fig. 2.

Variable	Component loadings	
	1	2
HAR	0.992	0.107
HL	0.992	0.102
HDW	0.987	0.055
HLD	0.982	0.121
HTT	0.979	0.107
HTTR	0.788	-0.616
Eigenvalues	5.486	0.430
Variance explained (%)	91.425	7.166

morphological variation and potential locomotor modes among the Ptolemaic and modern crocidurines.

Based on their relative MPRs, the postcranial morphologies of *C. suaveolens* (MPR = 21) and modern (MPR = 23) and Ptolemaic (MPR = 24) *C. religiosa* are functionally more ambulatory than any of the myosoricines. Modern *C. olivieri* (MPR = 33) is somewhat higher on the scale, between the myosoricines *M. cafer* and *M. varius*, whereas Ptolemaic *C. olivieri* (MPR = 48) ranks considerably higher, just above *M. geata* and *M. kihaulei*, and approaching the midpoint of the scale.

The mean difference between adjacent species on the MPR scale is 5  $\pm$  5 (SD) percentile ranks (Table 7). Differences between adjacent species of  $\geq$  10 percentile ranks, indicating relatively large differences in morphology, occur at three locations. The largest gap (16 percentile ranks) separates more fossorial *M. blarina* from Ptolemaic *C. olivieri*. Two smaller gaps (10 percentile ranks each) distinguish *M. varius* from modern *C. olivieri* and *M. zinki* from *S. norae*. Among just

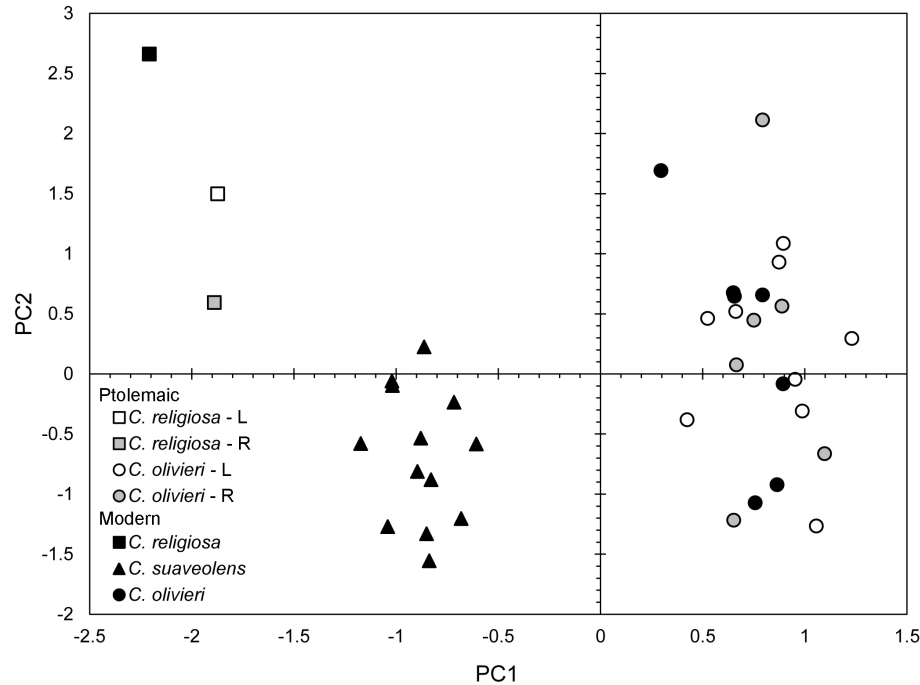
the crocidurines, a 15-percentile-rank gap separates modern and Ptolemaic *C. olivieri*, whereas modern and Ptolemaic *C. religiosa* are separated by only a single percentile rank (Fig. 4).

**5-index MPR model.**—Analysis of the reduced set of five indices from only the humerus yielded an MPR range of 14–94 (Table 7: MPR<sup>5</sup>). Myosoricines dominate the middle and upper regions of the scale (MPR range = 34–94), whereas the crocidurines occupy mostly the lower portion of the scale (MPR range = 14–35), indicating the humeri of the five crocidurine species are morphologically more ambulatory than most of the myosoricines (Fig. 5).

The mean difference between adjacent species on this MPR scale is six percentile ranks (Table 7). Gaps greater than this value occur at four locations: between Ptolemaic *C. religiosa* and modern *C. suaveolens* (nine percentile ranks); between *M. geata*/*M. kihaulei* and Ptolemaic *C. olivieri* (nine percentile ranks); between *M. varius* and *M. geata*/*M. kihaulei* (19 percentile ranks); and between *S. norae* and *C. phillipsorum* (23 percentile ranks). Among the crocidurines, 11 percentile ranks separate Ptolemaic and modern *C. religiosa*, but only a four-percentile-rank gap separates modern and Ptolemaic *C. olivieri* (Fig. 4).

## DISCUSSION

**Myosoricine scale.**—The relative positions of the nine species of myosoricines we used to establish a background scale of morphological variation remained relatively stable between our 12-index and 5-index models (Table 7). The sequence of myosoricine species also generally matches that reported by Woodman and Stabile (2015), despite their use of a wider range of 32 locomotor indices and their inclusion of two talpids—the ambulatory Chinese shrew-mole, *Uropsilus soricipes* and



**Fig. 3.**—Plot of Ptolemaic and modern *Crocidura* on the first two principal components from a PCA of six variables measured from the humerus (Table 6). Ptolemaic humeri are differentiated as left (L) and right elements (R).

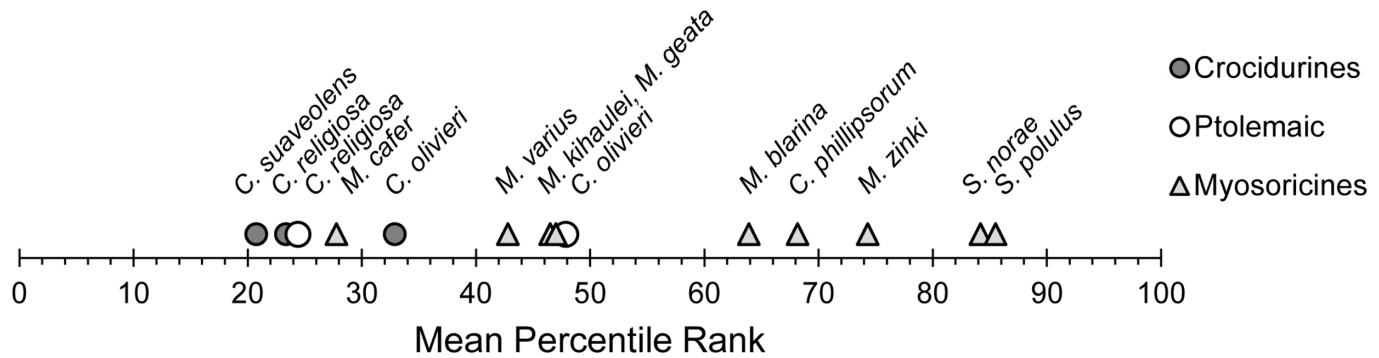
**Table 7.**—Percentile ranks calculated for 12 functional indices (Table 2) from two Ptolemaic (P) and three modern (M) species of crocidurine shrews and nine species of myosoricine shrews. Mean percentile ranks (MPR) were calculated 1) from all 12 indices (MPR<sup>12</sup>), and 2) from just the five humerus indices (MPR<sup>5</sup>). MPRs are interpreted as representing relative adaptation of a species for more ambulatory behavior (lower ranks) versus more fossorial behavior (higher ranks) on a scale of 0–100 (Figs. 3 and 4). Species are listed in order by MPR<sup>12</sup> within each subfamily. Abbreviations are explained in Table 1.

Taxa	SMI	HRI	HTI	TTP	HEB	OLI	OCI	URI	CI	FRI	FEB	DTA	MPR <sup>12</sup>	MPR <sup>5</sup>
Crocidurines:														
<i>C. suaveolens</i> <sup>M</sup>	32	18	32	4	32	10	20	40	30	8	15	8	21	24
<i>C. religiosa</i> <sup>M</sup>	82	7	4	14	18	—	—	—	—	23	15	—	23	25
<i>C. religiosa</i> <sup>P</sup>	4	7	25	32	4	—	—	—	—	—	—	75	24	14
<i>C. olivieri</i> <sup>M</sup>	68	39	14	25	11	—	—	—	—	58	15	—	33	31
<i>C. olivieri</i> <sup>P</sup>	50	39	14	46	25	50	20	40	90	58	50	92	48	35
Myosoricines:														
<i>M. cafer</i>	14	64	39	14	39	—	—	—	—	8	15	—	28	34
<i>M. varius</i>	50	64	64	82	54	30	50	10	10	23	35	42	43	63
<i>M. kahaulei</i>	14	39	50	61	54	—	—	—	—	58	50	—	47	44
<i>M. geata</i>	32	39	50	46	54	—	—	—	—	58	50	—	47	44
<i>M. blarina</i>	68	39	75	68	68	70	70	70	50	58	73	58	64	64
<i>C. phillipsorum</i>	68	75	82	46	75	—	—	—	—	58	73	—	68	69
<i>M. zinki</i>	32	82	64	75	82	—	—	—	—	92	92	—	74	67
<i>S. norae</i>	93	93	89	89	96	90	90	90	70	92	92	25	84	92
<i>S. polulus</i>	93	93	96	96	89	—	—	—	—	58	73	—	86	94

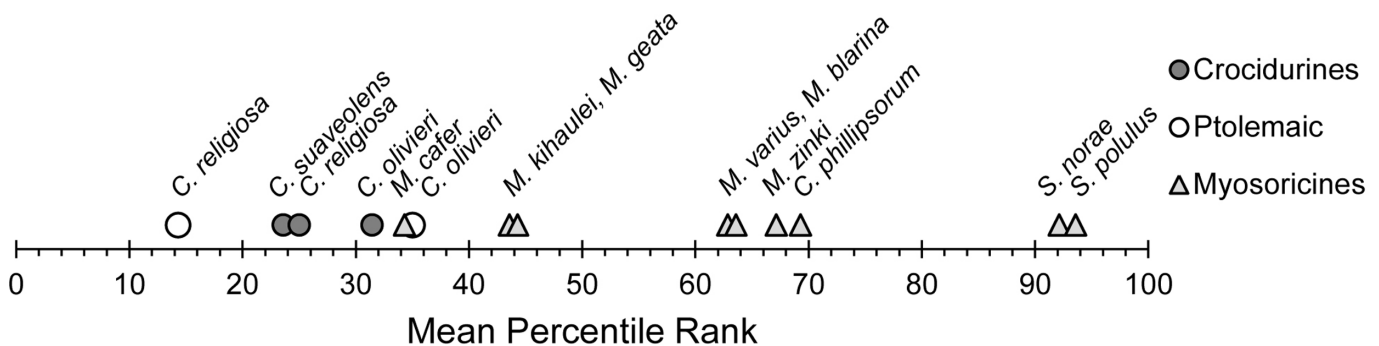
the semifossorial North American shrew-mole, *Neurotrichus gibbsii*—instead of five species of crocidurines. One exception is the position of *C. phillipsorum*, an enigmatic species whose skeletal morphology has a mixture of characteristics typical of both more ambulatory and more fossorial species (Woodman and Stabile 2015). In our analyses, *C. phillipsorum* is ranked among the more fossorial myosoricines, whereas it is positioned between the more ambulatory *M. kahaulei* and *M. varius* in Woodman and Stabile's (2015) analysis.

Within the context of the myosoricine scale, all of the five crocidurines rank below the midpoint of the scale, and most

are positioned toward the lower end in both MPR models (Table 7; Figs. 4 and 5). *Crocidura suaveolens* and Ptolemaic and modern *C. religiosa* rank below *M. cafer*, the most ambulatory of the myosoricines. Modern *C. olivieri* ranks just above (12-index model) or just below (5-index model) *M. cafer*, whereas Ptolemaic *C. olivieri* ranks well above (12-index model) or nearly equal with (5-index model) that species. In general, the characteristics of the available postcranial skeletons of the five samples of *Crocidura* in our study are consistent with those of soricids with a dominantly ambulatory mode of locomotion.



**Fig. 4.**—Results of mean percentile rank analysis of 12 morphological indices from two Ptolemaic and three modern species of crocidurine shrews and nine species of myosoricine shrews (Table 7). The scale is interpreted as representing relative functional mode of species from more ambulatory (lower scores) to more fossorial (higher scores).



**Fig. 5.**—Results of mean percentile rank analysis of five morphological indices of the humerus from two Ptolemaic and three modern species of crocidurine shrews and nine species of myosoricine shrews (Table 7). The scale is interpreted as representing relative functional mode of species from more ambulatory (lower scores) to more fossorial (higher scores).

*Individual indices.*—Individual characters summarized by the functional indices were typically, but not always, in accord between conspecific Ptolemaic and modern samples. The humerus is the most relevant postcranial element available. Variability of the humerus most closely tracks overall estimates of locomotor morphology (Woodman and Gaffney 2014; Woodman and Stabile 2015), and it is the most abundant postcranial bone preserved in the Djehuty Site, permitting the calculation of complete sets of indices for both Ptolemaic species.

For three of the five indices derived from the humerus (HRI, HTI, HEB), all five *Crocidura* samples have lower indices (Table 4) and correspondingly lower percentile ranks (Table 7) for these individual indices than any of the myosoricines. The *Crocidura* all have low values for a fourth index (TTP) as well, but are intermixed with three species of myosoricines with similarly low values. For any of these four indices, the Ptolemaic and modern *Crocidura* of the same species differ from each other by no more than 3%, and the values for some indices are equal (Table 4). These four indices measure 1) the robustness of the humerus and, thereby, its ability to resist bending and shearing stresses (HRI); 2) the length of the teres tubercle (HTI), which is a measure of the size of the latissimus dorsi and teres major muscles; 3) the distance from the proximal end of the humerus to the teres tubercle (TTP), which influences the mechanical advantage of muscles that insert on that process; and 4) the width of the distal end of the humerus, which acts as

the origin for various forearm muscles important for efficient digging (HEB). These four indices generally increase with increasing fossoriality (Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014; Woodman and Stabile 2015). The low indices of the crocidurines indicate they each possess a relatively slender humerus with small, more proximally located teres tubercle and a narrow distal end, typical of more ambulatory species.

The fifth humerus index, the shoulder moment index (SMI), measures the relative length of the deltopectoral crest of the humerus, providing a gauge of the size of the deltoid and pectoral muscle groups that insert on the crest and are involved in movement and rotation of the humerus. Like the other four humerus indices, SMI generally increases with increasing fossoriality (Sargis 2002; Samuels and Van Valkenburgh 2008). There are striking exceptions, however (e.g., *M. zinki*: Table 7; Woodman and Stabile 2015), possibly a result of the crest expanding in other dimensions, rather than lengthening, to accommodate the increased muscle mass associated with more fossorial species. Among the crocidurines in our study, the deltopectoral crest is somewhat straighter and slightly longer than expected in comparison with the more curved form of the crest observed among the humeri of myosoricines (Woodman and Stabile 2015) and soricines (Woodman and Gaffney 2014). A longer, straighter deltopectoral crest may prove to be characteristic of *Crocidura*, or possibly even the Crocidurinae, and the form of the crest may have locomotor implications related to activities other than digging.

Ptolemaic and modern humeri of *C. olivieri* have comparable indices, whereas those of the Ptolemaic (shorter crest) and modern (longer crest) humeri of *C. religiosa* differ by 7% (Table 4). This level of intraspecific variation is greater than expected for this index based on comparison with modern *C. olivieri* (mean  $\pm$  SD, range:  $47 \pm 2$ , 44–40%) and *C. suaveolens* ( $50 \pm 2$ , 47–53%; Table 5).

The ulna acts as a lever that pivots on the trochlear notch of the humerus, thereby transmitting force from the triceps brachii muscle of the upper arm to the forearm. Because of this role, the ulna varies in form between more ambulatory and more fossorial species. Three indices (OLI, OCI, URI) derived from the ulna can be important indicators of locomotor mode (Hildebrand 1985a, 1985b; Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014; Woodman and Stabile 2015). They measure 1) the difference in length between the olecranon process, on which the triceps brachii muscle inserts, and the functional arm of the ulna, which transmits the muscular force distally to the fore paw (OLD); 2) the length of the olecranon crest (OCI), which acts as a gauge of another dimension of the triceps brachii; and 3) the robustness of the ulna and its resistance to bending and shearing stresses (URI). We recovered only two ulnae of Ptolemaic *C. olivieri* from the Djehuty Site and none from *C. religiosa*. Obtaining ulnae from modern skeletons for comparison proved difficult, because the ulna is often cut in the traditional preparation of dried skins. We could compare our Ptolemaic *C. olivieri* only with modern *C. suaveolens* and three species of myosoricines. Both the Ptolemaic *C. olivieri* and modern *C. suaveolens* samples had low values (more ambulatory) for all three indices (Table 4). Despite being different species of different historical ages, they were within 2% of each other for each index.

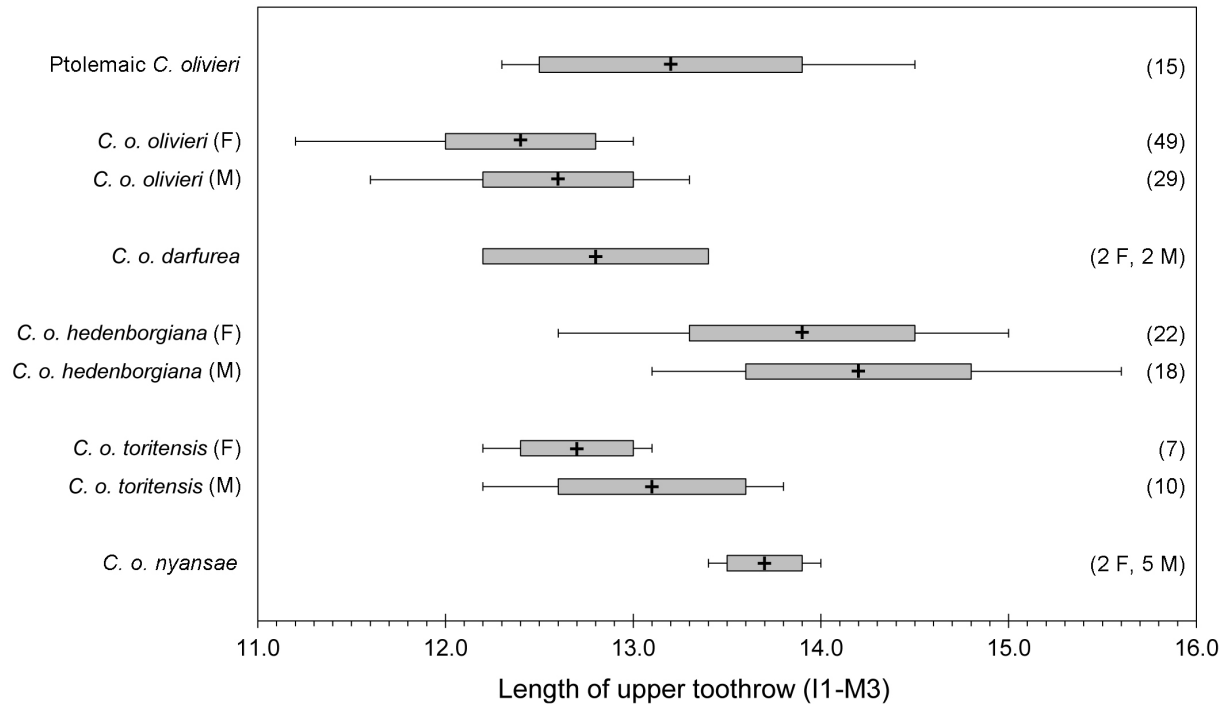
Four indices are based on measurements from the hind limb (CI, FRI, FEB, DTA). No femurs of Ptolemaic *C. religiosa* were recovered from the Djehuty Site, so three of these indices could not be calculated for that species. Because there are no complete tibiofibulae available for modern *C. olivieri* or *C. religiosa*, we could compare values for two indices (CI, DTA) from the Ptolemaic *C. olivieri* only to modern *C. suaveolens* and three myosoricines. The CI measures the length of the tibiofibula in relation to the length of the femur. Unlike the other indices, this index generally decreases with increasing fossoriality (Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014; Woodman and Stabile 2015). Ptolemaic *C. olivieri* have a relatively long tibiofibula and a correspondingly high index, as would be expected of an ambulatory shrew. In contrast, modern *C. suaveolens* has a relatively shorter tibiofibula and a low index (Table 4), characteristic of a more fossorial species. Two indices of the femur measure its relative robustness (FRI) and the relative breadth of the distal epicondyles (FEB), which serve as the origins of muscles involved in movement of the feet and toes and as the insertion for muscles that retract and adduct the femur (Reed 1951). Ptolemaic *C. olivieri* have moderately high values for each of these indices, yet both are within 2% of the values for modern *C. olivieri* (Table 4). The distal tibiofibular articulation index (DTA) measures the relative width (between the lateral and

medial malleoli) of the articulation for the astragalus. The indices calculated for Ptolemaic *C. olivieri* and *C. religiosa* are within 2% of each other, and both are much higher than that for *C. suaveolens*, the only modern species with which they could be compared for this index.

*Ptolemaic versus modern C. religiosa.*—Modern *C. religiosa* are endemic to Egypt, where records of their occurrence are mostly confined to the region of the Nile River Delta and the upper Nile Valley. Remains of several individuals recovered from owl pellets found at Karnak, across the river from the Djehuty Site, mark the known southern limit of the species (Goodman 1986; Happold 2013; Woodman et al. 2017).

Only two complete and one incomplete humerus and a single tibiofibula represent the Ptolemaic sample of *C. religiosa*, and we had only one incomplete modern skeleton of the species with which to compare them, making it difficult to gauge potential variation between them. Despite the low numbers of individuals, the mean MPRs of the Ptolemaic and modern *C. religiosa* resulting from the 12-index model are nearly the same, differing by one percentile rank. In contrast, the MPRs from the 5-index model, representing just the humerus, differ by a more considerable 11 percentile ranks. The two Ptolemaic humeri are longer than the single modern humerus (Table 2), but all three form a reasonably compact grouping in overall size as described by the PCA (Fig. 3). Moreover, preliminary study of larger samples of Ptolemaic and modern skulls of this species indicate no consistent size differences between the two populations, or between sexes within the modern population (N. Woodman, pers. obs.). The major morphological difference between the humeri of Ptolemaic and modern individuals appears to be in the relative length of the deltopectoral crest, represented by index SMI (Tables 4 and 6). This crest is relatively shorter on both of the Ptolemaic humeri than on the modern specimen. A shorter deltopectoral crest would be an indication of weaker deltoid and pectoral muscles, suggesting that Ptolemaic *C. religiosa* inhabited a different, possibly more restricted locomotor environment than modern members of the species. Might they represent a captive population? Given their similarity otherwise, however, it is more likely that the seeming difference in length of the deltopectoral crest is an artifact resulting from the low sample sizes available, and all three humeri probably are within the range of variation for both the modern and ancient Egyptian populations.

*Ptolemaic versus modern C. olivieri.*—Modern *C. olivieri* is widely distributed in central Africa, but within Egypt, the species is restricted to the Nile Delta and the al-Fayyum Oasis (*C. o. olivieri*). The nearest populations outside of Egypt are in southwestern (*C. o. darfurica*) and southern Sudan (*C. o. hedenborgiana*) and South Sudan (*C. o. toritensis*; Setzer, 1956; Churchfield and Hutterer 2013; Jacquet et al. 2015). Recent molecular studies confirmed that Egyptian and Sudanese populations are conspecific and identified them as belonging to the same subclade (i.e., Clade IV-B) of *C. olivieri* (Jacquet et al. 2015). Despite this, there is considerable body size variation among modern populations (Fig. 6). Modern *C. olivieri* also are sexually dimorphic in body size, with females, on average, smaller than males.



**Fig. 6.**—Box-and-whisker plots comparing length of the upper tooththrow of Ptolemaic *Crocidura olivieri* from the Djehuty Site with modern samples from northern Egypt (*C. o. olivieri*), southern Sudan (*C. o. hedenborgiana*), southwestern Sudan (*C. o. darfurea*), South Sudan (*C. o. toritensis*), and Kenya (*C. o. nyansae*). The sample of *C. o. nyansae* from Kenya provided the modern postcranial measurements for *C. olivieri* used in this study. The cross represents the population mean; the gray bar, the *SD*; the line, the range of measurements. The number in parentheses is the sample size. Length of upper tooththrow tracks greatest length of skull ( $y = 0.4301x + 0.5359$ ;  $R^2 = 0.9054$ ) and is an appropriate proxy for cranial size. Abbreviations: F, females; M, males. Plots for *C. o. darfurea* and of *C. o. nyansae* combine females and males because of low sample sizes.

The Djehuty Site is located well outside the modern distribution of *C. olivieri* in Egypt, and there are considerable differences in cranial size between the Ptolemaic population in Upper Egypt and the modern population in the delta region (Lower Egypt) (Fig. 6). The larger cranial size of the ancient population of this species has been noted previously based on specimens from other ancient Egyptian archaeological sites (Heim de Balsac and Mein 1971; Hutterer 1994). The larger inferred body size of the Ptolemaic populations may have resulted from a number of factors or combinations of factors that are the subject of our continued interest.

1. *Variation in local conditions:* Modern populations of *C. olivieri* can vary considerably in body size among localities (Fig. 6). Compared to modern conditions in the delta region, local biotic and abiotic conditions at Luxor during the Ptolemaic Period may have favored increased body size.
2. *Environmental change:* *Crocidura olivieri* was almost certainly more widespread through the Nile River Valley during the Ptolemaic Period. Gradual regional climatic change and resulting desertification (Brookfield 2010) likely led to its extirpation from the upper Nile Valley in Egypt and may also have influenced its body size.
3. *Human interference:* Like some other sacred animals (Kessler 2003; Kessler and Nur el-Din 2005), shrews may have been provided with official protected areas and supplemental food, or they may even have been raised in

captivity. The Romans are reported to have kept shrews as early as the 1st century AD (Pliny 1975). In the latter case, increased size could be a response to husbandry conditions or to human-mediated selection for larger individuals.

4. *External source population:* As has been documented for animal mummies elsewhere in ancient Egypt (Kessler and Nur el-Din 2005; von den Driesch et al. 2005), live or mummified shrews may have been transported to Luxor from other parts of Egypt for interment. The larger size of ancient shrews could, in part, reflect that of the source populations.

Based on differences in cranial measures (Fig. 6), we expect postcranial measurements of ancient *C. olivieri* from the Djehuty Site to be larger than those of the modern *C. olivieri*. However, our modern sample of this species is from a Kenyan population (*C. o. nyansae*) of a different molecular subclade (Clade IV-A—Jacquet et al. 2015), whose cranial measurements average much larger than modern *C. o. olivieri* from the Egyptian Delta and are slightly larger than those of the ancient population from the Djehuty Site (Fig. 6). The humeri of the modern Kenyan and Ptolemaic Djehuty populations reflect animals of nearly the same size, both in overall form as described by PCA (Fig. 3) and in individual variables (Table 2). The MPRs of the modern and Ptolemaic *C. olivieri* resulting from the 5-index humerus model differ by four percentile ranks, whereas those from the 12-index model differ by a more

considerable 15 percentile ranks (Table 7). The large difference in the 12-index model, however, is mostly a result of the lack of ulnae and tibiofibulae in our modern comparative material. Examination of the original mean functional indices (Table 4) shows that differences between the modern and Ptolemaic populations are not greater than 2% for any single index.

**Conclusions.**—Characteristics of the postcranial skeletons of modern *C. suaveolens* and modern and ancient Egyptian samples of *C. olivieri* and *C. religiosa* are consistent with those of soricids with an ambulatory locomotor mode. Ancient Egyptian and modern populations of *C. religiosa* reflect animals of approximately the same body size, and they concur in most features of the postcranial skeleton. One possible exception is the presence of a relatively longer deltopectoral crest of the humerus in the modern population. This difference may be an artifact of preservation or low sample size, or it may reflect an actual expansion or change in position of the deltoid and pectoral muscles.

The ancient Egyptian sample of *C. olivieri* has much larger cranial size than the modern Egyptian sample. The postcranial skeleton represents animals of approximately the same body size as modern *C. olivieri nyansae* from Kenya. The general agreement in characteristics and proportions of the humerus between ancient Egyptian and modern Kenyan populations suggests conservation in form and ambulatory function of the postcranial skeleton in *C. olivieri* through time and across space.

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#### LITERATURE CITED

BELL, C. J., AND J. I. MEAD. 2014. Not enough skeletons in the closet: collections-based anatomical research in an age of conservation conscience. *Anatomical Record* 297:344–348.

- BROOKFIELD, M. 2010. The desertification of the Egyptian Sahara during the Holocene (the last 10,000 years) and its influence on the rise of Egyptian civilization. Pp. 91–108 in *Landscapes and societies. Selected cases* (I. P. Martini and W. Chesworth, eds.). Springer, New York.
- BRUNNER-TRAUT, E. 1965. Spitzmaus und Ichneumon als Tiere des Sonnengottes. *Nachrichten der Akademie der Wissenschaften in Göttingen I. Philologisch-Historische Klasse* 7:123–163.
- BRUNNER-TRAUT, E. 1984. Spitzmaus. Pp. 1160–1161 in *Lexikon der Ägyptologie V* (W. Helck and E. Otto, eds.). Otto Harrassowitz, Wiesbaden, Germany.
- CHURCHFIELD, S., AND R. HUTTERER. 2013. *Crociodura olivieri* African giant shrew (Mann's musk shrew, Euchareena's musk shrew). Pp. 118–119 in *Mammals of Africa. Vol. 4. Hedgehogs, shrews and bats* (M. Happold and D. C. D. Happold, eds.). Bloomsbury Publishing, London, United Kingdom.
- DUBEY, S., N. SALAMIN, S. D. OHDACHI, P. BARRIÈRE, AND P. VOGEL. 2007. Molecular phylogenetics of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations. *Molecular Phylogenetics and Evolution* 44:126–137.
- DUBEY, S., N. SALAMIN, M. RUEDI, P. BARRIÈRE, M. COLYN, AND P. VOGEL. 2008. Biogeographic origin and radiation of the Old World crocidurine shrews (Mammalia: Soricidae) inferred from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 48:953–963.
- ELISSAMBURU, A., AND L. DE SANTIS. 2011. Fore limb proportions and fossorial adaptations in the scratch-digging rodent *Ctenomys* (Caviomorpha). *Journal of Mammalogy* 92:683–689.
- GALÁN, J. M. 2018. Proyecto Djehuty. Consejo Superior de Investigaciones Científicas, Madrid, Spain. <http://www.excavacionegipto.com/>. Accessed 16 January 2019.
- GOODMAN, S. M. 1986. The prey of barn owls (*Tyto alba*) inhabiting the ancient temple complex of Karnak, Egypt. *Ostrich* 57:109–112.
- HAPPOLD, D. C. D. 2013. *Crociodura religiosa* Egyptian pygmy shrew. Pp. 127–128 in *Mammals of Africa. Vol. 4. Hedgehogs, shrews and bats* (M. Happold and D. C. D. Happold, eds.). Bloomsbury Publishing, London, United Kingdom.
- HEIM DE BALSAC, H., AND P. MEIN. 1971. Les musaraignes momifiées des hypogées de Thèbes. Existence d'un metalophe chez les Crocidurinae (sensu Repenning). *Mammalia* 35:220–244.
- HILDEBRAND, M. 1985a. Walking and running. Pp. 38–57 in *Functional vertebrate morphology* (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, Massachusetts.
- HILDEBRAND, M. 1985b. Digging of quadrupeds. Pp. 89–109 in *Functional vertebrate morphology* (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, Massachusetts.
- HOPKINS, S. S. B., AND E. B. DAVIS. 2009. Quantitative morphological proxies for fossoriality in small mammals. *Journal of Mammalogy* 90:1449–1460.
- HOULIHAN, P. F. 1996. *The animal world of the pharaohs*. Thames and Hudson, New York.
- HUTTERER, R. 1994. Shrews of ancient Egypt: biogeographical interpretation of a new species. *Carnegie Museum of Natural History Special Publication* 18:407–414.
- IKRAM, S. 2005a. Divine creatures. Animal mummies. Pp. 1–15 in *Divine creatures. Animal mummies in ancient Egypt* (S. Ikram, ed.). American University in Cairo Press, New York.
- IKRAM, S. 2005b. Protective pets and cleaning crocodiles. Pp. 207–227 in *Divine creatures. Animal mummies in ancient Egypt* (S. Ikram, ed.). American University in Cairo Press, New York.

- IKRAM, S. 2005c. A moment in miniature: the eternal resting place of a shrew. *Denkschriften der Gesamtkademie* 33, Untersuchungen der Zweigstelle Kairo des Österreichischen Archäologischen Instituts 25:336–340.
- IKRAM, S. 2015. Speculations on the role of animal cults in the economy of ancient Egypt. Pp. 211–228 in *Apprivoiser le sauvage/taming the wild (CENiM 11)*. Vol. 3 (M. Massiera, B. Mathieu, and F. Rouffet, eds.). University Paul Valéry Montpellier, Montpellier, France.
- IKRAM, S., AND M. SPITZER. 2019. The cult of Horus and Thoth: a study of Egyptian animal cults in Theban tombs 11, 12, and -399-. In *Archaeozoology of Southwest Asia and Adjacent Areas XIII*. Proceedings of the thirteenth International Symposium, University of Cyprus, Nicosia, Cyprus, 7–10 June (J. Daujat, A. Hadjikoumis, R. Berthon, J. Chahoud, V. Kassianidou, and J.-D. Vigne, eds.). Lockwood Press, Atlanta, Georgia.
- JACQUET, F., ET AL. 2015. Phylogeography and evolutionary history of the *Crociodura olivieri* complex (Mammalia, Soricomorpha): from a forest origin to broad ecological expansion across Africa. *BMC Evolutionary Biology* 15:71.
- KESSLER, D. 1989. Die heiligen Tiere und der König. Teil I. Beiträge zur Organisation, Kult und Theologie der spätzeitlichen Tierfriedhöfe. *Ägypten und Altes Testament* 16:1–303, 10 pls.
- KESSLER, D. 2003. Tierische missverständnisse: grundsätzliches zu fragen des tierkultes. Internet-Beiträge zur Ägyptologie und Sudanarchäologie 4:33–16. <http://www2.rz.hu-berlin.de/nilus/net-publications/ibaes4/publikation/tierkulte.pdf>. Accessed 20 July 2018.
- KESSLER, D. 2007. Spitzmaus, Ichneumon und Ratte im Tierfriedhof. *Bulletin of the Egyptian Museum* 4:71–82.
- KESSLER, D., AND A. NUR EL-DIN. 2005. Tuna al-Gebel. Millions of ibises and other animals. Pp. 120–163 in *Divine creatures. Animal mummies in ancient Egypt* (S. Ikram, ed.). American University in Cairo Press, New York.
- LURKER, M. 1980. The gods and symbols of ancient Egypt. An illustrated dictionary. Thames and Hudson, London, United Kingdom.
- OSBORN, D. J., AND J. OSBORNOVÁ. 1998. The mammals of ancient Egypt. Aris & Phillips, Warminster, United Kingdom.
- PLINY [GAIUS PLINIUS SECUNDUS]. 1975. *Naturalis Historia*. Book VIII, transl. by W. H. S. Jones. Harvard University Press, Cambridge, Massachusetts.
- PRICE, M. V. 1993. A functional–morphometric analysis of forelimbs in bipedal and quadrupedal heteromyid rodents. *Biological Journal of the Linnean Society* 50:339–360.
- REED, C. A. 1951. Locomotion and appendicular anatomy in three soricoid insectivores. *American Midland Naturalist* 45:513–670.
- SAMUELS, J. X., AND B. VAN VALKENBURGH. 2008. Skeletal indicators of locomotor adaptations in living and extinct rodents. *Journal of Morphology* 269:1387–1411.
- SARGIS, E. J. 2002. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *Journal of Morphology* 253:10–42.
- SETZER, H. W. 1956. Mammals of the Anglo-Egyptian Sudan. *Proceedings of the United States National Museum* 106:447–587.
- VON DEN DRIESCH, A., D. KESSLER, F. STEINMANN, V. BERTEAUXAND, AND J. PETERS. 2005. Mummified, deified and buried at Hermopolis Magna—the sacred birds from Tuna El-Gebel, middle Egypt. *Ägypten und Levante* 15:203–244.
- WILKINSON, G. 1847. The manners and customs of the ancient Egyptians. 3rd ed. John Murray, London, United Kingdom.
- WILLOWS-MUNRO, S., AND C. A. MATTHEE. 2011. Exploring the diversity and molecular evolution of shrews (family Soricidae) using mtDNA cytochrome *b* data. *African Zoology* 46:246–262.
- WOODMAN, N., AND S. A. GAFFNEY. 2014. Can they dig it? Functional morphology and degrees of semifossoriality among some American shrews (Mammalia, Soricidae). *Journal of Morphology* 275:745–759.
- WOODMAN, N., C. KOCH, AND R. HUTTERER. 2017. Rediscovery of the type series of the sacred shrew, *Sorex religiosus* I. Geoffroy Saint-Hilaire, 1826, with additional notes on mummified shrews of ancient Egypt (Mammalia: Soricidae). *Zootaxa* 4341:1–24.
- WOODMAN, N., AND F. A. STABILE. 2015. Functional skeletal morphology and its implications for locomotory behavior among three genera of mysoricine shrews (Mammalia: Eulipotyphla: Soricidae). *Journal of Morphology* 276:550–563.

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## APPENDIX I

### *Specimens Examined*

#### MODERN SPECIMENS

*Crociodura suaveolens* (13).—AFGHANISTAN: USNM 600146, 600147, 600148, 600150, 600151, 600153, 600460, 600461, 600462, 602173, 602174, 602175, 602179.

*Crociodura olivieri* (7).—KENYA: USNM 589794, 589795, 589796, 589797, 589798, 589799, 589800.

*Crociodura religiosa* (1).—EGYPT: USNM 341933.

PTOLEMAIC SPECIMENS (Djehuty Site, Excavation Unit 194)

*Crociodura olivieri* (24 remains).—Left humeri (11): 194 I.2 (#22), 194 III.1 (#10–12), 194 IV (#01–06), 833 II.2 (#28); right humeri (7): 194 I.2 (#26), 194 III.1 (#13–15), 194 IV (#07–09). Left tibiofibulae (2): 194 III.2 (#17, 18); right tibiofibula (1): 194 III.2 (#19). Left ulna (1): 194A III.2 (#21); right ulna (1): 194A III.2 (#20). Left femur (1): 194 III.3 (#29).

*Crociodura religiosa* (4 remains).—Left humeri (2): 194 I.2 (#23, 24); right humerus (1): 194 I.2 (#25). Left tibiofibula (1): 194 I.2 (#27).