Skeletal variation among short-eared shrews (*Cryptotis*) indicates differing degrees of fossoriality

Sarah Gaffney[1,2] and Neal Woodman[2]

[1]Smith College, Northampton, Massachusetts, [2]USGS Patuxent Wildlife Research Center, National Museum of Natural History, Smithsonian Institution, Washington, DC

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Introduction

Species of genus *Cryptotis* (small-eared shrews) are distributed from northeastern North America to northern South America. Based on their postcranial morphology, some species are strongly suspected to be semifossorial, meaning they burrow underground but forage above ground. Fossorial mammals burrow and forage underground while terrestrial mammals rarely dig (Samuels and Van Valkenburgh 2008). Previous studies of fossorial mammals (e.g., moles) show that certain skeletal modifications are related to an increased mechanical advantage in digging. For example, the humerus has more prominent processes and the bones of the fore-foot are broader. Similar modifications have been seen in shrews (Woodman and Timm 1999), though due to lack of behavioral information, their functional relation to fossoriality is not definitively known. We documented variation in the postcranial skeletons of 13 species of shrews to investigate the differing degrees of fossoriality.

Fig. 1. Dried skins from the genus *Cryptotis*: **A.** *C. lacertosus*. **B.** *C. nigrescens*.

Fig. 2. Postcranial measurements used in this study: **FDW**=distal width of femur; **FG3**=width from greater trochanter to third trochanter; **FL**=length of femur; **FLD**=least mediolateral diameter of femur; **FTW**=width from greater trochanter to lesser trochanter; **HDAW**=width of distal articular surface of humerus; **HDPC**=length of deltopectoral crest; **HDW**=distal width of humerus; **HL**=length of humerus; **HLD**=least mediolateral diameter of humerus; **HLER**=lateral epicondyle input lever for rotation; **HTTR**=teres tubercle input lever for rotation; **SAM** =acromion to metacromion; **RDW**=distal width of radius; **RL**=length of radius; **SL**=greatest length of scapula; **TDA**=width of distal articular surface of tibia; **TDW**=distal width of tibia; **TL**=length of tibia; **UFL**=functional length of ulna; **UL**= length of ulna; **ULD**=least mediolateral diameter of ulna; **UOP**=length of olecranon process; and **UPC**=width of proximal crest of ulna.

Materials and Methods

We measured 80 specimens for fore and hind foot data and 33 specimens for post-cranial data. Thirteen species of *Cryptotis* (Soricidae, Soricinae) were examined in this study (Fig. 1). We also measured a terrestrial mole (Talpidae), *Uropsilus*; a semi-fossorial mole, *Neurotrichus;* and a semifossorial African shrew (Soricidae, Myosoricinae), *Surdisorex*, to act as guides for determining fossoriality in *Cryptotis*.

The femur, humerus, radius, scapula, tibia, and ulna were photographed and measured in Adobe Photoshop C3 Extended with the custom measurement tool. Measurements (mm) were recorded to the nearest 0.01 mm and are described in Fig. 2.

We x-rayed the fore and hind feet of specimens using a Kevex X-Ray Source and Varian Image Viewing and Acquisition (VIVA) software. Digital x-ray images were converted into positive images, saved in Adobe Photoshop C3 Extended, and the metacarpal, phalanges, and claw of each digit measured using the custom measurement tool (Fig. 3). The measurements recorded are described in Fig. 4.

We calculated 15 indices (Table 1) previously used for determining substrate use, including fossoriality (Samuels and Van Valkenburgh 2008) and plotted measurements to see if there were consistent groupings of species.

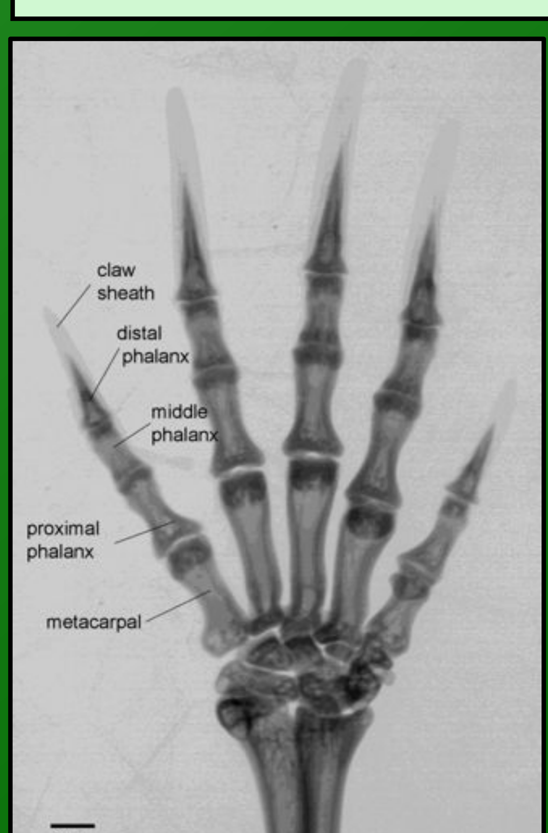

Fig. 3. Digital x-ray image and bones measured of the right manus of *Cryptotis lacertosus* (USNM 569503).

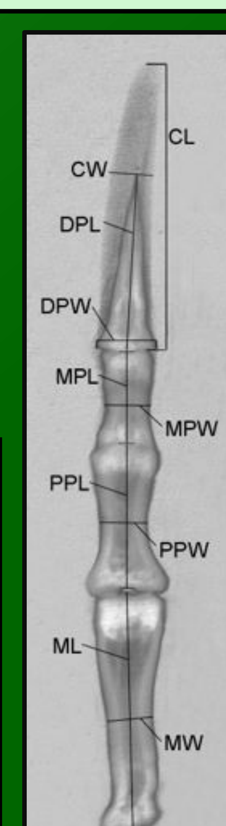

Fig. 4. Fore and hind foot measurements used in this study: **CL** = claw length, **CW** = claw width, **DPL** = distal ph. length, **DPW** = distal ph. width, **MPL** = middle ph. length, **MPW** = middle ph. width, **PPL** = proximal ph. length, **PPW** = proximal ph. width, **ML** = metacarpal length, and **MW** = metacarpal width .

ID	SMI	BI	HRI	HEB	OLI	URI	MANUS	CLAW	CI	FRI	FEB	TRI	PES	IM	HFI
Uropsilus soricipes	0.463	1.262	0.094	0.432	0.126	0.038	0.728	0.985	1.878	0.086	0.254	0.137	0.429	0.701	0.892
Cryptotis nigrescens	0.406	0.948	0.089	0.344	0.193	0.063	0.611	0.887	1.495	0.100	0.227	0.137	0.443	0.724	0.940
C. parvus	0.424	1.025	0.087	0.359	0.180	0.057	0.537	0.919	1.451	0.082	0.227	0.135	0.456	0.710	0.859
C. mexicanus	0.438		0.108	0.456											
C. phillipsii	0.421		0.107	0.418											
C. meridensis	0.439	1.034	0.102	0.400	0.212	0.063	0.466	0.856	1.654	0.090	0.249	0.134		0.690	0.900
C. endersi	0.420		0.090	0.416				1.168		0.093	0.272		0.475		0.901
C. thomasi	0.436		0.107				0.518	1.008		0.096	0.235		0.451		0.898
C. gracilis	0.457		0.109	0.438			0.592	0.929		0.105	0.271	0.144	0.537		0.916
C. goodwini	0.437		0.130	0.521			0.582	1.237		0.095	0.266		0.417		0.837
C. mam	0.477	1.059	0.131	0.515	0.256	0.076	0.585	1.328	1.514	0.089	0.259	0.149	0.439	0.715	0.874
C. oreoryctes	0.444	1.050	0.133	0.531	0.301	0.073	0.586	1.312	1.501	0.093	0.266	0.141	0.435	0.665	0.820
C. lacertosus	0.419	1.054	0.151	0.610	0.277	0.091	0.601	1.253	1.502	0.100	0.293	0.157	0.388	0.749	0.912
San Lorenzo	0.432		0.133	0.575			0.598	1.192		0.091	0.272		0.440		0.899
Neurotrichus gibbsii	0.591	1.147	0.216	0.534	0.276	0.073	0.604	1.400	1.676	0.103	0.265	0.164	0.633	0.698	0.870
Surdisorex norae	0.520	0.999	0.164	0.603	0.286	0.081	0.533	1.404	1.340	0.124	0.272	0.161	0.386	0.723	0.846

Table 1. Indices of substrate use: Brachial index (**BI**) = RL/HL; crural index (**CI**) = TL/FL; claw length index(**CLAW**) = 3DPL/3DPtL; femoral epicondylar index (**FEB**) = FDW/FL; femoral robustness index (**FRI**) = FLD/FL; humeral epicondylar index (**HEB**) = HDW/HL; humerofemoral index (**HFI**) = HL/FL; humeral robustness index (**HRI**) = HLD/HL; intermembral index (**IM**) = (HL + RL)/(FL +TL); manus proportions index (**MANUS**) = 3PPL/3ML; olecranon length index (**OLI**) = UOP/UFL; pes length index (**PES**) = 3MtL/FL; shoulder moment index (**SMI**) = HDPC/HL; tibial robustness index (**TRI**) = TDW/TL; and ulnar robustness index (**URI**) = ULD/UFL.

Results

Of the 15 indices, four (CLAW, HEB, HRI, and OLI) indices corresponding to features of the feet, humerus, and ulna showed repeating, cohesive groupings that correspond to functional groups of species as determined by our outgroup standards (*Uropsilus*, *Neurotrichus*, *Surdisorex*). The terrestrial mole, *Uropsilus*, always was at the lower end of the plots or index values while the semi-fossorial species *Neurotrichus* and *Surdisorex* had higher index values and were near the higher end of the plots. The placement of these species allowed us to judge degrees of semi-fossoriality among *Cryptotis*.

In general, the indices showed gradual variation among species of shrews and moles. However, distinct breaks in the pattern divide the species into two to four groupings with consistent species membership (Fig. 5A, B). These groups were also seen in the three plotted measurements.

The plot of the lateral epicondyle input lever and the teres tubercle input lever (Fig. 5C) measurements showed a positive correlation between the sizes of the processes among the species. The plot of the distal phalanx measurements shows that the width of the distal phalanges increases as length increase (Fig. 5D).

Based on the indices and plots, *Cryptotis* separates into four groups that we believe represent step-like variation in fossoriality: 1. *C. nigrescens*, *C. parvus*. 2: *C. meridensis*, *C. endersi*, *C. thomasi*, *C. gracilis*, *C. phillipsii*, and *C. mexicanus* with *Uropsilus*. 3: *C. goodwini*, *C. mam*, and *C. oreorycites*. 4: San Lorenzo and *C. lacertosus*, together with *Neurotrichus* and *Surdisorex*.

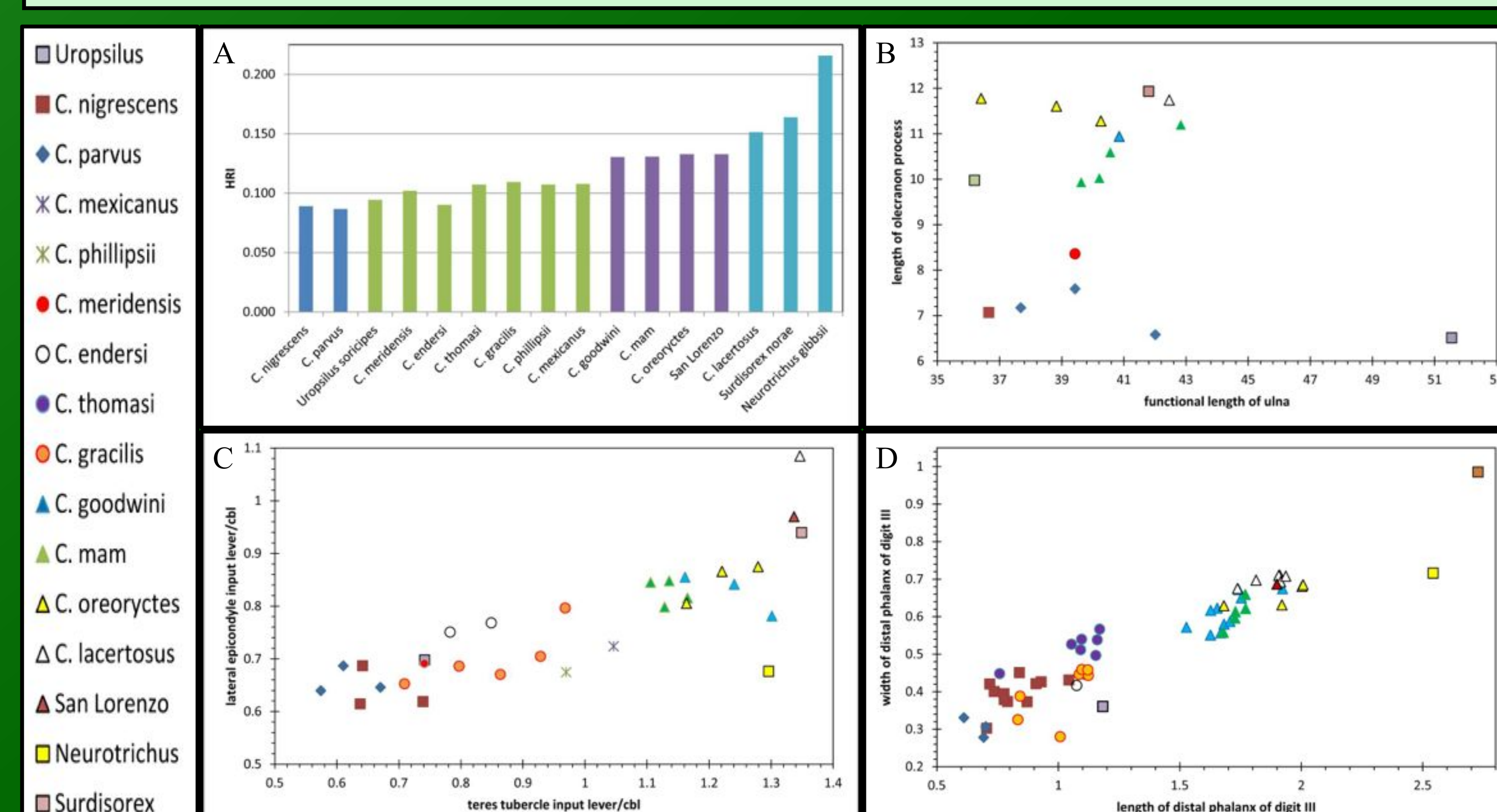

Figure 5. **A:** Graph of humeral robustness index (HRI). **B:** Plot of length of olecranon process against the functional length of ulna. **C:** Plot of lateral epicondyle input lever against the teres tubercle input lever, both standardized by cranium length. **D:** Plot of distal phalanx width against length of digit III.

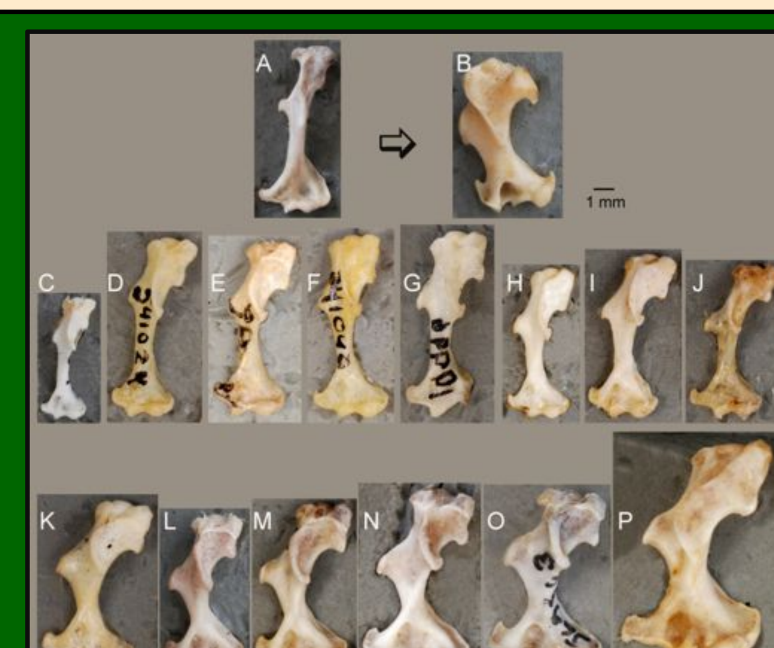

Fig. 6. Humerus variation in *Cryptotis* with increasing fossoriality following the trend in moles. **A:** *Uropsilus*; **B:** *Neurotrichus*; **C:** *Cryptotis parvus*; **D:** *C. nigrescens*; **E:** *C. meridensis*; **F:** *C. endersi*;; **G:** *C. thomasi*; **H:** *C. gracilis*; **I:** *C. phillipsii*; **J:** *C. mexicanus*; **K:** *C. goodwini*; **L:** *C. mam*; **M:** *C. oreorycites*; **N:** San Lorenzo; **O:** *C. lacertosus*; **P:** *Surdisorex norae*.

Discussion

Postcranial bones of fossorial mammals must be adapted to perform the required motions and withstand the stress of digging. Behavioral observations of *Cryptotis* are limited; however, some species show skeletal modifications similar to those found in semifossorial mammals. Our comparison of the postcranial bones of *Cryptotis* to those of terrestrial and semifossorial species suggests that these shrews are semifossorial in varying degrees.

Semifossorial and fossorial species tend to have more robust humeri with more prominent processes (teres tubercle and condyles) than terrestrial species (Shimer 1903). *Cryptotis* exhibits wide variation in humerus morphology (Fig. 6). The humeral epicondylar index (HEB) shows the relationship between distal width and length of the humerus; greater epicondylar breadth corresponds to greater area for origination of muscles involved in flexing and extending the forearm, manus, and digits (Reed 1951). Muscles inserting on the teres tubercle are crucial to humerus rotation (Reed 1951). The humeral robustness index (HRI) is the relationship between length and diameter of the humerus and represents the ability of the humerus to withstand stress (Fig 5A). These modifications enhance digging ability, as the mammal can exert more force with larger muscles attached to stronger bone.

The longer olecranon processes of fossorial species (OLI, Fig. 5B) have increased attachment for muscles involved in extending and adducting digits, flexing the manus, and extending the forearm (Reed 1951). Furthermore, the ulna acts a lever during digging. Input force (F_i) from the triceps brachii is received by the olecranon process, the input lever arm (L_i), and transmitted to the ulna's functional length, the output lever arm (L_o). The resulting output force (F_o) is determined in part by the lengths of the two arms, such that: $(F_i)(L_i) = (F_o)(L_o)$; and, $F_o = (F_i)(L_i/L_o)$. Hence, the efficiency of the ulna can be expressed as L_i/L_o, which is the percentage of the exerted force transmitted to digging. In terrestrial *Uropsilus*, L_i/L_o = 12.6%, whereas, in semifossorial *Neurotrichus*, L_i/L_o = 27.6%. Among *Cryptotis*, values of L_i/L_o range from 18% in *C. parvus* to 30.1% in *C. oreorycites* (see index OLI in Table 1).

Forefeet of fossorial mammals have short, broad metacarpals and phalanges and elongate, broad distal phalanges and claws, which is seen in some *Cryptotis* and assumed to increase mechanical advantage in digging as the bones and claws are sturdier (Shimer 1903; Woodman and Morgan 2005). *Cryptotis* exhibits gradation in the CLAW index, which compares the size of the fore-claws to the hind-claw, showing increase in fore-claw length

Our study indicates considerable variation in degree of fossoriality among the 13 species of *Cryptotis* studied, with the majority of the indices calculated ranging from terrestrial to semifossorial. Specific characteristics of the humerus, ulna, and digit III also correspond well with four functional groups.

Cryptotis nigrescens and *C. parvus* appear to be the most terrestrial members of the genus, while the group containing *C. meridensis*, *C. endersi*, *C. thomasi*, *C. gracilis*, *C. phillipsii*, and *C. mexicanus* are slightly more semifossorial. Even more semifossorial is the group with *C. goodwini*, *C. mam*, and *C. oreorycites*, followed by the most fossorial group containing *C. lacertosus* and the population from San Lorenzo.

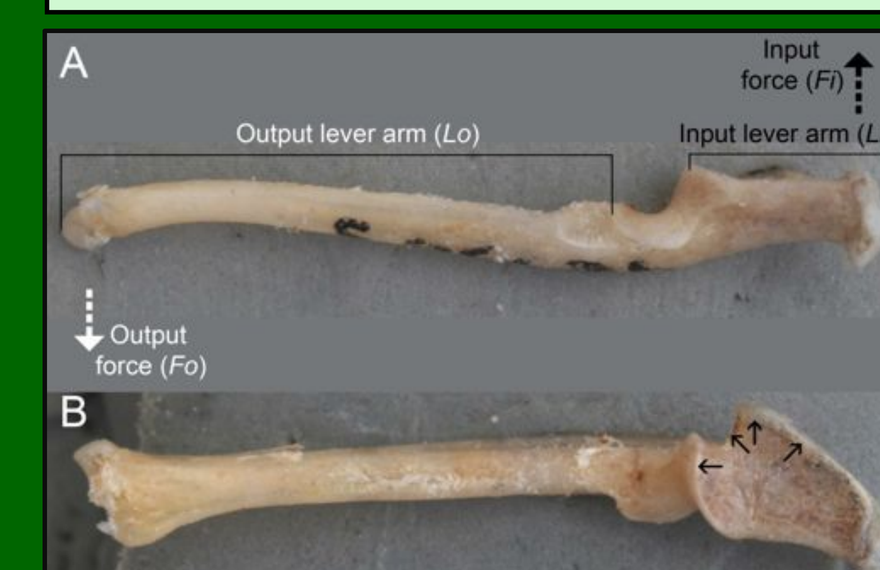

Fig. 7. Palmar (**A**) and anterior (**B**) views of right ulna of *Cryptotis lacertosus* (USNM 569503). **A:** The ulna acts as a lever arm. Olecranon process (input lever arm, L_i) receives input force (F_i), transmits it to the functional length (output lever arm, L_o). Output force (F_o) determined by lengths of the two arms, such that: $(F_i)(L_i) = (F_o)(L_o)$ and $F_o = (F_i)(L_i/L_o)$. Fossorial mammals typically have relatively longer input lever arms and shorter output lever arms, thereby decreasing load. **B:** Olecranon process has expansive region for attachment of triceps brachii (arrows).

Conclusions

Variation in postcranial morphology results in differences in mechanics and functionality. The characteristics we measured show gradation among *Cryptotis*. When compared to other species that are known to be terrestrial and semifossorial, *Cryptotis* ranges between the two extremes, and can be divided into as many as four distinct functional groups that correspond to differing degrees of semi-fossoriality. Species of *Cryptotis* with more complex and robust humeri, larger olecranon processes, and broader claws and phalanges are more highly adapted for digging.

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