Functional Limb Morphology of African Myosoricine Shrews (Mammalia, Soricidae)

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INTRODUCTION

Shrews (family Soricidae) are small-bodied, predatory mammals distributed across North America, Europe, and Asia. Members of this family show considerable variation in skeletal morphology. Because the postcranial skeleton can reflect the mode of substrate use, this variation may be useful for predicting the burrowing ability of shrew species, particularly for those whose behavior is difficult to observe in the field. For example, the medial epicondyle at the base of the humerus is the origin of the flexor carpi radialis and flexor carpi ulnaris muscles.[1] If this epicondyle is enlarged, it can support larger flexor muscles, which then provide greater force for digging through the soil. The claws of the forefeet can also be indicators of digging behavior, since relatively long, robust claws more easily cut through the soil and increase the amount of substrate that can be moved per stroke.[1,2]

Variation in skeletal morphology has previously been linked to substrate use in species of shrews, moles, and rodents.[1,2] For example, the burrowing ability of shrews in the genus *Cryptotis* was inferred from variation in the postcranial skeleton.[3,4] As in that genus, there are clear differences in skeletal morphology among species in Myosoricinae, a subfamily that includes three genera of African shrews. Species in the genus *Surdisorex* have elongated claws[5] and field observations have shown that these species are active burrowers.[6] However, little is known about the other two genera, *Myosorex* and *Congosorex*. Our study examines differences in the postcranial morphology of species from each of the three myosoricine genera. Our analysis of the skeletal morphology of *Surdisorex* should help us to understand which characters are important for burrowing in this subfamily and to predict the burrowing behavior of the less studied *Myosorex* and *Congosorex* species.

QUESTION IN THIS STUDY

How do African shrews of the subfamily Myosoricinae vary in their functional limb morphology and how might this be related to substrate use?

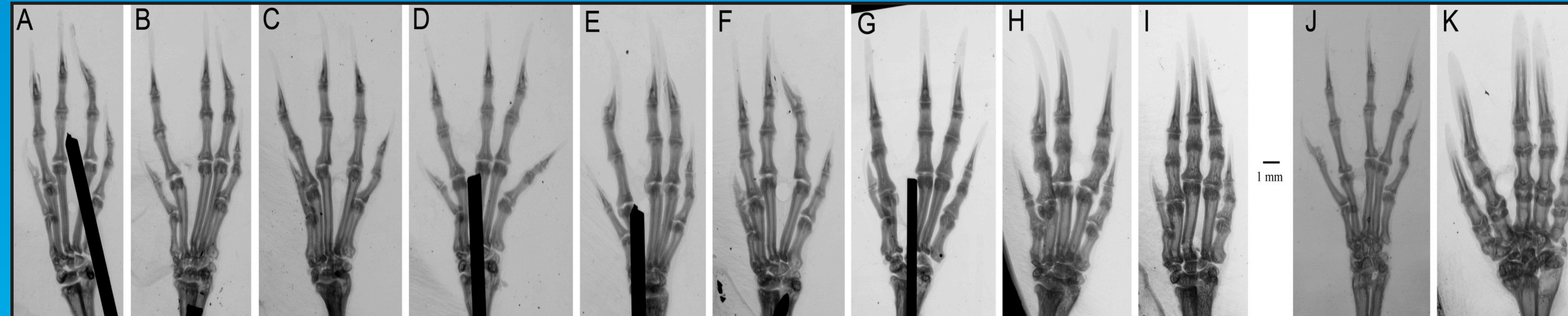


Figure 3. Positive x-ray images of the left forefoot. Shrews: **A,** *M. cafer*; **B,** *M. kihaulei*; **C,** *M. geata*; **D,** *C. phillipsorum*; **E,** *M. varius*; **F,** *M. blarina*; **G,** *M. zinki*; **H,** *S. polulus*; **I,** *S. norae*; Moles: **J,** *U. soricipes*; **K,** *N. gibbsii*.

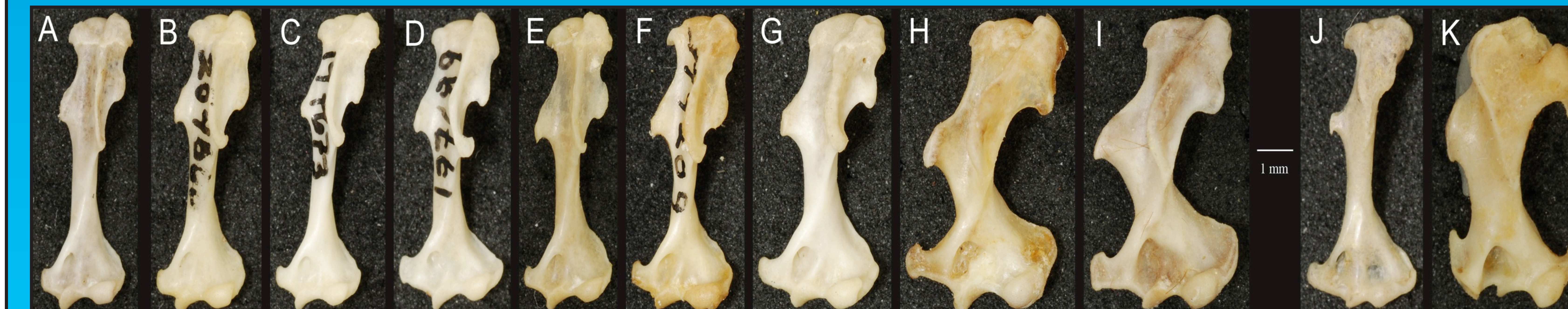


Figure 4. Digital photographs of the humerus, shown with the head facing down. Shrews: **A,** *M. cafer*; **B,** *M. kihaulei*; **C,** *M. geata*; **D,** *C. phillipsorum*; **E,** *M. varius*; **F,** *M. blarina*; **G,** *M. zinki*; **H,** *S. polulus*; **I,** *S. norae*; Moles: **J,** *U. soricipes*; **K,** *N. gibbsii*.

METHODS

We examined and measured 124 individuals representing 9 species of shrews and 2 species of moles. Images of the bones of forefeet and hind feet of dried skin specimens were obtained using digital x-ray imaging and acquisition software. The long bones of the fore limb and hind limb of skeletal specimens were digitally photographed. These images were imported into Adobe Photoshop CS3 and measured in mm using the Custom Measuring Tool. A total of 82 measurements were taken for each individual (Figures 1, 2). These measurements were used to calculate 20 standard indices that have been previously used as indicators of locomotion in shrews,[3] rodents,[7] and other mammals[8] Based on the indices, we ranked the species for burrowing adaptation. A cluster analysis was run and the resulting phenogram was compared to our rankings. The shrews were compared to *Uropsilus soricipes*, a terrestrial mole, and *Neurotrichus gibbsii*, a semifossorial mole.[9,10] Moles (family Talpidae) are generally considered to be the sister-group to shrews[11] and thus served as an approximate comparison of digging ability.

Figure 1. Dorsal view of manual ray III showing the measurements of the long bones of the manus and pes.

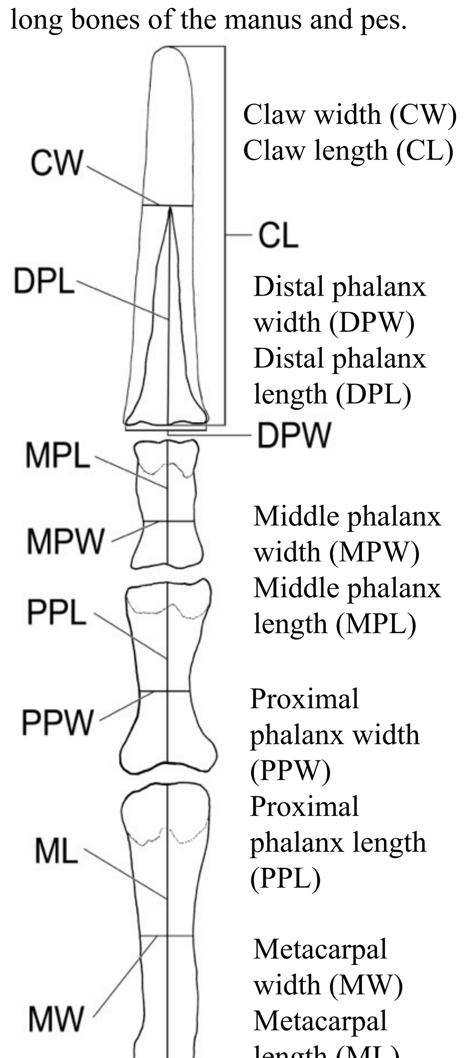
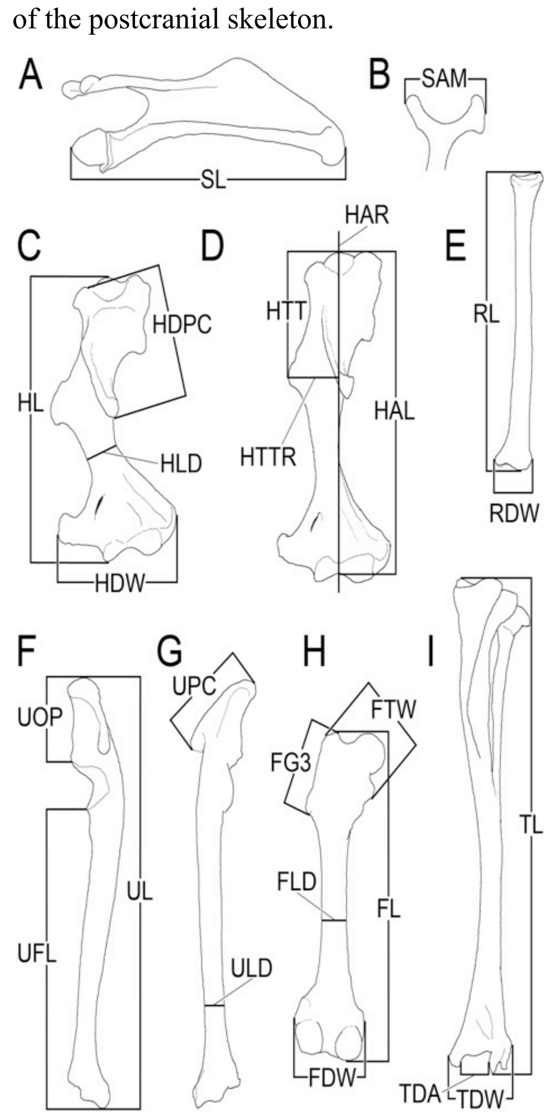


Figure 2. Measurements of the long bones of the postcranial skeleton.



A. Scapula: greatest length (SL). B. Scapula: acromion-metacromion distance (SAM).
C. Humerus: length (HL); distal width (HDW); length of the deltopectoral crest (HDPC); least mediolateral diameter of humerus (HLD).
D. Humerus: axis of rotation (HAR); teres tubercle input lever of rotation (HTTR); length along the axis of rotation (HAL); length along the axis of rotation from the head to the teres tubercle (HTT).
E. Radius: length (RL); distal width (RDW).
F. Ulna: total length (UL); functional length (UFL); length of the olecranon process (UOP).
G. Ulna: width of the proximal crest (UPC); least mediolateral diameter (ULD).
H. Femur: length (FL); greater trochanter-lesser trochanter distance (FTW); greater trochanter-third trochanter distance (FG3); distal width (FDW); least mediolateral diameter (FLD).
I. Tibiofibula: length (TL); width of the distal articular surface (TDA); distal width (TDW).

RESULTS AND DISCUSSION

Our ranking system produced three groupings of myosoricine shrews. (Table 1). Four species—*M. cafer*, *M. kihaulei*, *M. geata*, and *C. phillipsorum*—are generally similar to the terrestrial mole *Uropsilus*. The remaining members of *Myosorex*—*M. zinki*, *M. blarina*, and *M. varius*—are intermediate between the morphology of *Uropsilus* and *Neurotrichus*. Two species of *Surdisorex* were most similar to the semifossorial mole *Neurotrichus*. The ideal range of the proportional ranks is from 0 to 100. The range of burrowing adaptation for the species we examined is from 16 to 88, with the terrestrial *Uropsilus* ranked at 34 and the semifossorial *Neurotrichus* at 84. The results of our ranking system matched well with the phenogram generated from the cluster analysis (Figure 5).

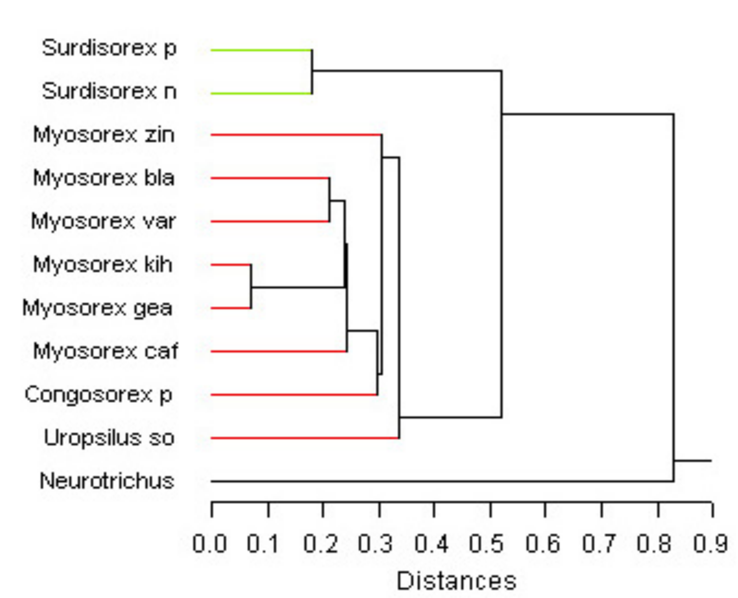


Figure 5. Cluster analysis of the eleven species based on 82 measurements. Distances indicate degrees of similarity.

For the species in this study, the bones of the manus and the humerus are the most consistent indicators of fossoriality. Smaller but thicker proximal manual long bones are more resistant to stress and elongated distal phalanges and claws can move more soil.[1,2] Thicker humeri can bear more of the bending and shearing stress from digging through the soil.[4] A larger deltopectoral crest can support bigger deltoid and pectoral muscles, just as an enlarged teres tubercle allows for a larger teres major muscle.[9] Bigger epicondyles at the base of the humerus also provide space for larger muscle attachments.[1] Thus, it makes the most sense to focus on the indices that best represent these characters; namely, %DPL, %CL, MW3, HRI, HEB, HTI, and SMI.

Based on these features, shrews in the subfamily Myosoricinae can be put on a range of predicted substrate use, from terrestrial to semifossorial. *C. phillipsorum*, *M. cafer*, *M. kihaulei*, and *M. geata* are closer to *Uropsilus* and represent primarily terrestrial species. Their morphology suggests a life spent mostly on the surface, with little if any deep burrowing. The remaining *Myosorex*, however, do show some adaptations for burrowing and likely engage in a greater amount of digging. The two members of *Surdisorex* are most similar to the semifossorial mole *Neurotichus* and are best equipped to burrow.

Table 1. Mean indices calculated for each species. Proportional rankings are based on the number of taxa available for a given index.

Taxon	CLAW	SHI	SMI	HRI	HTI	HTTD	HEB	RDW	OLI	OCI	URI	%DPL	%CL	%CLS	MW3	FRI	FEB	%HDPL	%HCL	%HCLS	PROPORTIONAL RANK
M. cafer	100	92	46	10	15	36	32	—	—	—	—	19	36	51	11	8	21	15	26	58	16
M. kihaulei	97	94	46	9	16	40	35	—	—	—	—	23	46	49	12	10	23	19	32	59	27
M. geata	93	94	47	9	16	39	35	—	—	—	—	21	42	50	13	10	23	19	31	62	30
U. soricipes	81	125	44	10	16	39	44	9	16	17	4	22	40	55	12	9	26	18	30	60	34
C. phillipsorum	113	104	50	11	18	42	42	—	—	—	—	23	39	59	13	10	24	18	32	56	44
M. varius	109	99	48	10	18	43	35	13	19	30	5	27	52	52	14	9	22	20	34	60	47
M. blarina	107	100	50	9	19	41	39	15	24	31	8	28	57	49	15	10	24	23	39	59	55
M. zinki	120	108	47	13	18	42	47	—	—	—	—	29	61	48	16	11	25	21	34	60	62
S. polulus	162	113	62	17	39	55	58	—	—	—	—	45	76	59	20	10	24	25	39	64	79
N. gibbsii	123	174	62	22	38	50	54	19	26	36	7	68	104	65	41	10	27	30	46	65	84
S. norae	143	120	62	17	35	51	60	17	31	40	9	46	78	60	20	11	25	27	38	69	88

1. CLAW – compares the length of the distal phalanx of manual ray III to the length of the distal phalanx of pedal ray III.
2. SHI – compares the length of the scapula to the length of the humerus and reflects scapular elongation.
3. SMI – compares the length of the deltopectoral crest (origin of deltoid and pectoral muscles) to the length of the humerus.
4. HRI – compares the width of the humerus to its length and indicates robustness and resistance to bending and shearing stress.
5. HTI – compares the length of the teres tubercle to length of humerus and reflects the size of the teres major muscle.
6. HTTD – indicates the location of the teres tubercle along the humerus and reflects the amount of force transferred.
7. HEB – represents the relative area of the lower extremity of the humerus available for muscle attachments.
8. RDW – compares the width of the radius to its length and indicates robustness and resistance to bending and shearing stress.
9. OLI – compares the length of the olecranon process to the length of the ulna and reflects the amount of force transferred.
10. OCI – compares the length of the olecranon crest to the length of the ulna and reflects muscle attachments.
11. URI – compares the width of the ulna to its length and indicates robustness and resistance to bending and shearing stress.
12. %DPL – compares the length of the distal phalanx of manual ray III to the length of the first three proximal phalanges.
13. %CL – compares the claw length of manual ray III to the combined length of the first three proximal phalanges.
14. %CLS – compares the length of the distal phalanx of manual ray III to claw length and shows proportion of claw support.
15. MW3 – compares the width of the metacarpal of manual ray III to its length and indicates the thickness of the metacarpals.
16. FRI – compares the width of the femur to its length and indicates robustness and resistance to bending and shearing stress.
17. FEB – represents the relative area of the femur available for muscle attachments.
18. %HDPL – compares the length of the distal phalanx of pedal ray III to the length of the first three proximal phalanges.
19. %HCL – compares the claw length of pedal ray III to the combined length of the first three proximal phalanges.
20. %HCLS – compares the length of the distal phalanx of pedal ray III to claw length and shows proportion of claw support.

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