



Variation in the myosoricine hand skeleton and its implications for locomotory behavior (Eulipotyphla: Soricidae)

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Substrate use and locomotory behavior of mammals are typically reflected in external characteristics of the forefeet, such as the relative proportions of the digits and claws. Although skeletal anatomy of the forefeet can be more informative than external characters, skeletons remain rare in systematic collections. This is particularly true for the Myosoricinae (Eulipotyphla: Soricidae), a small clade of African shrews that includes both ambulatory forest shrews (*Myosorex*) and semifossorial mole shrews (*Surdisorex*). Most species in this subfamily have restricted distributions, and their behavior and ecology are mostly unstudied. To better understand the potential range of locomotory behavior among myosoricines, we used digital x-rays to image and facilitate measuring the forefoot skeletons of 9 species. As a gauge of potential variation, we compared them with the ambulatory talpid *Uropsilus* (Talpidae) and the semifossorial talpid *Neurotrichus*. The hand morphologies of myosoricines show a graded range of potential substrate use between ambulatory and semifossorial. Some of these shrews exhibit adaptations for increased burrowing efficiency that are similar to those seen in talpids and other mammals, such as longer, broader distal phalanges and claws and shorter, wider metacarpals and proximal and middle phalanges. They also, however, have characteristics that are distinct from talpids, such as maintenance of forefoot asymmetry and an increased emphasis of ray III.

Key words: anatomy, Insectivora, manus, Myosoricinae, postcranial, ray, semifossorial, Soricomorpha.

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Myosoricinae is a well-supported clade (Qu erouil et al. 2001; Willows-Munro and Matthee 2011) of small- to medium-sized shrews (Eulipotyphla: Soricidae) that includes 3 recent African genera and at least 25 species: the mouse shrews and forest shrews, *Myosorex* Gray, 1838 (19 spp.); the mole shrews, *Surdisorex* Thomas, 1906 (3 spp.); and the Congo shrews, *Congosorex* Heim de Balsac and Lamotte, 1956 (3 spp.—Meester 1953; Hutterer 2005; Stanley et al. 2005; Kerbis Peterhans et al. 2008, 2009, 2010, 2013; Taylor et al. 2013). Species of *Myosorex* are generally assumed to be terrestrial and ambulatory in their substrate use and behavior (Hutterer 1985). They typically have short foreclaws, obvious pinnae, moderately large eyes, and medium to long tail lengths (Hutterer et al. 2002). In contrast, the 3 species of *Surdisorex* are strongly semifossorial, appearing “more like a mole than a shrew” (Thomas 1906:223). They produce shallow runs under leaf litter and dig actively for earthworms, which comprise a large portion of their diet (Duncan and Wrangham 1971; Coe and Foster 1972). These shrews also possess a number of external

characteristics that typically are associated with semifossoriality and fossoriality among mammals, including tiny eyes, small pinnae, a short tail, and enlarged foreclaws (Duncan and Wrangham 1971; Meester 1953; Kerbis Peterhans et al. 2009). The habits of *Congosorex* are poorly known. Although these shrews have external characters associated with semifossorial and fossorial behaviors in mammals, such as tiny eyes, short tails, and reduced pinnae (e.g., Shimer 1903), the foreclaws are short (Hutterer et al. 2002), making them unlikely to be strong burrowers.

Beyond traditional cranial and external characters (Hollister 1916; Kerbis Peterhans et al. 2008, 2009, 2010; Stanley and Esselstyn 2010), little effort has been made to examine the potential diversity in form and function of myosoricines. Study of forefoot skeletal morphology among some soricine shrews has helped to identify a broader array of ecological diversity in the subfamily than had been appreciated (Woodman and Timm 1999; Woodman 2010, 2011a; Woodman and Gaffney 2014), and variation in the bones of the forefoot is of

sufficient magnitude to distinguish species and even subspecies (Woodman and Morgan 2005; Woodman and Stephens 2010; Woodman 2011b). As for other vertebrates, complete prepared skeletons of shrews and many other small mammals are relatively scarce in systematic collections (Bell and Mead 2014). The skeleton of the forefoot is typically preserved in traditional dried skin preparations, however, and it can be imaged using digital x-ray technology (Woodman and Morgan 2005; Woodman and Stephens 2010; Sargis et al. 2013a, 2013b). To study variation within and among species of myosoricines, we x-rayed the forefeet of 9 species of these shrews encompassing all 3 recognized genera. We examined the resulting images and measured the bones of the rays to quantitatively compare and contrast the morphology of the forefoot among these shrews. Our purpose was to test whether forefoot characteristics that distinguish grades of locomotion in soricines and talpids reveal a similar pattern among myosoricines.

MATERIALS AND METHODS

We use the term “digit” to refer to the tissues associated with the phalanges (finger) and “ray” to refer to tissues associated with the phalanges and metacarpal (finger and palm). We obtained digital x-ray images of forefeet from dried study skins of myosoricine shrews using a Kevex-Varian (Palo Alto, California) digital x-ray system in the Division of Fishes, National Museum of Natural History, Washington, D.C., following the procedure of Woodman and Morgan (2005; see also Woodman and Stephens 2010; Sargis et al. 2013a, 2013b). The resulting digital images were transferred to Adobe Photoshop CS3 Extended (Knoll et al. 2007), trimmed, converted to positive images, and measured with the custom Measurement Scale in the Analysis menu. We measured 8 variables from ray I of the manus and 10 variables from each of rays II–V (38 total; see Fig. 1 for explanation and abbreviations of variables). All measurements are in millimeters (mm), and all forefoot measurements are rounded to the nearest 0.01 mm. Summary statistics include mean, *SD*, and total range (Supporting Information S1). We recorded 2 proxies for body size from specimen labels, where available: field weight (WT) rounded to the nearest 0.1 g and head-and-body length (HB), which was determined by subtracting tail length from total length and rounded to the nearest mm (Table 1). Although WT can be a better measure of overall body size, it is not available for all specimens or all species in our study. Fortunately, among myosoricines HB and WT are correlated (0.88; Supporting Information S2), and we use it as a proxy for body size in comparisons among variables.

We measured the forefeet of 82 individuals representing 3 genera and 9 species of myosoricines (Appendix I): *Congosorex phillipsorum* ($n = 7$), *Myosorex blarina* ($n = 3$), *M. cafer* ($n = 2$), *M. geata* ($n = 12$), *M. kahaulei* ($n = 12$), *M. varius* ($n = 4$), *M. zinki* ($n = 2$), *Surdisorex norae* ($n = 17$), and *S. polulus* ($n = 14$). Mean WT among these species ranges from 7.8 to 22.5 g, and HB is 71–99 mm (Table 1; Fig. 2A). Moles (Talpidae) and shrews are likely sister groups (Meredith et al. 2011), and moles are among the most stereotypically semifossorial and fossorial small mammals. As an aid

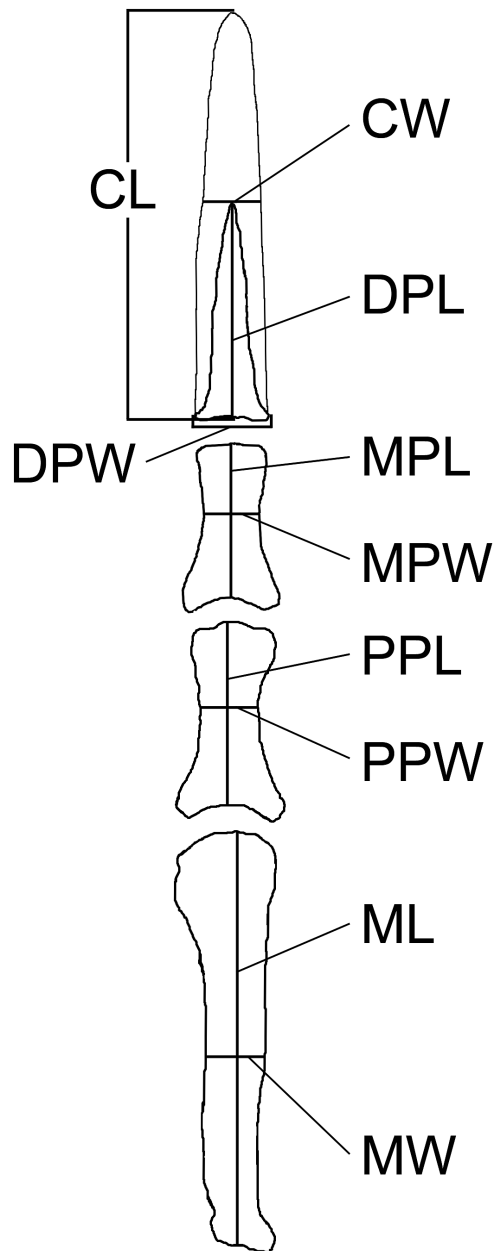


Fig. 1.—Myosoricine left ray III illustrating variables measured: CL = claw length; CW = claw width; DPL = distal phalanx length; DPW = distal phalanx width; ML = metacarpal length; MW = metacarpal width; MPL = middle phalanx length; MPW = middle phalanx width; PPL = proximal phalanx length; PPW = proximal phalanx width. A numeral before an abbreviation designates the ray to which an element belongs (e.g., 4MW = width of metacarpal IV).

in understanding the potential similarities and differences among terrestrial and semifossorial myosoricines, we also examined and measured the forefeet of the ambulatory Chinese shrew mole, *Uropsilus soricipes* Milne-Edwards (1871; $n = 9$) and the semifossorial shrew mole, *Neurotrichus gibbsii* (Baird, 1857; $n = 14$). Specimens used in this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); and National Museum of Natural History, Washington, D.C. (USNM).

Table 1.—Body size measures and indices from ray III of the manus of myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and talpids (*Neurotrichus* and *Uropsilus*). Abbreviations are explained in “Materials and Methods.” Summary statistics include mean \pm *SD* and total range.

Species	HB	WT	%CLS	PI	IPR	M3W	3P3L/HB	3TSL/HB	3TOT/HB
<i>Congosorex phillipsorum</i> (<i>n</i> = 7)	71 \pm 2 69–74	7.8 \pm 0.3 7.4–8.3	60 \pm 3 54–62	87 \pm 4 79–92	57 \pm 3 52–60	13 \pm 2 10–13	8.0 \pm 0.4 7.5–8.5	9.8 \pm 0.5 9.2–10.3	11.1 \pm 0.6 10.3–11.8
<i>Myosorex blarina</i> (<i>n</i> = 3)	86 \pm 5 81–91	15.0 13.5–16.5 (<i>n</i> = 2)	49 \pm 4 45–53	84 \pm 5 79–88	68 \pm 11 55–77	15 15–15 (<i>n</i> = 2)	7.3 \pm 0.3 7.0–7.5	9.4 \pm 0.4 8.9–9.7	11.5 \pm 0.3 11.2–11.8
<i>M. cafer</i> (<i>n</i> = 2)	80 76–84	11.3 9.5–13.0	51 47–56	91 90–91	67 66–67	11 11–12	9.1 8.7–9.5	10.8 10.4–11.2	12.4 11.8–13.1
<i>M. geata</i> (<i>n</i> = 12)	78 \pm 5 68–83	10.1 \pm 1.5 7.6–12.0 (<i>n</i> = 11)	50 \pm 4 43–58	90 \pm 4 85–97 (<i>n</i> = 11)	68 \pm 4 62–73 (<i>n</i> = 11)	13 \pm 0 12–13 (<i>n</i> = 11)	8.0 \pm 0.6 7.3–9.4 (<i>n</i> = 11)	9.7 \pm 0.6 9.1–11.1 (<i>n</i> = 11)	11.4 \pm 0.8 10.6–13.4 (<i>n</i> = 11)
<i>M. kihaulei</i> (<i>n</i> = 12)	76 \pm 4 67–82 (<i>n</i> = 11)	10.1 \pm 1.6 7.0–12.5 (<i>n</i> = 11)	49 \pm 2 46–54	89 \pm 5 82–97 (<i>n</i> = 11)	68 \pm 6 54–79	12 \pm 2 9–14 (<i>n</i> = 11)	8.2 \pm 0.6 7.5–9.2 (<i>n</i> = 11)	10.1 \pm 0.7 9.3–11.0 (<i>n</i> = 11)	12.0 \pm 0.9 10.8–13.1 (<i>n</i> = 11)
<i>M. varius</i> (<i>n</i> = 4)	84 \pm 2 83–87	12.8 \pm 1.0 12.0–14.0	52 \pm 6 44–57	88 \pm 5 84–95	70 \pm 6 64–77	14 \pm 2 12–16	7.5 \pm 0.2 7.3–7.8	9.6 \pm 0.4 9.2–10.0	11.5 \pm 0.3 11.0–11.7
<i>M. zinki</i> (<i>n</i> = 2)	93 91–95	15.0 14.5–15.5	48 43–52	86 84–87	67 64–70	16 15–17	7.6 7.4–7.8	9.8 9.7–9.8	12.2 11.8–12.5
<i>Surdisorex norae</i> (<i>n</i> = 17)	99 \pm 4 90–108	21.5 \pm 2.9 17.5–26.7 (<i>n</i> = 10)	60 \pm 4 54–68 (<i>n</i> = 16)	82 \pm 9 53–92 (<i>n</i> = 15)	69 \pm 5 61–79 (<i>n</i> = 16)	20 \pm 1 18–22	7.0 \pm 0.5 6.1–7.9 (<i>n</i> = 16)	10.2 \pm 0.5 9.2–11.3 (<i>n</i> = 16)	12.4 \pm 0.6 11.013.3 (<i>n</i> = 15)
<i>S. polulus</i> (<i>n</i> = 23)	95 \pm 3 89–100 (<i>n</i> = 22)	22.5 (<i>n</i> = 1) (<i>n</i> = 22)	60 \pm 6 50–75	84 \pm 4 74–92	70 \pm 4 62–78	20 \pm 1 18–21	7.7 \pm 0.4 6.4–8.3 (<i>n</i> = 22)	11.1 \pm 0.6 9.2–12.2 (<i>n</i> = 22)	13.5 \pm 0.9 10.8–14.9 (<i>n</i> = 22)
<i>Uropsilus</i> (<i>n</i> = 9)	71 \pm 6 65–83	9.0 \pm 0.7 8.0–9.8 (<i>n</i> = 5)	55 \pm 6 46–64	104 \pm 4 97–109	59 \pm 7 47–70	12 \pm 1 12–13	8.4 \pm 0.7 6.8–9.2 (<i>n</i> = 8)	10.2 \pm 0.8 8.5–11.2 (<i>n</i> = 8)	11.7 \pm 1.1 9.6–12.9 (<i>n</i> = 8)
<i>Neurotrichus</i> (<i>n</i> = 15)	74 \pm 7 67–87 (<i>n</i> = 7)	—	65 \pm 4 60–73	135 \pm 8 119–150	66 \pm 3 60–70	41 \pm 3 37–46	5.5 \pm 0.4 4.8–5.9 (<i>n</i> = 7)	9.1 \pm 0.6 7.9–9.6 (<i>n</i> = 7)	11.0 \pm 0.9 9.0–11.8 (<i>n</i> = 7)

We calculated pairwise Pearson’s product-moment correlations (Supporting Information S2) to examine intensities of association among variables and coefficients of variation (*V*; Supporting Information S2) to gauge the magnitude of interspecific and intraspecific variation among variables having different means. Enlargement of the forefoot and changes in symmetry and the relative proportions of bones and claws commonly accompany adaptation of the mammalian forefoot for burrowing (Reed 1951; Hildebrand 1985; Morgan and Verzi 2011). We examined symmetry of the forefoot by comparing the total lengths (TOT) of rays I, II, IV, and V as proportions of the total length of ray III (Lemelin 1999); TOT is total length of the ray including claw (= ML + PPL + CL for ray I; ML + PPL + MPL + CL for rays II–V; see Fig. 1 for variable abbreviations). To determine how total length of the ray skeleton (3TSL = 3ML + 3PPL + 3MPL + 3DPL) varied among species of different body size (HB), we regressed 3TSL on HB. In examining variation among the individual bones of the forefoot, we calculated a number of indices and proportions, all of which are expressed as percentages. The claw support index (%CLS = 3DPL/3CL) represents the amount of support

for the claw that is provided by the underlying distal phalanx. This measure increases with greater semifossoriality in soricines (Woodman and Gaffney 2014). The phalangeal index (PI) and interphalangeal ratio (IPR) are common morphological proxies for inferring substrate use among extant and fossil groups of mammals. Because these indices can vary considerably among the rays of an individual or species, ray III is typically used for interspecific comparisons (Lemelin 1999; Weisbecker and Warton 2006; Weisbecker and Schmid 2007; Kirk et al. 2008). The PI compares the length of the digit (not including the claw) relative to the metacarpal, and a higher PI represents a longer digit (Supporting Information S3). For ray III, PI = [(3PPL + 3MPL)/3ML]. The IPR measures the length of the middle phalanx as a percentage of the proximal phalanx (3MPL/3PPL). A larger IPR indicates a relatively longer middle phalanx (Supporting Information S3). We also plotted the relative lengths of the metacarpal (3ML), proximal phalanx (3PPL), and middle phalanx (3MPL) of ray III on the ternary diagrams of mammals provided in Kirk et al. (2008), which they used to distinguish different mammalian guilds of substrate use. Relative shortening and broadening of the phalanges

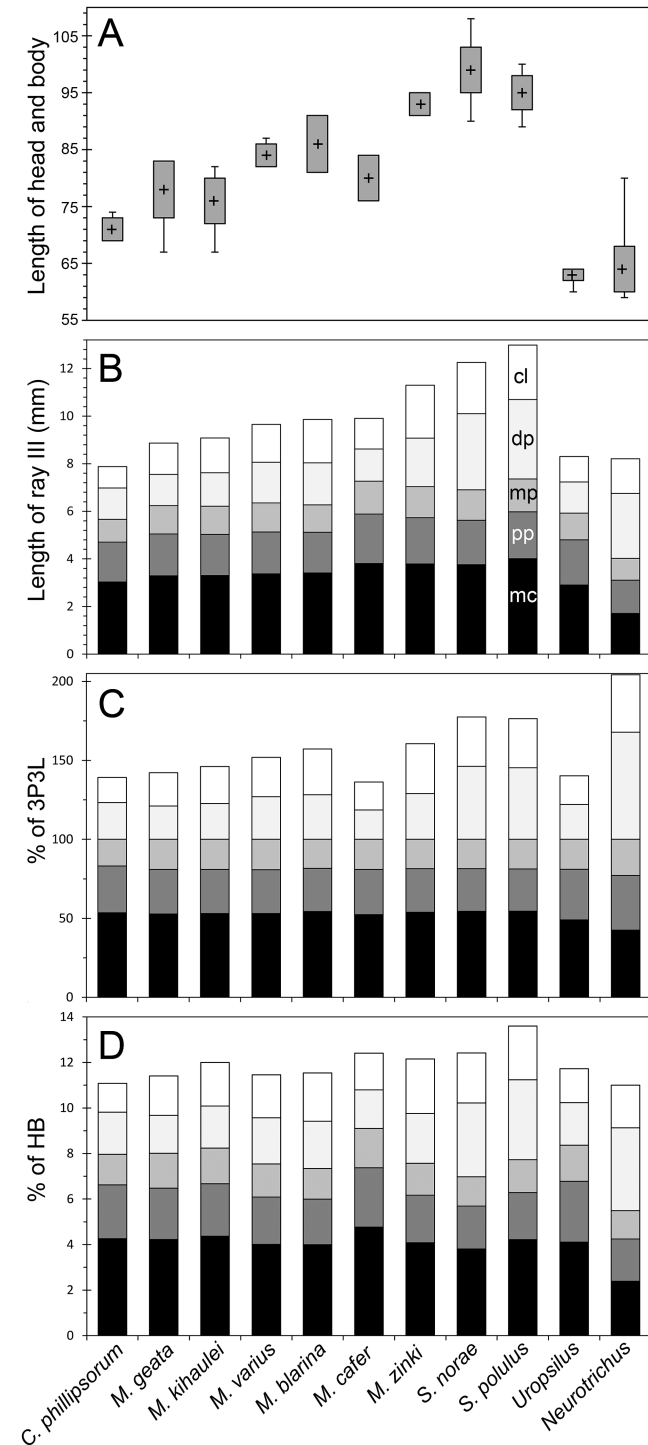


Fig. 2.—Graphs of body size and the relative proportions of elements comprising ray III of myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and 2 talpids (*Neurotrichus* and *Uropsilus*). A) Box-and-whisker plot of body size as represented by head-and-body length in millimeters (mm). A cross represents the mean, the box shows *SD*, and “whiskers” represent the range. B) Mean lengths of individual elements of ray III in mm. Colors and abbreviations in B, C, and D: cl, claw; dp, distal phalanx; mp, middle phalanx; pp, proximal phalanx; mc, metacarpal. C) Mean lengths of individual elements of ray III expressed as a proportion of the combined length of the proximal 3 elements (3P3L). The distal end of each middle phalanx is at 100%. D) Mean lengths of individual elements of ray III expressed as a proportion of body size.

and metacarpals has been documented for many semifossorial and fossorial mammals (Hildebrand 1985; Morgan and Verzi 2011). The metacarpal width index (MW3) measures the width of the metacarpal relative to its length, simultaneously taking into account both aspects of this bone. This index increases with increasing fossoriality among soricines (Woodman and Morgan 2005; Woodman and Gaffney 2014).

We carried out principal component analyses (PCAs) individually on 7 variables (1CL, 1DPL, 1DPW, 1ML, 1MW, 1PPL, 1PPW) from ray I and 9 variables (CL, DPL, DPW, ML, MW, MPL, MPW, PPL, PPW) from each of rays II–V. To remove possible allometric effects, each variable was \log_{10} -transformed and standardized by dividing by the geometric mean of all 7 or 9 variables for its individual respective ray following Mosimann and James (1979). Regression and multivariate statistical analyses were performed using Systat 11.00.01 (Wilkinson et al. 2004).

RESULTS

General variation in the myosoricine forefoot.—The external forefoot exhibits considerable qualitative variation in the proportions of the digits and claws among myosoricines (Fig. 3). *C. phillipsorum* and most species of *Myosorex* have relatively long, narrow fingers tipped with relatively short, narrow claws. In contrast, the 2 species of *Surdisorex* have relatively short, broad fingers with long, broad claws on digits II, III, and IV. The forefoot of *M. zinki* is intermediate between the general condition for *Myosorex* and that for *Surdisorex*. The claws, in particular, are notably longer and broader than those of other *Myosorex*.

Inspection of the x-ray images of the forefoot skeletons reveals corresponding qualitative variation in proportions of the bones of the manus (Figs. 2B and 4). The metacarpals and proximal and middle phalanges of *Congosorex* and most *Myosorex* are relatively long and narrow, while the distal phalanges are short (Fig. 2C) and narrow. In general proportions, the manus of these species is comparable to that of the ambulatory talpid *Uropsilus* (Fig. 4J). In *Surdisorex*, the metacarpals and proximal and middle phalanges are relatively shorter (Fig. 2D) and more robust, while the distal phalanges are long (Fig. 2D) and have a wide proximal base. These characteristics are superficially similar to those in the forefoot of the semifossorial talpid *Neurotrichus* (Fig. 4K). The bones of the manus of *M. zinki* (Fig. 4G) are of intermediate proportions between those of the manus of most other *Myosorex* and those of *Surdisorex*. The robust metacarpals and phalanges and more elongate distal phalanges and claws of *M. zinki* suggest a species that is more semifossorial in its habits than other members of the genus. Because of the distinctiveness of its manus, we treated *M. zinki* separately from other *Myosorex* in our quantitative analyses.

Symmetry of the forefoot.—In general, semifossorial and fossorial talpids have evolved a forefoot in which the lengths of the radial rays (I, II) and ulnar rays (IV, V) are closer to that of central ray III. Moreover, complementary rays from the 2

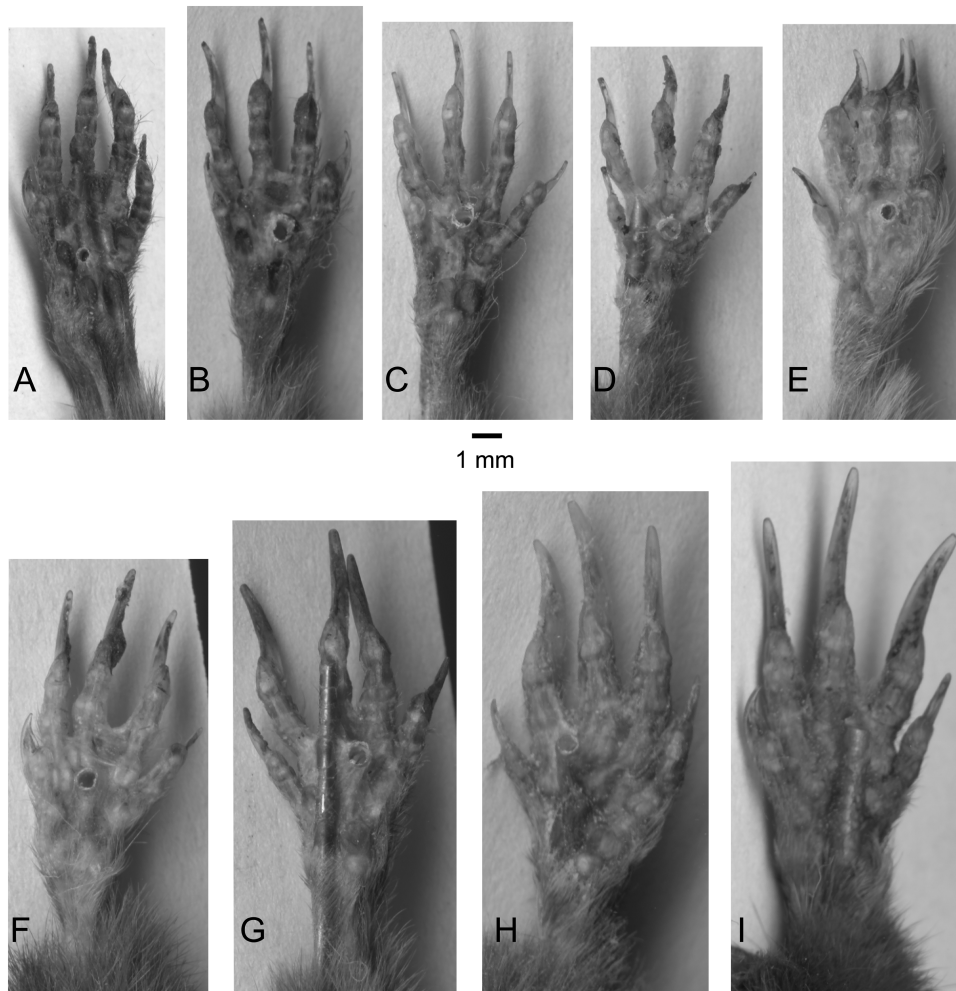


Fig. 3.—Palmar view of myosoricine left forefeet illustrating variation in the external morphology of the digits and claws: A) *Myosorex cafer* (FMNH 165587), B) *M. kihalaei* (FMNH 204858), C) *M. geata* (FMNH 197670), D) *Congosorex phillipsorum* (FMNH 177685), E) *M. varius* (FMNH 165589), F) *M. blarina* (FMNH 26285), G) *M. zinki* (FMNH 174117), H) *Surdisorex polulus* (USNM 589820), and I) *S. norae* (FMNH 190626).

sides of the manus (I and V; II and IV) are nearly the same length. The result is that the tips of the digits and, more importantly, the tips of the claws form a more nearly bilaterally symmetrical arc centered on ray III (Reed 1951). In both *Uropsilus* and *Neurotrichus*, e.g., the average difference in total length of ray II from ray III is only 7%, and ray IV differs from ray III by 2–4% (Table 2). Rays I and V, from opposite sides of the manus, differ in length by only 3–7%, and rays II and IV differ in length by 3–5%. In more fossorial forms, the differences among the lengths of the rays can be even less (Reed 1951).

Shrews typically have more asymmetrical forefeet than moles. The rays and digits differ more in length and generally decrease in the order: III, IV, II, V, I. Rays I and II on the radial side of the manus are shorter than their counterparts (rays V and IV, respectively) on the ulnar side (Woodman and Stephens 2010). Myosoricines maintain the general soricid asymmetry, although this is most apparent for complimentary rays I and V, which average 9–15% difference in length. Rays II and IV average only 2–6% difference, similar to differences between those rays in *Uropsilus* and *Neurotrichus*. Comparing the relative lengths

of the myosoricine rays directly with those of *Uropsilus* and *Neurotrichus*, the most consistent difference is in ray I, which averages 8–20% shorter (Table 2). Ray V averages 4–11% shorter for *M. blarina*, *M. zinki*, and the 2 *Surdisorex*, and rays II and IV average 2–7% shorter for *Surdisorex*. There appears to be a subtle, but not universal, trend for the longer clawed myosoricines to have relatively shorter rays on either side of ray III, particularly rays I and V. This is most apparent for the 2 species of *Surdisorex*, but slight shortening of the rays appears to have taken place in the forefeet of *M. blarina* and *M. zinki* as well. In adapting to a more semifossorial mode, the myosoricines have maintained an asymmetrical forefoot that further emphasizes central ray III and reduces rays I and V. This pattern is in contrast with the more symmetrical, spade-like foot of talpids.

Relative proportions of ray III.—Among myosoricines, mean total length of the 4 bones comprising ray III (TSL) varies from 6.98 to 10.70 mm, and mean total length of the ray including the claw (TOT) ranges from 7.88 to 12.99 mm (Fig. 2B). For both measures, *C. phillipsorum* has the shortest ray III and *S. polulus* has the longest.

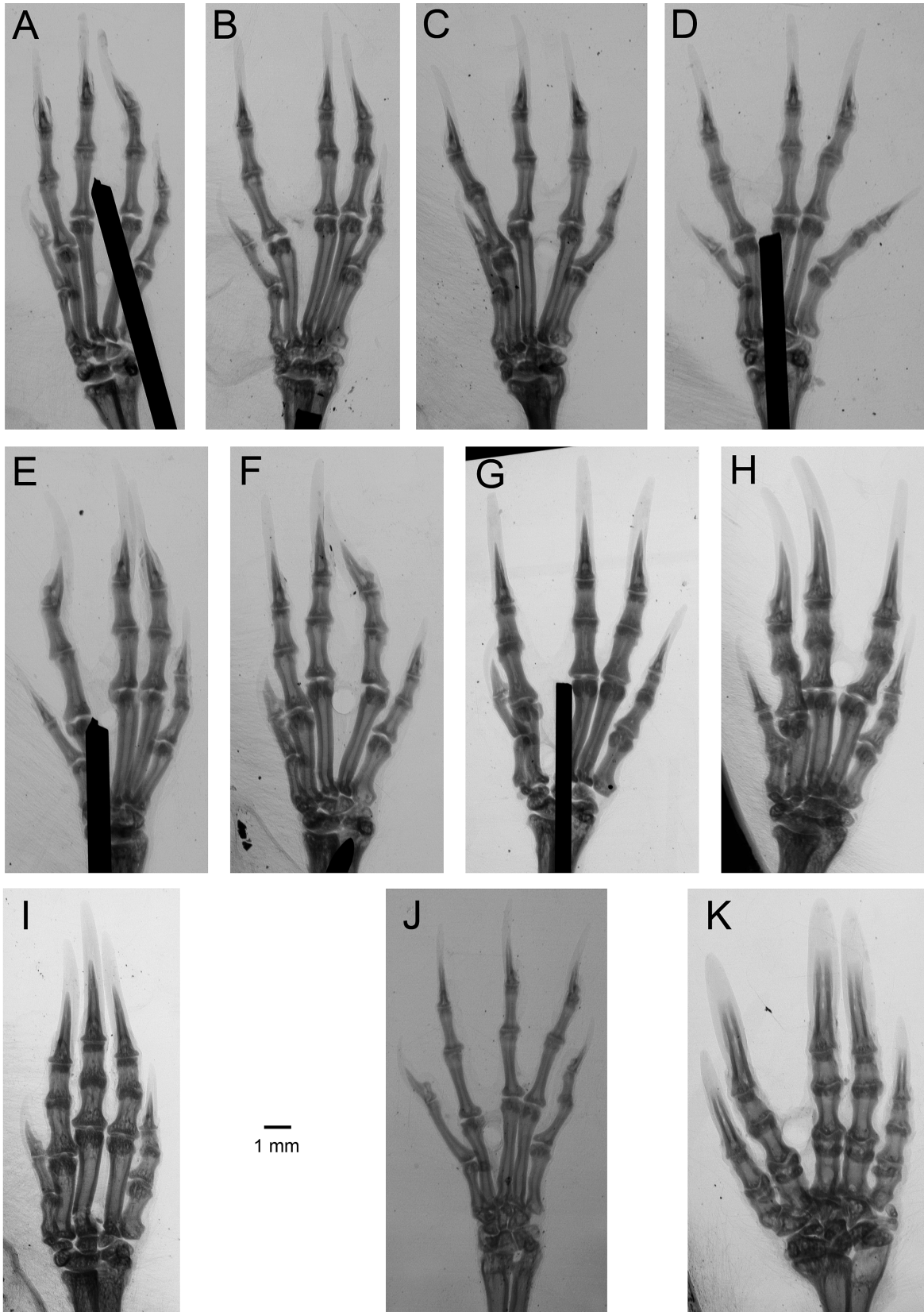


Fig. 4.—X-ray views of left manus skeletons of myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and 2 talpids (*Neurotrichus* and *Uropsilus*), illustrating variation in proportions of the bones and claws: A) *Myosorex cafer* (FMNH 165585), B) *M. kishaulei* (FMNH 155621), C) *M. geata* (FMNH 197670), D) *Congosorex phillipsorum* (FMNH 177688), E) *M. varius* (FMNH 165591), F) *M. blarina* (FMNH 26285), G) *M. zinki* (FMNH 174117), H) *Surdisorex polulus* (USNM 163982), I) *S. norae* (USNM 182581), J) *Uropsilus soricipes* (USNM 574298), and K) *Neurotrichus gibbsii* (USNM 65707).

Table 2.—Proportional lengths of rays I, II, IV, and V relative to the total length (TOT) of ray III for myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and talpids (*Neurotrichus* and *Uropsilus*). Summary statistics include mean \pm SD and total range. All numbers are percentages.

	Ray I	Ray II	Ray IV	Ray V
<i>Congosorex</i>	50 \pm 1	94 \pm 2	96 \pm 2	64 \pm 2
<i>phillipsorum</i> (n = 7)	49–52 (n = 6)	91–96 (n = 4)	94–100	62–67
<i>Myosorex blarina</i> (n = 3)	48 47–49 (n = 2)	91 89–92 (n = 2)	96 \pm 5 92–101	57 56–58 (n = 2)
<i>M. cafer</i> (n = 2)	50 50–50	92 92–92	95 95–95	65 64–65
<i>M. geata</i> (n = 11)	52 \pm 1 50–54 (n = 10)	92 \pm 3 87–96 (n = 10)	96 \pm 1 94–98	66 \pm 1 64–68 (n = 10)
<i>M. kihaulei</i> (n = 11)	50 \pm 2 48–53 (n = 9)	92 \pm 3 87–96 (n = 8)	95 \pm 2 90–98	63 \pm 2 60–66
<i>M. varius</i> (n = 4)	51 \pm 3 49–55	93 \pm 1 92–95	96 \pm 1 94–98	63 \pm 2 60–65
<i>M. zinki</i> (n = 2)	51 50–51	90 90–90	96 94–98	62 62–63
<i>Surdisorex norae</i> (n = 15)	43 \pm 2 39–46 (n = 12)	88 \pm 2 86–91 (n = 14)	91 \pm 3 85–94	56 \pm 3 47–59 (n = 13)
<i>S. polulus</i> (n = 23)	47 \pm 2 42–50 (n = 16)	90 \pm 3 82–97	94 \pm 3 86–99	58 \pm 2 54–63 (n = 22)
<i>Uropsilus</i> (n = 8)	60 \pm 3 53–63 (n = 7)	93 \pm 2 89–96	96 \pm 2 92–99 (n = 7)	67 \pm 3 63–71 (n = 7)
<i>Neurotrichus</i> (n = 15)	63 \pm 3 58–67 (n = 14)	93 \pm 2 88–97	98 \pm 2 94–102 (n = 14)	66 \pm 2 63–72 (n = 14)

Regression analysis of total length of ray III (TSL) on body size (HB) for all myosoricines shows a significant positive trend of increasing digit length with increasing body size within the subfamily (Fig. 5; $TSL = 0.1216 HB - 1.5893$; $F_{1,76} = 278.32$, $P = 0.000$, $R_{ADJ}^2 = 0.783$; $n = 78$). Individuals of *C. phillipsorum* and *M. kihaulei* are about equally distributed on either side of this regression line. Most *M. blarina*, *M. geata*, *M. varius*, *M. zinki*, and *S. norae*, however, plot below the line, indicating a shorter ray III than expected for myosoricines. In contrast, *M. cafer* and *S. polulus* plot primarily above the regression, indicating a longer ray III than expected. A 2nd regression, calculated for species of *Myosorex* alone, has a much lower slope and indicates a different trend within that genus than for the subfamily ($TSL = 0.0541 HB + 3.5166$; $F_{1,31} = 20.732$, $P = 0.000$, $R_{ADJ}^2 = 0.381$; $n = 33$). Both species of *Surdisorex* have much longer rays for their body size than is predicted for *Myosorex*, and *M. cafer* and *M. zinki* have proportionally longer rays than other members of the genus. In contrast, *C. phillipsorum* has proportionally shorter rays than predicted for *Myosorex*. Hence, ray III has a different relationship to body size in each of the 3 genera. In general, however, a longer ray III is associated with greater semifossoriality among myosoricines. Superficially, this appears to be distinct from the talpid pattern

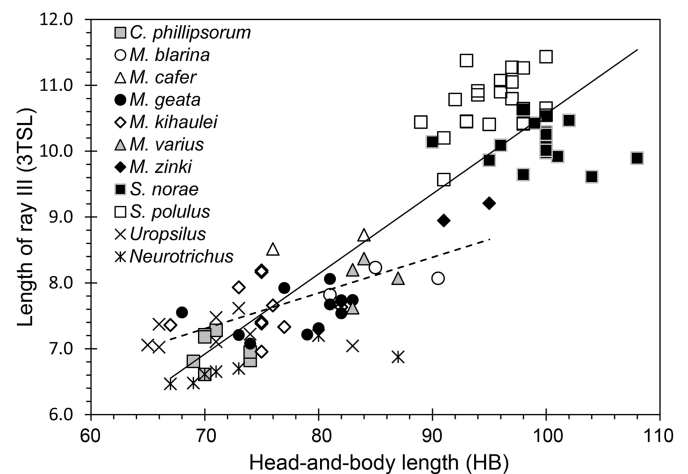


Fig. 5.—Plot of total length of ray III skeleton (TSL) on body size (HB) for myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and 2 talpids (*Neurotrichus* and *Uropsilus*). Regression analysis of all myosoricines (long solid line) shows a significant positive trend of increasing ray length with increasing body size within the subfamily ($3TSL = 0.1216 HB - 1.5893$; $F_{1,76} = 278.32$, $P = 0.000$, $R_{ADJ}^2 = 0.783$; $n = 78$). Regression analysis of *Myosorex* (short dashed line) also shows a significant positive trend, but with a much lower slope ($3TSL = 0.0541 HB + 3.5166$; $F_{1,31} = 20.732$, $P = 0.000$, $R_{ADJ}^2 = 0.381$; $n = 33$).

in which a proportionally shorter ray III accompanies increasing semifossoriality and fossoriality (Fig. 2D; Reed 1951).

The elongation of ray III among more semifossorial myosoricines is not simply a result of allometric increase of each of the individual elements. The increased length results entirely from much longer distal phalanges and claws in those species (Fig. 2D). The more proximal elements of the ray (i.e., metacarpal and proximal and middle phalanges) are, instead, all shorter in more semifossorial species. An interesting contrast to the semifossorial pattern is *M. cafer*, an ambulatory species that has a relatively long ray III, but a short distal phalanx and claw. In that species, the length of ray III is a result of the long metacarpal, proximal phalanx, and middle phalanx (Figs. 2B–D). Hence, both myosoricines and talpids increase the lengths of the distal phalanx and claw and decrease the lengths of the proximal bones of the ray with increasing semifossoriality. The difference results from the much more extensive shortening of the metacarpals and proximal and middle phalanges in talpids, resulting in a shorter ray III (Figs. 2B–D and 4; Supporting Information S4).

Relative lengths of individual elements.—With the exception of ray I, which lacks a middle phalanx, the mean contribution of each particular element to the length of its respective ray is remarkably consistent among rays within a species (Supporting Information S4). When expressed as a proportion of the total length of the ray skeleton (TOT), the maximum intraspecific difference in length of an individual element among rays II–V is 6% (Supporting Information S4). Elements of rays III and IV are the most similar to each other, followed by those of rays II and V (Supporting Information S4). Although rays II–V are not quite scaled mirror images of each other, their average proportions are remarkably consistent.

As described above, a large proportion of the variation in the lengths of the rays, both among rays within species and among species for a given ray, results from variation in the length of the distal phalanx and claw (Figs. 2B and 2C; Supporting Information S4). Because the distal phalanx provides support for the claw, one would expect these 2 elements to covary in length. Regression analysis (Fig. 6) shows a significant positive trend of increasing claw III length with increasing length of distal phalanx III (CL = 1.4665DPL + 0.7073; $F_{1,79} = 1130.720$, $P = 0.000$, $R_{\text{ADJ}}^2 = 0.934$; $n = 81$) among myosoricines. The distal phalanx typically lengthens at a faster rate than the claw, so the amount of support provided by the distal phalanx generally increases as both elements elongate. Species of *Myosorex* have a range of support of 48–52%, *Surdisorex* averages 60%, and *Congosorex*, despite its shorter claws, also averages 60% (Table 1: %CLS).

The soricine genus *Cryptotis* exhibits a similar trend (CL = 1.44 DPL + 0.552; $F_{1,99} = 962.78$, $P = 0.000$, $R_{\text{ADJ}}^2 = 0.907$; $n = 101$ —Woodman and Morgan 2005), with a regression slope not significantly different from the myosoricine slope ($t_{0.05[1,178]} = 0.310$, $P = 0.757$). Support for claw III ranges 37–52% for more ambulatory species of *Cryptotis* and 51–58% for more semifossorial species (Woodman and Morgan 2005; Woodman 2011a). The similar regression equations suggest a common, generalized pattern of support for the claw among species of Soricidae, although, in reality, there is considerable variation even within our small sample of myosoricines. *M. zinki*, e.g., plots

above the myosoricine regression line, indicating a longer claw III than expected relative to distal phalanx III (less support for the claw), whereas *C. phillipsorum* plots below the regression, indicating greater support for the claw than expected.

The 2 talpids exhibit a trend superficially similar to that for the myosoricines (Fig. 6), but the regression slope (CL = 1.2691 DPL + 0.7235; $F_{1,22} = 411.889$, $P = 0.000$, $R_{\text{ADJ}}^2 = 0.947$; $n = 24$) is offset and significantly different ($t_{0.05[1,101]} = 2.590$, $P = 0.011$). The distal phalanx of these talpids provides greater support for the claw than does that of myosoricines, and this support increases at a higher rate as the claw lengthens.

Phalangeal and interphalangeal indices.—Average PIs for ray III among species of myosoricines range from 84 to 91 (Table 1; Supporting Information S3) and are highest for *M. cafer* and lowest for *M. blarina*, *S. norae*, and *S. polulus*. These values are close to values calculated for terrestrial (79 ± 8) and fossorial (81 ± 7) hystricognath rodents (Weisbecker and Schmid 2007), terrestrial didelphids (83–89—Lemelin 1999), and diprotodontian marsupials (60–125—Weisbecker and Warton 2006), but are mostly lower than those calculated for 3 soricine shrews (91–99—Woodman and Stephens 2010). Mean values calculated for the ambulatory mole *Uropsilus* (104) and the semifossorial mole *Neurotrichus* (135) are much higher. In myosoricines, the length of digit III generally increases relative to the length of the palm with increasing semifossoriality. This is opposite to the pattern seen in rodents and moles.

IPRs for ray III primarily serve to quantify the longer proximal phalanx and shorter middle phalanx of *C. phillipsorum* (Table 1; Figs. 2B–D; Supporting Information S3). The IPR of

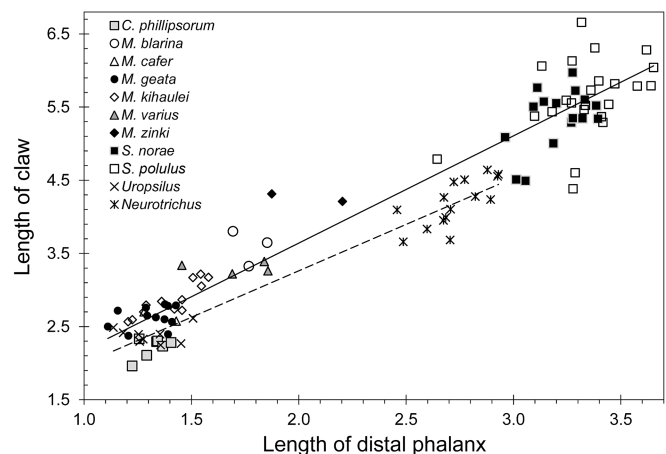


Fig. 6.—Regressions of length of claw III (3CL) on length of distal phalanx III (3DPL) for myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and 2 talpids (*Neurotrichus* and *Uropsilus*). The regression on myosoricines (longer solid line) has a significant positive slope indicating increasing claw length with increasing distal phalanx length (CL = 1.4665 DPL + 0.7073; $F_{1,79} = 1130.720$, $P = 0.000$, $R_{\text{ADJ}}^2 = 0.934$; $n = 81$). A regression on the talpids (shorter dashed line; CL = 1.2691 DPL + 0.7235; $F_{1,22} = 411.889$, $P = 0.000$, $R_{\text{ADJ}}^2 = 0.947$; $n = 24$) has a significantly different slope ($t_{0.05[101]} = 2.590$, $P = 0.011$). These analyses show that the claw has less support from the underlying distal phalanx among myosoricines (except *Congosorex phillipsorum*), and support increases with the elongation of the claw at a slower rate than for talpids.

this shrew is most similar in magnitude to those of *Uropsilus*. IPRs for *Myosorex* and *Surdisorex* are all much larger and closer in magnitude to those of *Neurotrichus*. Given the broad taxonomic and locomotory range covered by *Myosorex* and *Surdisorex*, the longer proximal phalanx and shorter middle phalanx of *Congosorex* are more likely the consequence of divergent phylogeny than locomotory adaptation.

Plots of the relative lengths of the metacarpal (ML), proximal phalanx (PPL), and middle phalanx (MPL) from ray III (Supporting Information S4) on Kirk et al. (2008) ternary diagrams (not shown) functionally associate mysoricine forefeet most closely with those of terrestrial carnivores, terrestrial rodents, and terrestrial treeshrews. In general, mysoricines are more similar to other terrestrial mammals in proportions than are soricine shrews (Woodman and Stephens 2010). The most distinctive of the mysoricines is *C. phillipsorum*, whose distribution on the plots generally does not overlap that of any other mammal, indicating the unique proportions of the manus of this species. The terrestrial mole *Uropsilus* is associated with arboreal carnivores, terrestrial didelphids, and terrestrial and arboreal rodents, and the semifossorial mole *Neurotrichus* with extant primates and arboreal marsupials and rodents. The associations of the talpids with arboreal mammals are probably the result of their very short metacarpals (Reed 1951), rather than the long proximal and middle phalanges common to grasping arboreal mammals (Kirk et al. 2008).

Relative widths of individual elements.—Relative shortening and broadening of the metacarpals and proximal and middle phalanges can be seen qualitatively (Fig. 2) and quantitatively (Fig. 7) among the more semifossorial mysoricines. The metacarpal III width index (MW3), which quantifies this variation, increases gradually in the genus *Myosorex*, from the species with the longest and narrowest metacarpals (*M. cafer*) to that with the shortest and widest (*M. zinki*; Table 1). Compared with those for *Myosorex*, the MW3 for *C. phillipsorum* is low to intermediate. This species has relatively higher width indices for rays I and V, a result of more consistent widths of bones among all 5 rays than is shown by the other mysoricines (Supporting Information S3). Other mysoricines tend to have narrower elements comprising rays I and V.

Indices for the 2 *Surdisorex* are much larger than any other mysoricines, and they equal or exceed even those for *Neurotrichus*. In fact, many of the metacarpals and phalanges of *Surdisorex* are as wide as or wider than those of *Neurotrichus* (Fig. 7; Supporting Information S1). *Surdisorex* retains longer metacarpals and longer proximal and middle phalanges in the manus than does *Neurotrichus*, and the additional leverage probably increases bending and shearing forces on those bones while digging. The greater broadening of those elements could be a means of resisting these stresses.

Principal component analyses.—PCAs of variables from each of the 5 rays provided approximately similar results, and we use our analysis of ray III as an example of the general pattern for each of them. Variable loadings on the 1st principal component (PC1) from this analysis, which explains nearly 79% of the variance in the model, indicate a contrast of variables representing widths of the phalanges plus length of the

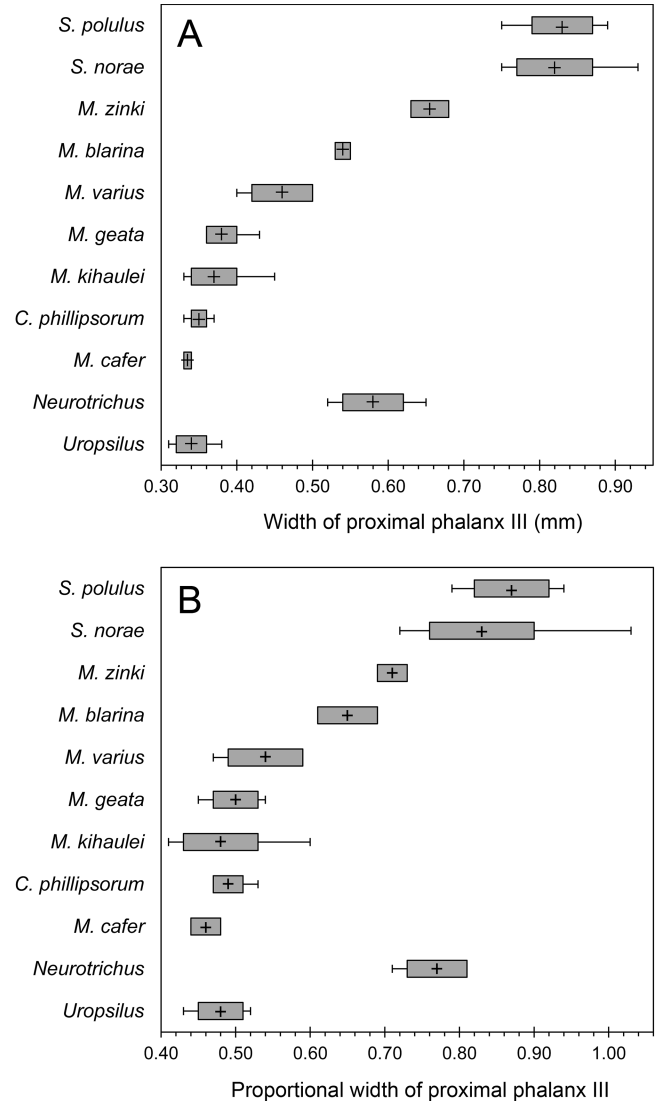


Fig. 7.—Box-and-whisker plots of widths of proximal phalanx III of mysoricines (*Congosorex*, *Myosorex*, and *Surdisorex*) and 2 talpids (*Neurotrichus* and *Uropsilus*). A) Proximal phalanx III as measured in millimeters (mm). B) Proximal phalanx III as a percentage of body size (HB). The cross represents the mean, the box shows SD, and “whiskers” represent the range.

distal phalanx with those representing lengths of the metacarpal and proximal and middle phalanges (Table 3). Only claw length and width of the metacarpal did not contribute strongly to this axis. The 2nd principal component (PC2) accounted for a little more than 11% of the variance, and it was most heavily influenced by a contrast between width of the metacarpal and length of the claw. In a plot of factor scores on these first 2 principal components (Fig. 8), PC2 does little to segregate species or groups of species, although *M. kahaulei* has an uncommonly broad distribution on this axis. PC1, however, essentially provides a scale of adaptation for semifossoriality (Table 4). *Congosorex* and most species of *Myosorex* cluster along the lower end of this axis. Within this grouping, there is a gradation of species with increasingly longer, wider distal phalanges and shorter, wider metacarpals and proximal and middle

phalanges. *M. cafer* averages the shortest distal phalanx and longest, narrowest metacarpal and proximal and middle phalanges, followed by *M. geata* and *M. kihaulei*, *C. phillipsorum*, and *M. varius*. *M. blarina* and *M. zinki* are distinct from other species of *Myosorex*, and their distribution does not overlap any

other species. The longest, broadest distal phalanges and shortest, broadest metacarpal and proximal and middle phalanges on this scale are present in *S. polulus* and *S. norae*.

DISCUSSION

Myosoricines present a range of morphological characters of the forefoot that we interpret as representing grades of adaptation

Table 3.—Component loadings and eigenvalues for the first 2 principal components from PCA of 9 log₁₀-transformed and size-standardized variables from digit III of myosoricines (Fig. 8).

Variable	Component loadings	
	1	2
3PPL	-0.987	0.027
3ML	-0.986	0.018
3MPL	-0.970	-0.038
3DPW	0.942	-0.017
3MPW	0.935	0.077
3DPL	0.916	-0.192
3PPW	0.906	0.109
3CL	0.739	-0.517
3MW	0.502	0.821
Eigenvalues	7.107	0.999
Percent of total variance explained	78.97	11.10

Table 4.—Mean scores for myosoricine (*Congosorex*, *Myosorex*, and *Surdisorex*) species on PC1. This axis serves as a scale of relative adaptation for ambulatory (more negative) to semifossorial (more positive) locomotory behavior.

Species	Mean score on PC1
<i>Myosorex cafer</i>	-1.5864317
<i>M. geata</i>	-1.0878649
<i>M. kihaulei</i>	-1.0755349
<i>Congosorex phillipsorum</i>	-0.9333924
<i>M. varius</i>	-0.5714566
<i>M. blarina</i>	-0.1469821
<i>M. zinki</i>	0.0104264
<i>Surdisorex polulus</i>	0.9477095
<i>S. norae</i>	1.0142225

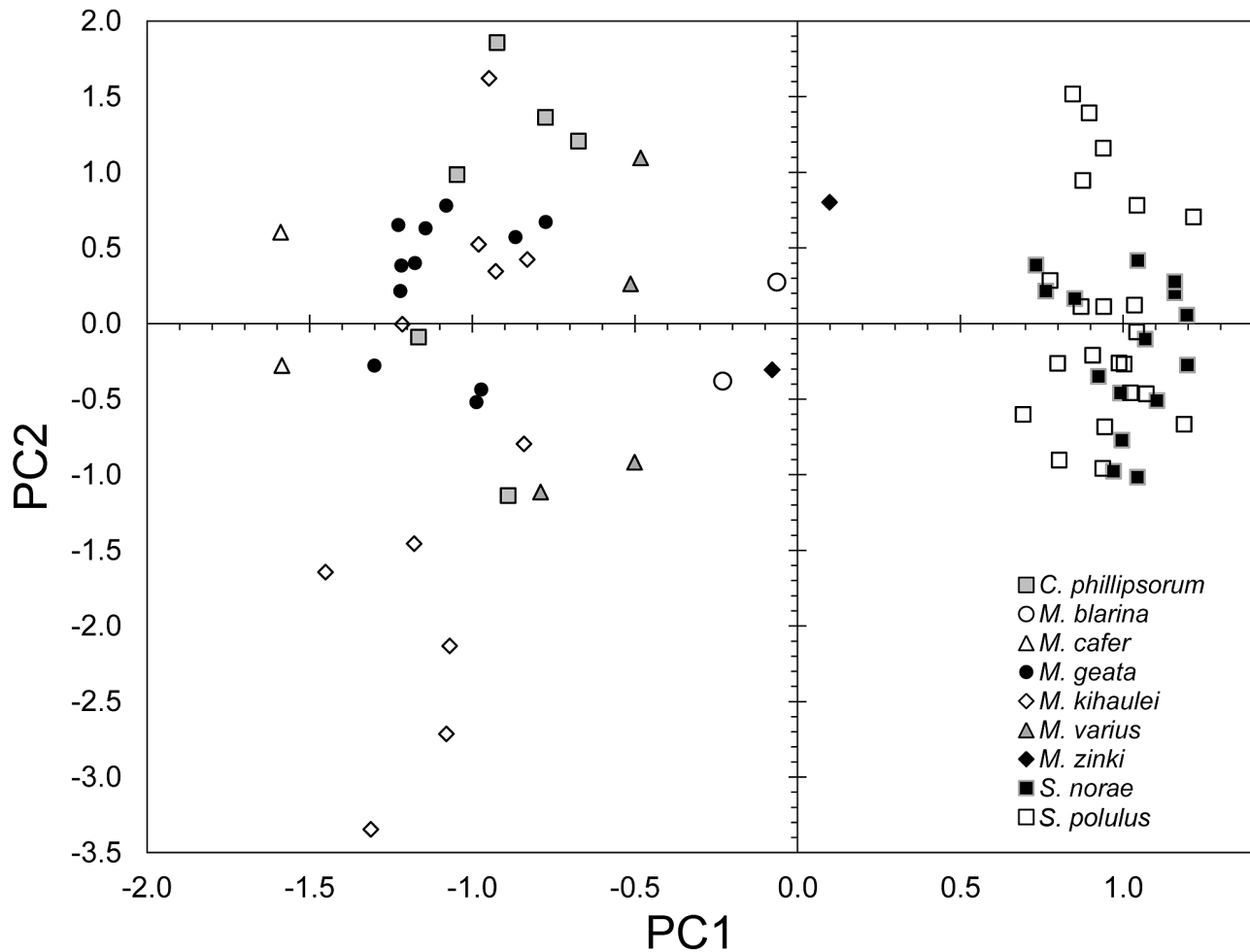


Fig. 8.—Plot of factor scores on PC1 (79% of variation) and PC2 (11%) from PCA of 9 variables from ray III of myosoricines (*Congosorex*, *Myosorex*, and *Surdisorex*; see Table 3).

for increased digging efficiency. In common with many other mammals (Reed 1951; Hildebrand 1985), these grades are most consistently marked by increased length and width of the distal phalanx and claw (particularly on rays II–IV), and by shorter, wider, and more robust metacarpals and phalanges. The myosoricine distal phalanx generally elongates at a faster rate than the claw, so that it provides proportionally greater support to the claw in species better adapted for digging. The metacarpals and the proximal and middle phalanges, in contrast, show slight reductions in length. More semifossorial myosoricines tend to have larger body size, but body size is not an exclusive characteristic, as ambulatory myosoricines can also be large.

Even along this spectrum, there is considerable variation within the Myosoricinae. The 3 genera comprising the subfamily have different relationships, e.g., between body size and various mutable characteristics of the manus. *Congosorex*, in particular, shows subtle variation that is distinctive among myosoricines, such as short foreclaws associated with relatively long distal phalanges, unique proportions of the proximal and middle phalanges, and more consistent robustness of bones among rays. Comparison of quantitative forefoot characteristics of all the species in our study provides an approximate ranking of adaptations for burrowing. Although this ranking gives the appearance of a gradual series of adaptation, it should not be interpreted as an evolutionary sequence. Each of the species is extant and represents the current tip of its respective phylogenetic branch. The different degrees of adaptation for digging reflect each species' unique means of providing for its needs within the physical and biological contexts of the environment it inhabits.

Kerbis Peterhans et al. (2010) partitioned members of the genus *Myosorex* into 2 morphological groups based upon the predominant shape of the skull. A group comprised of *M. cafer*, *M. varius*, and 6 other species was described as having a narrow, subtly hexagonal skull, and a group of 8 species that includes *M. blarina*, *M. geata*, *M. kihalaei*, and *M. zinki* was described as having a broad, more markedly hexagonal skull. This difference in skull shape may be phylogenetic, ecological, or related to some other factor, but there is no evidence that this bipartite division correlates with the morphology of the manus. Instead, individuals with both skull morphologies span large, overlapping segments of our scale of forefoot locomotory adaptation. Hence, skull shape and degree of adaptation of the manus for digging appear to be independent.

In contrast with talpids, semifossorial myosoricines retain the asymmetrical forefoot typical of soricids but have a longer central ray III and shorter rays I and V. Myosoricines also retain long metacarpals and proximal and middle phalanges relative to moles. In the most semifossorial species, however, these elements can be more robust than in semifossorial talpids. The significance of these characteristics as they relate to the locomotory behaviors of ambulation, scratch digging, and humeral-rotation digging await comprehensive analysis of the myosoricine forelimb, but it is clear that the metacarpals and proximal and middle phalanges, which form the palm and proximal portion of the digits, are functionally distinct from those of semifossorial moles.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (j mammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Measurements of bones and claws of rays I–V from 9 species of myosoricines and 2 talpids. Abbreviations are explained in Materials and Methods. Summary statistics include mean \pm standard deviation and total range.

Supporting Information S2.—Variable correlations and coefficients of variation.

Supporting Information S3.—Forefoot indices.

Supporting Information S4.—Relative lengths of bones of the manus.

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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.
- COE, M. J., AND J. B. FOSTER. 1972. The mammals of the northern slopes of Mt. Kenya. *Journal of the East African Natural History Society and National Museum* 131:1–18.
- DUNCAN, P., AND R. W. WRANGHAM. 1971. On the ecology and distribution of subterranean insectivores in Kenya. *Journal of Zoology (London)* 164:149–163.
- HILDEBRAND, M. 1985. 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.
- HOLLISTER, N. 1916. Descriptions of a new genus and eight new species and subspecies of African mammals. *Smithsonian Miscellaneous Collections* 66:1–8.

- HUTTERER, R. 1985. Anatomical adaptations of shrews. *Mammal Review* 15:43–55.
- HUTTERER, R. 2005. Order Soricomorpha. Pp. 220–311 in *Mammal species of the world: a taxonomic and geographic reference*. 3rd ed. (D. E. Wilson and D. M. Reeder, eds.). The Johns Hopkins University Press, Baltimore, Maryland.
- HUTTERER, R., P. BARRIERE, AND M. COLYN. 2002. A new myosoricine shrew from the Congo Basin referable to the forgotten genus *Congosorex* (Mammalia: Soricidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 71(Supplement):7–16.
- KERBIS PETERHANS, J. C., ET AL. 2010. African shrews endemic to the Albertine Rift: two new species of *Myosorex* (Mammalia: Soricidae) from Burundi and the Democratic Republic of Congo. *Journal of East African Natural History* 99:103–128.
- KERBIS PETERHANS, J. C., R. HUTTERER, P. KALIBA, AND L. MAZIBUKO. 2008. First record of *Myosorex* (Mammalia: Soricidae) from Malawi with description as a new species, *Myosorex gnoskei*. *Journal of East African Natural History* 97:19–32.
- KERBIS PETERHANS, J. C., M. H. HUHDORF, A. J. PLUMPTRE, R. HUTTERER, P. KALEME, AND B. NDARA. 2013. Mammals, other than bats, from the Misotshi-Kabogo highlands (eastern Democratic Republic of Congo), with the description of two new species (Mammalia: Soricidae). *Bonn Zoological Bulletin* 62:203–219.
- KERBIS PETERHANS, J. C., W. T. STANLEY, R. HUTTERER, T. C. DEMOS, AND B. AGWANDA. 2009. A new species of *Surdisorex* Thomas, 1906 (Mammalia, Soricidae) from western Kenya. *Bonner Zoologische Beiträge* 56:175–183.
- KIRK, E. C., LEMELIN, M. W. HAMRICK, D. M. BOYER, AND J. I. BLOCH. 2008. Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. *Journal of Human Evolution* 55:278–299.
- KNOLL, T., ET AL. 2007. Adobe Photoshop CS3 Extended. Version 10.0.1. Adobe Systems, Inc., San Jose, California.
- LEMELIN, P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *Journal of Zoology (London)* 247:165–175.
- MEESTER, J. 1953. The genera of African shrews. *Annals of the Transvaal Museum* 22:205–214.
- MEREDITH, R. W. ET AL. 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg extinction on mammal diversification. *Science* 334:521–524.
- MORGAN, C. C., AND D. H. VERZI. 2011. Carpal-metacarpal specializations for burrowing in South American octodontoid rodents. *Journal of Anatomy* 219:167–175.
- MOSIMANN, J. E., AND F. C. JAMES. 1979. New statistical methods for allometry with applications to Florida red-winged blackbirds. *Evolution* 32:444–459.
- QUÉROUIL, S., R. HUTTERER, P. BARRIÈRE, MARC COLYN, J. C. KERBIS PETERHANS, AND E. VERHEYEN. 2001. Phylogeny and evolution of African shrews (Mammalia: Soricidae) inferred from 16s rRNA sequences. *Molecular Phylogenetics and Evolution* 20:185–195.
- REED, C. A. 1951. Locomotion and appendicular anatomy in three soricoid insectivores. *American Midland Naturalist* 45:513–670.
- SARGIS, E. J., N. WOODMAN, A. T. REESE, AND L. E. OLSON. 2013a. Using hand proportions to test taxonomic boundaries within the *Tupaia glis* species complex (Scandentia, Tupaiidae). *Journal of Mammalogy* 94:183–201.
- SARGIS, E. J., N. WOODMAN, N. C. MORNINGSTAR, A. T. REESE, AND L. E. OLSON. 2013b. Morphological distinctiveness of Javan *Tupaia hypochrysa* (Scandentia, Tupaiidae). *Journal of Mammalogy* 94:938–947.
- SHIMER, H. W. 1903. Adaptations to aquatic, arboreal, fossorial and cursorial habits in mammals. III. Fossoriality. *American Naturalist* 37:819–825.
- STANLEY, W. T., AND J. A. ESSELSTYN. 2010. Biogeography and diversity among montane populations of mouse shrew (Soricidae: *Myosorex*) in Tanzania. *Biological Journal of the Linnean Society* 100:669–680.
- STANLEY, W. T., M. A. ROGERS, AND R. HUTTERER. 2005. A new species of *Congosorex* from the Eastern Arc Mountains, Tanzania, with significant biogeographical implications. *Journal of Zoology (London)* 265:269–280.
- TAYLOR, P. J., T. C. KEARNEY, J. C. KERBIS PETERHANS, R. M. BAXTER, AND S. WILLOWS-MUNRO. 2013. Cryptic diversity in forest shrews of the genus *Myosorex* from southern Africa, with the description of a new species and comments on *Myosorex tenuis*. *Zoological Journal of the Linnean Society* 169:881–902.
- THOMAS, O. 1906. Two new genera of small mammals discovered by Mrs. Holms-Tarn in British East Africa. *Annals and Magazine of Natural History, Series 7*, 18:222–226.
- WEISBECKER, V., AND S. SCHMID. 2007. Autopodial skeletal diversity in hystricognath rodents: functional and phylogenetic aspects. *Mammalian Biology* 72:27–44.
- WEISBECKER, V., AND D. I. WARTON. 2006. Evidence at hand: diversity, functional implications, and locomotor prediction in intrinsic hand proportions of diprotodontian marsupials. *Journal of Morphology* 267:1469–1485.
- WILKINSON, L., ET AL. 2004. Systat. Version 10.00.01. Systat Software, Inc., San Jose, California.
- 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. 2010. Two new species of shrews (Soricidae) from the western highlands of Guatemala. *Journal of Mammalogy* 91:566–579.
- WOODMAN, N. 2011a. Patterns of morphological variation amongst semifossorial shrews in the highlands of Guatemala, with the description of a new species (Mammalia, Soricomorpha, Soricidae). *Zoological Journal of the Linnean Society* 163:1267–1288.
- WOODMAN, N. 2011b. Nomenclatural notes and identification of small-eared shrews (Mammalia: genus *Cryptotis*) from Cobán, Guatemala, in The Natural History Museum, London. *Proceedings of the Biological Society of Washington* 124:249–258.
- 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., AND J. J. P. MORGAN. 2005. Skeletal morphology of the forefoot in shrews (Mammalia: Soricidae) of the genus *Cryptotis*, as revealed by digital x-rays. *Journal of Morphology* 266:60–73.
- WOODMAN, N., AND R. B. STEPHENS. 2010. At the foot of the shrew: manus morphology distinguishes closely-related *Cryptotis goodwini* and *Cryptotis griseoventris* (Mammalia, Soricidae) in Central America. *Biological Journal of the Linnean Society* 99:118–134.
- WOODMAN, N., AND R. M. TIMM. 1999. Geographic variation and evolutionary relationships among broad-clawed shrews of the *Cryptotis goldmani*-group (Mammalia: Insectivora: Soricidae). *Fieldiana: Zoology* 91:1–35.

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APPENDIX I

Specimens examined: Specimens of myosoricines and talpids examined for this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); National Museum of Natural History, Washington (USNM).

Soricidae:

Congosorex phillipsorum ($n = 7$).—Tanzania: Iringa District (FMNH 177683–177689).

Myosorex blarina ($n = 3$).—Uganda: Kasese District (FMNH 144209, 144211); Zaire: Ruwenzori (FMNH 26285).

Myosorex cafer ($n = 2$).—South Africa: Kwazulu Natal Prov. (FMNH 165585, 165587).

Myosorex geata ($n = 12$).—Tanzania: Kilosa District (FMNH 166767, 166775, 166777, 197667, 197670–197673); Morogoro District (FMNH 158299–158302); Mpwapa District (FMNH 166767).

Myosorex kahaulei ($n = 12$).—Tanzania: Kilombero District (FMNH

155620–155622); Makete District (FMNH 204685, 204856, 204858, 204860, 204862); Rungwe District (FMNH 163552, 163554, 163558, 163559).

Myosorex varius ($n = 4$).—South Africa: Kwazulu Natal Prov. (FMNH 165589–165592).

Myosorex zinki ($n = 2$).—Tanzania: Kilimanjaro Region (FMNH 174117, 174119).

Surdisorex norae ($n = 17$).—Kenya: Aberdare Mountains (AMNH 187262; FMNH 190622–190624, 190626; USNM 182581–182586, 589811–589813, 589815, 589817, 589819).

Surdisorex polulus ($n = 23$).—Kenya: Mount Kenya (USNM 163975, 163976, 163979, 163981, 163982, 163984, 163987, 163989–163991, 163993, 163996–164000, 164002–164007, 589820).

Talpidae:

Neurotrichus gibbsii gibbsii ($n = 15$).—United States: Oregon (USNM 13410, 65707, 79788, 80217, 80437–80441, 89023, 204484–204487, 264887).

Uropsilus soricipes ($n = 9$).—China: Sichuan (USNM 175142, 256119, 260743, 260751, 574297–574301).