

Comparative functional skeletal morphology among three genera of shrews: implications for the evolution of locomotor behavior in the Soricinae (Eulipotyphla: Soricidae)

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The clade comprising the soricid tribes Blarinellini (*Blarinella*) and Blarinini (*Blarina* and *Cryptotis*) is notable within the Soricidae (Eulipotyphla) for the large proportion of reportedly semifossorial species. To better define locomotor modes among species in these two tribes, we quantified purported locomotor adaptations by calculating 23 functional indices from postcranial measurements obtained from museum specimens of *Blarina* and *Blarinella* and published measurements for 16 species of *Cryptotis*. We then analyzed relative ambulatory–fossorial function of each species using principal component analyses and mean percentile rank (MPR) analysis of the indices. Species within the Blarinellini–Blarinini clade exhibit a graded series of morphologies with four primary functional groupings that we classified as “ambulatory,” “intermediate,” “semifossorial,” and “fossorial.” To obtain a preliminary overview of evolution of locomotor modes in this group, we mapped MPRs on a composite phylogeny and examined the resulting patterns. That analysis revealed that the most recent common ancestor of the Blarinellini–Blarinini clade most likely had an intermediate or semifossorial locomotor morphology. Individual subclades subsequently evolved either more ambulatory or more fossorial morphologies. Hence, evolution of locomotor traits within this clade is complex. Multiple shifts in locomotor mode likely occurred, and no single directional tendency is apparent either among the major modes or in levels of complexity.

Key words: anatomy, digging, fossorial, Insectivora, Soricomorpha, substrate use, terrestrial

Shrews (Eulipotyphla: Soricidae) engage in a range of locomotor behaviors that include climbing, swimming, and burrowing in a variety of substrates. A preliminary classification by Hutterer (1985) indicated the dominant eco-locomotor mode among 266 species of shrews (Eulipotyphla: Soricidae) is terrestrial ambulation (77%), followed by semifossorial (11%), scansorial (6%), and semiaquatic (4%) locomotion. Despite being less common than strictly ambulatory species, semifossorial shrews are represented in all three soricid subfamilies, and they are geographically widespread, occurring in Africa, Eurasia, and the Americas (Hutterer 1985; Churchfield 1990).

Within the subfamily Soricinae, the unnamed clade (Dubey et al. 2007; Chen et al. 2012) that comprises the tribes Blarinellini (*Blarinella*) and Blarinini (*Blarina* + *Cryptotis*) is notable for the large proportion of species (76%) classified as semifossorial. These include all *Blarina* and *Blarinella* and most species of *Cryptotis* (Hutterer 1985). Externally, all three

genera exhibit reduced pinnae and relatively short tails, both of which are adaptations typically associated with burrowing habits (Shimer 1903; Hildebrand 1985b; Hoffmann and Lunde 2008).

The North American northern short-tailed shrew, *Blarina brevicauda*, was once described as “the most fossorial of the American shrews” (Banfield 1974:22). It constructs burrow systems and spends relatively little time on the surface of the ground. Hypogeal prey, particularly earthworms (Annelida), can form a considerable portion of its diet (George et al. 1986). Other species of *Blarina* have generally similar habits, although they may spend more time at the ground surface and consume more epigeal prey than *B. brevicauda* (Thompson et al. 1986; Whitaker et al. 1994; McCay 2001; Ritzi et al. 2005).

Accounts of digging behavior among the small-eared shrews of the genus *Cryptotis* are restricted to observations of individuals of only a few species (Chamberlain 1929; Davis

and Joeris 1945; Guevara 2017). The most common reports involve the North American least shrew, *Cryptotis parvus*, which constructs shallow subterranean tunnels and nests, often under logs, rocks, or other solid objects (Whitaker 1974). It also uses narrow surface runways, which it often leaves to search for prey (Gottschang 1965). In contrast, the Mexican small-eared shrew, *C. mexicanus*, is an active burrower of tunnels 2–3 cm below the ground surface, and it spends most of its time underground (Guevara 2017). Studies of the skeletal morphology of the limbs and feet of a variety of species of *Cryptotis* revealed considerable interspecific variation, suggesting a broader spectrum of locomotor modes, from mostly ambulatory to mostly fossorial, exists within the genus (Woodman and Morgan 2005; Woodman and Gaffney 2014).

Asian short-tailed shrews (genus *Blarinella*, herein abbreviated as *Bl.* to distinguish it from *Blarina*) are reported to be active burrowers (Hoffmann and Lunde 2008; Smith et al. 2013), “tunneling in light soil and leaf mould” (Allen 1938:115), and the Sichuan short-tailed shrew, *Blarinella quadraticauda* has been compared to *Blarina brevicauda* in its form and semifossorial habits (Thomas 1911; Allen 1938; Hoffmann and Lunde 2008). In general, however, there is little tangible

documentation of the eco-locomotor modes of any of the three species in this genus.

One of the issues faced in identifying locomotor mode of soricids is that observations of locomotor behavior are rare or nonexistent for most species. Instead, dominant locomotor mode is often inferred from external characteristics thought to be linked to locomotor behavior, such as shape of the body and the sizes of the eyes, ears, tail, fore feet, and fore claws (Shimer 1903; Hildebrand 1985b). Locomotor-associated traits can be assessed by qualitative studies of the internal anatomy of the skeleton and associated musculature of the limbs (Reed 1951; Gaughran 1954), but such studies also are rare. A promising alternative means of appraising such traits is by quantitative analyses of the skeleton to provide morphological proxies of potential function and substrate use (Hildebrand 1985b; Lemelin 1999; Sargis 2002; Weisbecker and Warton 2006; Weisbecker and Schmid 2007; Kirk et al. 2008; Samuels and Van Valkenburgh 2008; Hopkins and Davis 2009; Elissamburu and De Santis 2011). Subsequent statistical analyses of morphological proxies have been shown to successfully distinguish functional groups of species of a priori known locomotor mode (Samuels and Van Valkenburgh, 2008), and such analyses been used to predict potential locomotor mode based upon combined

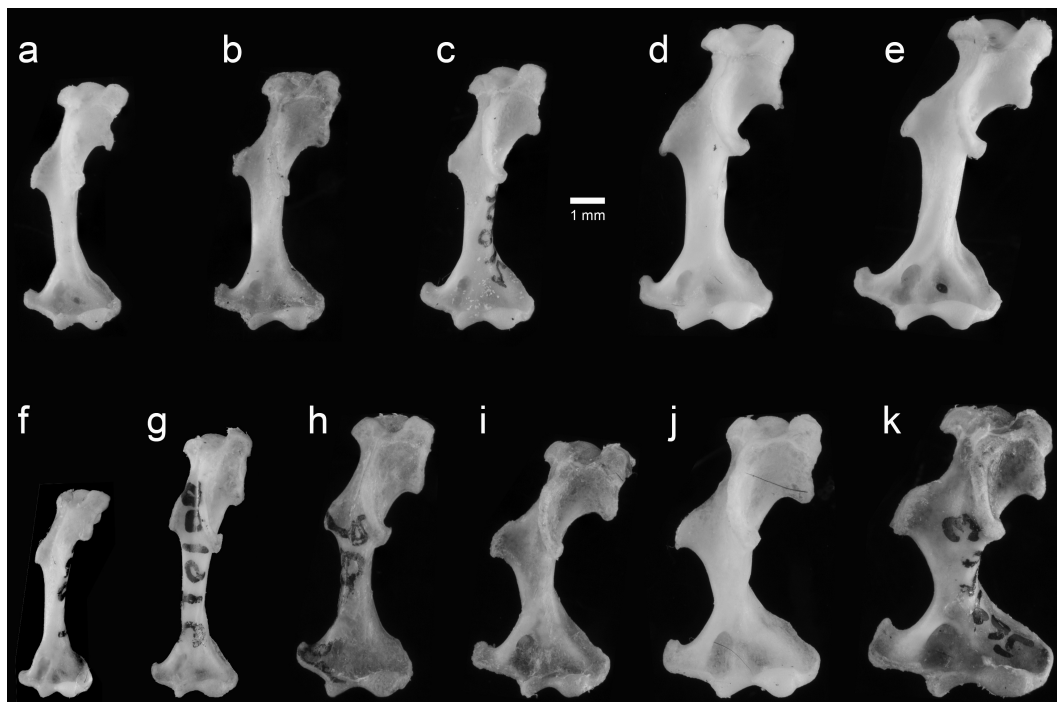


Fig. 1.—Anterior aspect of the left humerus illustrating some of the variation present among the Blarinellini and Blarinini: a) *Blarinella quadraticauda* (USNM 574288), b) *Blarina carolinensis* (USNM 267175), c) *B. peninsulae* (USNM 568067), d) *B. brevicauda jerrychoatei* (USNM 569836), e) *B. brevicauda talpoides* (USNM 568645), f) *Cryptotis parvus* (USNM 568975), g) *C. merriami* (USNM 570108), h) *C. meridensis* (USNM 385101), i) *C. mam* (USNM 569555), j) *C. oreoryctes* (USNM 569878), k) *C. lacertosus* (USNM 569503).

morphological traits (Woodman and Gaffney 2014; Woodman and Stabile 2015b).

To better understand variation in morphological traits associated with ambulatory and semifossorial locomotor modes in the Blarinellini and Blarinini, we quantified functional aspects of the postcranial skeleton and compared them among species-group taxa of *Blarina*, *Blarinella*, and *Cryptotis* to obtain a classification of these functional modes in this clade. We then used this classification in an attempt to discern potential patterns of locomotor function across species, genera, and tribes by

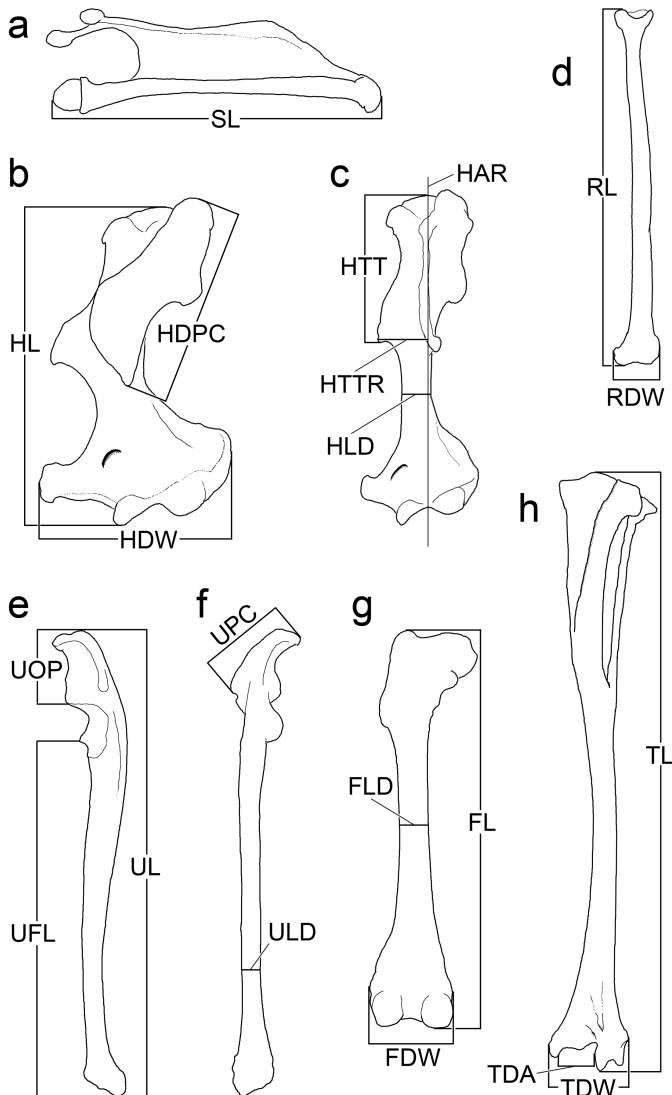


Fig. 2.—Postcranial measurements. a) Scapula: SL, greatest length of scapula. b) Humerus: HL, length of humerus; HDW, distal width of humerus; HDPC, length of delto-pectoral crest. c) Humerus: HAR, axis of rotation of the humerus; HLD, least mediolateral diameter of humerus; HTT, length from head of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

mapping our locomotor mode assessments onto a composite phylogeny of the Blarinini and Blarinellini.

MATERIALS AND METHODS

For our purposes in this paper, we employ “ambulatory” to refer to terrestrial shrews that move on the surface of the ground and lack morphological traits clearly associated with focused aquatic, fossorial, or scansorial behavior (Brown and Yalden 1973). “Digit” refers to the bones and tissues associated with the manual or pedal structure supported by the phalanges, whereas “ray” refers to tissues associated with the structure

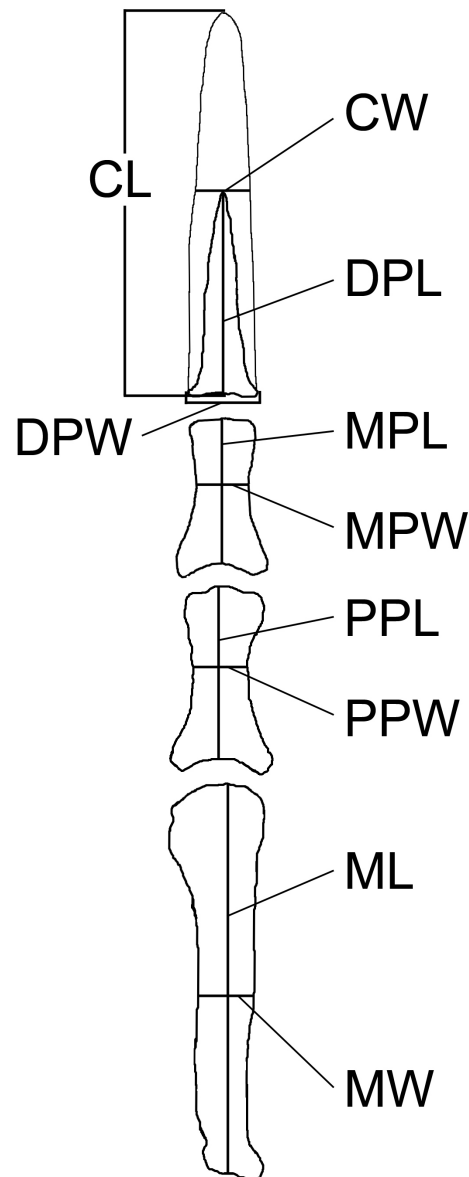


Fig. 3.—Ray III of the manus illustrating variables measured on the manus and pes: CL, length of claw; CW, width of claw; ML, length of metacarpal; PPL, length of proximal phalanx; MPL, length of middle phalanx; DPL, length of distal phalanx; MW, width of metacarpal; PPW, width of proximal phalanx; MPW, width of middle phalanx; DPW, width of distal phalanx.

supported by the phalanges and metacarpal or metatarsal. As a proxy for body size, we used head-and-body length (HB), calculated by subtracting tail length from total length as recorded by the original collectors. All measurements reported herein are in mm (Supplementary Data SD1).

The small size of individual limb bones of many sorcids makes them difficult to manipulate or to measure accurately or precisely (Fig. 1). To overcome this problem, we followed procedures detailed by Woodman and Gaffney (2014) and Woodman and Morgan (2005; see also Woodman and Stephens 2010; Sargis et al. 2013a, 2013b; Woodman and Stabile 2015a, 2015b). The scapula, humerus, ulna, radius, femur, and tibiofibula were digitally photographed, and images of the manus and pes were obtained by digitally x-raying the feet and hands of dried skins. Variables were measured from the resulting images using the program ImageJ (Schneider et al. 2012; program available at: <https://imagej.nih.gov/>), calibrated with a scale included within each image.

We obtained 41 measurements from long bones of the postcranial skeleton (Fig. 2) and ray III of the manus and pes (Fig. 3) from 95 individuals representing *Bl. quadraticauda* and four taxa of North American short-tailed shrews of the genus *Blarina*: *B. brevicauda jerrychoatei*; *B. b. talpoides*; *B. carolinensis*; and *B. peninsulae* (Appendix I). Individual sample sizes were limited by the availability of skeletons and dried skins (Bell and Mead 2014), which also limited our selection of the taxa included in our study. Although we had complete specimens of only *Bl. quadraticauda* available to represent the Blarinellini in this study, that species appears to be representative of the genus *Blarinella*, which includes three recognized species that differ primarily in size and pelage coloration (Jiang et al. 2003; Hoffmann and Lunde 2008; Smith et al. 2013). In fact, Chen et al. (2012) indicated that *Bl. quadraticauda* is poorly differentiated genetically from *Bl. griselda*. Moreover, our comparison of the bones of the manus and pes of a single specimen of the smaller *Bl. wardi* (not included in our study because no skeleton was preserved) with our sample of *Bl. quadraticauda* indicated that the claws and distal phalanges of *Bl. wardi* are relatively longer and narrower, but the other bones of the manus and pes are proportionally similar between the two species.

For the genus *Cryptotis*, we used measurements obtained by Woodman and Gaffney (2014) for 16 species (not including *C. phillipsii*) following the same methodologies that we used. Those samples include members of all five species groups within the genus *Cryptotis* that have proven to be clades (He et al. 2015; Baird et al. 2017): *C. parvus* group (*C. parvus*, *C. tropicalis*); *C. nigrescens* group (*C. merriami*, *C. merus*, *C. nigrescens*); *C. mexicanus* group (*C. mexicanus*); *C. goldmani* group (*C. cavatorculus*, *C. celaque*, *C. gracilis*, *C. lacertosus*, *C. mam*, *C. mccarthyi*, *C. oreoryctes*); and *C. thomasi* group (*C. endersi*, *C. meridensis*, *C. thomasi*). Populations designated as “Celaque,” “Cusuco,” and “Las Minas” in Woodman and Gaffney (2014) are now recognized as *C. celaque*, *C. mccarthyi*, and *C. oreoryctes*, respectively. The traditional *C. mexicanus* group (sensu lato), which included

Table 1.—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 (2015b) for additional information on the significance of these measures. Abbreviations of measurements are explained in Figs. 2 and 3; “h” indicates a hind limb variable.

1. Distal phalanx length index (CLAW = 3DPL/3hDPL).
2. Claw length index (CLI = 3CL/3hCL).
3. Scapulohumeral index (SHI = SL/HL).
4. Shoulder moment index (SMI = HDPC/HL).
5. Humeral robustness index (HRI = HLD/HL).
6. Humeral rotation lever index (HTI = HTTR/HAL).
7. Teres tubercle position index (TTP = HTT/HAL).
8. Humeral epicondylar index (HEB = HDW/HL).
9. Radial distal width index (RDW = RDW/RL).
10. Olecranon length index, or index of fossorial ability (OLI = UOP/UFL).
11. Olecranon crest index (OCI = UPC/UFL).
12. Ulnar robustness index (URI = ULD/UFL).
13. Relative length of the manual distal phalanx [%DPL = 3DPL/(3ML + 3PPL + 3MPL)].
14. Relative length of the manual claw [%CL = 3CL/(3ML + 3PPL + 3MPL)].
15. Relative support for the claw (%CLS = 3DPL/3CL).
16. Metacarpal width index (MW3 = 3MW/3ML).
17. Manus proportions index (MANUS = 3PPL/3ML).
18. Pes length index (PES = 3hML/FL).
19. Femoral robustness index (FRI = FLD/FL).
20. Femoral epicondylar index (FEB = FDW/FL).
21. Relative length of the pedal distal phalanx [%hDPL = 3hDPL/(3hML + 3hPPL + 3hMPL)].
22. Relative length of the pedal claw [%hCL = 3hCL/(3hML + 3hPPL + 3hMPL)].
23. Relative support for the pedal claw (%hCLS = 3hDPL/3hCL).

the *C. goldmani* group, proved to be polyphyletic (Guevara and Cervantes 2014; He et al. 2015). We use a narrower definition of the *C. mexicanus* group that includes only the clade consisting of *C. magnus*, *C. mexicanus*, *C. nelsoni*, *C. obscurus*, and *C. phillipsii*.

To assess locomotor function, we used postcranial, manual, and pedal measurements for each taxon to calculate up to 23 osteological indices (Table 1) that have been used previously to characterize locomotor mode and adaptations for substrate use among sorcids (Woodman and Gaffney 2014; Woodman and Stabile 2015b), rodents (Price 1993; Weisbecker and Schmid 2007; Samuels and Van Valkenburgh 2008; Elissamburu and De Santis 2011), and other mammals (Lemelin 1999; Sargis 2002; Weisbecker and Warton 2006; Kirk et al. 2008; Hopkins and Davis 2009). To partly overcome the problem of missing data, we calculated indices from mean values of variables (Supplementary Data SD1). All indices are expressed as whole number percentages (Table 2). Higher values for each of these indices are associated with more fossorial traits and lower values with more ambulatory traits. The 23 indices used herein are a reduced set of the most relevant of 33 indices whose individual performances were assessed for sorcids in Woodman and Gaffney (2014) and Woodman and Stabile (2015b). We also examined limb proportions as they related to locomotor patterns by calculating: 1) the proportional length of each element of the fore limb relative to the total length of the skeleton of the fore limb (calculated as HL + RL + ML + PPL + MPL + DPL); 2) the length of each element of the hind limb relative to the total length of the hind limb (FL + TL + hML + hPPL

+ hMPL + hDPL); 3) the length of each bone and the claw of ray III of the manus relative to the total length of the ray (ML + PPL + MPL + CL); and 4) the length of each bone and the claw of ray III of the pes relative to the total length of the ray (hML + hPPL + hMPL + hCL).

We used two methods and three models to analyze the indices and calculate a summary functional score for each species. The summary scores from each of the three models provide an overview of interspecific postcranial variation and permit us to define relative ambulatory versus fossorial morphology for each taxon (Woodman and Gaffney 2014). For our first analysis, we used principal component analysis (PCA) of a covariance matrix of the 23 indices (Table 3). A covariance matrix for this analysis is appropriate because all indices were measured on the same 0–100 scale, making standardization of variable scales unnecessary. The combined variation in traits represented by the 23 indices was summarized as a score for

each taxon along the first factor axis (PC1). Missing indices in this analysis reduced our species sample to three *Blarina*, *Blarinella quadricaudata*, and eight *Cryptotis*. For our second analysis, we reduced our PCA matrix to nine indices calculated from measurements of just the humerus and the fore foot, two of the structures that are more commonly preserved and that exhibit obvious modifications related to semifossorial behavior in eulipotyphlans (Reed 1951; Woodman and Stabile 2015b) and other quadrupedal vertebrates (Hildebrand 1985b; Samuels and Van Valkenburgh 2008). This analysis included all four *Blarina*, *Bl. quadricaudata*, and 14 species of *Cryptotis*. For the third analysis, we computed percentile ranks for each of the morphological indices for each of the 21 species. We then averaged the percentile ranks to obtain a mean percentile rank (MPR) for each species that represents its relative potential locomotor adaptation on a possible scale from 0 (most ambulatory) to 100 (most fossorial). Univariate statistics were calculated in Excel

Table 2.—Mean functional indices calculated for 23 soricine shrews from variables in Supplementary Data SD1. Taxa are listed in order by mean percentile rank (see Table 7). Abbreviations of indices are explained in Table 1.

Taxon	CLAW	CLI	SHI	SMI	HRI	HTI	TTP	HEB	RDW	OLI	OCI	URI	%DPL
<i>C. parvus</i>	94	105	100	42	9	17	40	36	13	18	24	6	16
<i>C. merus</i>	93	98	94	46	9	12	37	36	—	—	—	—	13
<i>C. tropicalis</i>	81	105	101	45	10	18	42	34	13	17	24	6	13
<i>C. nigrescens</i>	89	96	94	43	9	18	39	35	13	20	29	7	16
<i>C. merriami</i>	99	96	94	44	9	17	38	35	12	20	27	7	15
<i>C. meridensis</i>	97	108	97	44	10	18	45	40	14	21	26	6	19
<i>C. endersi</i>	117	145	96	42	9	20	41	42	—	—	—	—	—
<i>C. thomasi</i>	99	113	101	44	11	24	44	—	—	—	—	—	19
<i>Bl. quadricaudata</i>	106	108	100	43	10	21	46	39	13	22	24	6	20
<i>C. gracilis</i>	93	105	106	46	11	21	46	44	—	—	—	—	21
<i>B. carolinensis</i>	112	126	109	48	12	21	45	45	14	28	30	7	24
<i>B. peninsulæ</i>	117	136	107	49	12	19	45	44	15	29	32	8	23
<i>B. b. talpoides</i>	114	130	106	45	12	23	45	43	17	32	35	8	23
<i>B. b. jerrychoatei</i>	108	125	110	45	13	24	46	44	17	29	36	7	23
<i>C. mexicanus</i>	121	128	110	44	11	25	49	46	—	—	—	—	26
<i>C. celaque</i>	123	142	112	45	13	31	49	51	14	26	33	8	33
<i>C. mccarthyi</i>	117	124	—	43	13	30	46	51	—	—	—	—	35
<i>C. mam</i>	133	134	113	46	13	32	51	52	16	25	33	7	35
<i>C. oreoryctes</i>	127	138	116	44	13	34	51	54	15	29	37	7	36
<i>C. cavatorculus</i>	134	153	—	50	12	32	48	52	15	28	34	7	37
<i>C. lacertosus</i>	125	131	123	44	15	33	51	58	17	28	40	9	36

Taxon	%CL	%CLS	MW3	MANUS	PES	FRI	FEB	%hDPL	%hCL	%hCLS
<i>C. parvus</i>	35	44	9	54	46	8	23	13	26	49
<i>C. merus</i>	30	45	10	57	45	9	22	12	25	48
<i>C. tropicalis</i>	30	43	10	60	48	8	21	13	23	55
<i>C. nigrescens</i>	31	51	12	59	43	9	22	14	26	55
<i>C. merriami</i>	29	52	10	62	44	10	22	12	23	50
<i>C. meridensis</i>	38	49	11	49	—	9	25	16	29	55
<i>C. endersi</i>	—	45	—	—	48	9	27	12	21	56
<i>C. thomasi</i>	40	49	12	52	45	10	24	15	28	55
<i>Bl. quadricaudata</i>	39	51	11	60	50	10	25	15	29	52
<i>C. gracilis</i>	41	50	12	58	53	10	27	16	28	57
<i>B. carolinensis</i>	45	53	13	61	41	9	25	16	27	59
<i>B. peninsulæ</i>	44	51	13	57	—	—	—	15	26	60
<i>B. b. talpoides</i>	43	53	14	54	41	10	26	17	28	60
<i>B. b. jerrychoatei</i>	41	55	14	56	45	10	25	17	27	63
<i>C. mexicanus</i>	48	55	15	57	—	—	—	17	29	58
<i>C. celaque</i>	58	57	17	55	44	9	28	20	31	66
<i>C. mccarthyi</i>	62	57	19	59	—	—	—	22	37	60
<i>C. mam</i>	62	56	17	60	45	9	26	20	36	56
<i>C. oreoryctes</i>	64	57	17	58	44	9	27	21	34	62
<i>C. cavatorculus</i>	60	61	19	60	—	—	—	22	31	69
<i>C. lacertosus</i>	63	58	20	58	41	10	28	23	38	60

97-2003 (Microsoft Corp., Redmond, Washington) and multivariate statistics in Systat 11.00.01 (Systat Software, Inc., Chicago, Illinois).

A comprehensive phylogeny of the Blarinellini–Blarinini clade remains elusive, although relationships of the two tribes and their component genera are well established (Dubey et al. 2007; Chen et al. 2012). To obtain a preliminary overview of the potential distribution of locomotor adaptation among species in this clade, we manually combined phylogenetic tree topologies for the Soricinae by Dubey et al. (2007), for *Blarina* by Reilly et al. (2005), for *Blarinella* by Chen et al. (2012), and for *Cryptotis* from Baird et al. (2017) and Zeballos et al. (2018). Because these studies used different gene combinations and include nonoverlapping gene sequences, the resulting tree is speculative. We mapped MPRs of terminal taxa on the combined tree and examined it for patterns.

Table 3.—Component loadings and eigenvalues for the first factor axis from principal component analysis (PCA) of 23 morphological indices from 12 taxa of soricine shrews (see Fig. 4).

Variable	Component loading
CLI	0.488
CLAW	0.480
%CL	0.401
%DPL	0.267
SHI	0.257
HEB	0.247
HTI	0.197
OCI	0.144
TTP	0.137
%HCL	0.129
%CLS	0.124
%HCLS	0.120
OLI	0.116
%HDPL	0.108
MW3	0.100
FEB	0.070
HRI	0.058
RDW	0.044
URI	0.022
SMI	0.016
FRI	0.007
MANUS	-0.015
PES	-0.033
Eigenvalue	1,065.805
Percent of total variance explained	88.465

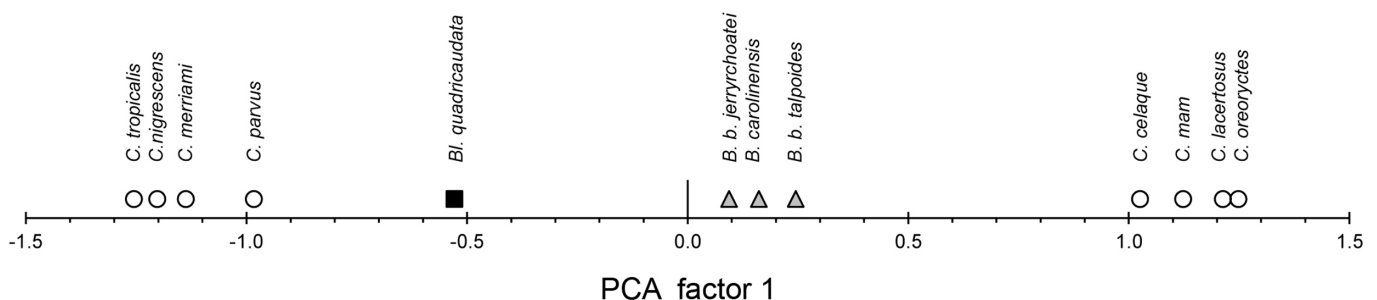


Fig. 4.—Results of principal component analysis (PCA) of 23 morphological indices among 12 taxa of soricine shrews (Tables 3 and 4). The scale is interpreted as representing relative functional mode of species from ambulatory (lower scores) to fossorial behavior (higher scores).

RESULTS

23-index PCA.—The first principal component (PC) from our PCA of 23 indices explained > 88% of the variance (Table 3). All of the indices, with the exceptions of MANUS and PES, contributed positively to this axis, which we interpret as a summary of the indices for each species and a scale of relative locomotor function among the 12 taxa included in the model (Fig. 4; Table 4). The scale here runs from -1.26 (the most ambulatory species, *C. tropicalis*) to 1.25 (the most fossorial species, *C. oreoryctes*). Individual species are grouped along the intervening scale, suggestive of grades of function.

The average difference in scores between adjacent species and subspecies on this scale is 0.23 (Table 4). Differences in adjacent scores greater than that value occur at three places, which are marked by obvious gaps in Fig. 4. These gaps separate the included taxa into four associations, from lowest to highest: 1) *C. nigrescens* and *C. parvus* groups; 2) *Bl. quadricaudata*; 3) species and subspecies of *Blarina*; and 4) *C. goldmani* group. Unfortunately, representatives from only three of the five species groups of *Cryptotis* (*C. goldmani*, *C. nigrescens*, and *C. parvus* groups) are represented in this model, so a large portion of the known morphological and functional diversity is missing.

9-index PCA.—Principal component analysis of a reduced set of nine indices from the humerus and the fore foot permitted inclusion of 19 of the 21 taxa, providing superior coverage of taxonomic and morphological diversity relative to the previous 23-index model. All of the indices contributed positively to the first PC, which explains > 94% of the variance in the model (Table 5). As in the 23-index model, we interpret this component as a general summary of the indices and a scale of relative locomotor function (Fig. 5; Table 6).

The scale for this analysis extends from the most ambulatory species at -1.36 (*C. merus*) to the most fossorial species at 1.49 (*C. lacertosus*). The average difference in scores between adjacent species and subspecies on this scale is 0.16 (Table 6). Differences in adjacent scores greater than that value occur in four regions of the scale, from lowest to highest scores (Fig. 5): 1) between *C. parvus* and *C. meridensis*; 2) between *Bl. quadricaudata* and *C. gracilis*; 3) between *B. carolinensis* and *C. mexicanus*; and 4) between *C. mexicanus* and *C. celaque*. These gaps effectively divide the scale into five functional groups of taxa: 1) *C. nigrescens* and *C. parvus* groups;

2) *C. thomasi* group, plus *Bl. quadricaudata*; 3) *C. gracilis*, plus all *Blarina*; 4) *C. mexicanus*; and 5) *C. goldmani* group (except *C. gracilis*).

Mean percentile ranks.—Mean percentile rank analysis permitted inclusion of all 21 taxa regardless of missing indices. Within a hypothetical range from 0 (most ambulatory) to 100 (most fossorial), MPRs among *Blarina*, *Blarinella*, and *Cryptotis* range from 19 to 82 (Table 7; Fig. 6). *Cryptotis* is functionally the most diverse genus, as well as being the most speciose. Based on these MPRs, the most ambulatory shrews

Table 4.—Rounded scores on the first factor axis from principal component analysis (PCA) of 23 morphological indices from 12 taxa of soricine shrews. The score is interpreted as representing relative adaptation of species for more ambulatory behavior (lower scores) versus more fossorial behavior (higher scores) (see Fig. 4).

Taxon	Factor 1 score
<i>C. tropicalis</i>	-1.26
<i>C. nigrescens</i>	-1.20
<i>C. merriami</i>	-1.14
<i>C. parvus</i>	-0.98
<i>Bl. quadricaudata</i>	-0.53
<i>B. b. jerrychoatei</i>	0.09
<i>B. carolinensis</i>	0.16
<i>B. b. talpoides</i>	0.24
<i>C. celaque</i>	1.03
<i>C. mam</i>	1.12
<i>C. lacertosus</i>	1.21
<i>C. oreoryctes</i>	1.25

Table 5.—Component loadings and eigenvalues for the first factor axis from principal component analysis (PCA) of nine morphological indices from 19 taxa of soricine shrews (see Fig. 5).

Variable	Component loading
%CL	12.375
%DPL	8.501
HEB	7.097
HTI	6.438
%CLS	4.264
TTP	3.857
MW3	3.344
HRI	1.635
SMI	0.391
Eigenvalue	364.295
Percent of total variance explained	94.613

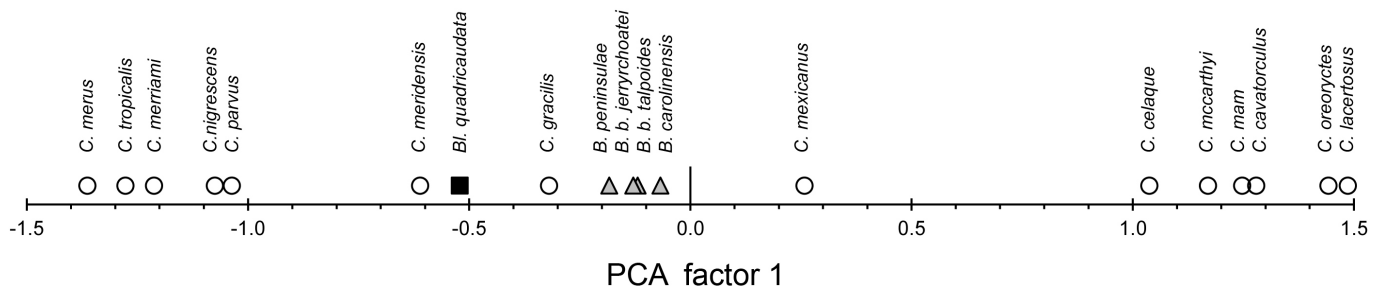


Fig. 5.—Results of principal component analysis (PCA) of nine morphological indices from the humerus and manus among 19 taxa of soricine shrews (Tables 5 and 6). The scale is interpreted as representing relative functional mode of species from ambulatory (lower scores) to fossorial behavior (higher scores).

among the 21 species we examined are *C. parvus* and *C. merus* (MPR = 19), and the most fossorial are *C. cavatorculus* and *C. lacertosus* (MPR = 82). Individual species of *Cryptotis* are distributed along most of the intervening scale, indicating a gradient of functionality. The order of the species groups of *Cryptotis*, and the positioning of *Blarina* and *Blarinella* relative to those species groups, is the same as in the previous two analyses. However, the order of individual species within the genus *Blarina* and within the species groups of *Cryptotis* is shuffled. The species groups of *Cryptotis* provide the background scale of variation for understanding the remaining taxa, particularly *Bl. quadricaudata* and the species and subspecies of *Blarina*.

The average difference in MPR between adjacent taxa on the scale is 3 percentile points (Table 7). Differences > 6 percentile points occur at only three locations, and within just the genus *Cryptotis*, gaps > 6 percentile points occur at four places and partly demarcate subclades (i.e., species groups) as well as functional groups. At the lower end of the scale, a gap of 8 percentile points between *C. merriami* (MPR = 24) and *C. meridensis* (32) separates a mixture of species belonging to the more ambulatory *C. nigrescens* and *C. parvus* groups from the *C. thomasi* group. The largest gap occurs in the middle of the scale, where 13 percentile points separate *C. thomasi* (39) of the *C. thomasi* group from *C. gracilis* (52), which is sister to other members of the *C. goldmani* group (Baird et al. 2017). *Cryptotis gracilis* is separated from *C. mexicanus* (*C. mexicanus* group) by a 10-percentile-point gap. Finally, 8 percentile points separate *C. mexicanus* (62) from *C. celaque* (70) and the remaining members of the *C. goldmani* group on the higher end of the scale.

The four species and subspecies of *Blarina* (54–62) cluster together just above the middle of the scale, bridging the gap between *C. gracilis* and *C. mexicanus*. Among the four North American short-tailed shrews, *B. carolinensis* is ranked as the most ambulatory and *B. b. jerrychoatei* as the most fossorial. *Blarinella quadricaudata* (40) is most closely associated with members of the *C. thomasi* group (32–39) near the lower part of the middle of the percentile rank scale (Table 7; Fig. 6).

Because the MPR analysis alone ranked all 21 taxa in our study, we hereafter use MPRs to represent relative locomotor function of individual species and clades. Four primary functional groups within the Blarinini and Blarinellini are delineated

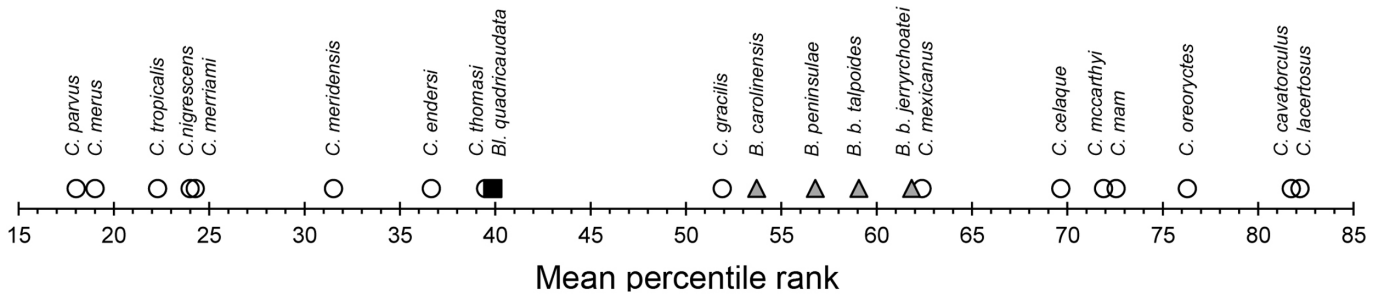


Fig. 6.—Results of mean percentile rank analysis of 23 morphological indices among 21 taxa of soricine shrews (Table 7). The scale is interpreted as representing relative functional mode of species from ambulatory (lower scores) to fossorial behavior (higher scores).

by large gaps in the MPR scale, and we label these as follows: taxa with ranks 19–24, “ambulatory”; 32–40, “intermediate”; 52–62, “semifossorial”; and 70–82, “fossorial.” These terms are relative and are defined only within the parameters of this group of genera and species for the purpose of further discussion below. However, approximately similar functional groups can be identified from scores calculated for species of mysoricine shrews (Woodman and Stabile 2015b), suggesting that the groupings could reflect more generalized functional grades of ambulatory–fossorial adaptation among soricids.

Distribution of functional modes.—The sister relationship of the Blarinellini and Blarinini, and that of the genera *Blarina* and *Cryptotis* within the Blarinini, are well established (Dubey et al. 2007; Chen et al. 2012). The last common ancestor of the Blarinellini and Blarinini is estimated to have been extant at 12.1 Ma, and the oldest fossil member of the genus *Cryptotis* has been dated at 9 Ma (Harris 1998; Dubey et al. 2007), indicating that the last common ancestor of the Blarinini existed some time prior to the latter date. Although species groups within *Cryptotis* generally represent clades, relationships among species groups, and among species within those groups, remain mostly unresolved, as many branches are poorly supported and species sampling is incomplete (Guevara and Cervantes 2014; He et al. 2015; Baird et al. 2017).

The combined phylogeny shows the hypothesized relationships of species within each of the genera and associates MPR functional scores with each of the terminal taxa (Fig. 7). *Blarinella quadricaudata*, representing the Blarinellini, exhibits intermediate locomotor morphology, whereas the four *Blarina* form a clade of semifossorial taxa (Fig. 7). *Cryptotis* exhibits the greatest diversity in morphology and function among the three genera, including species representing all four functional locomotor modes. With one exception, however, any single species group within *Cryptotis* is limited to a single functional group: the largest group—the *C. goldmani* group—includes both semifossorial and fossorial locomotor modes. Overall, the correspondence between species groups and functional groups is remarkable considering that the species groups of *Cryptotis* were originally defined primarily on the basis of external and cranial characters (Choate 1970; Hall 1981).

Semifossorial *C. mexicanus*, representing the *C. mexicanus* group, is sister to all other *Cryptotis* (Baird et al. 2017). The *C. nigrescens* group (*C. merus*, *C. nigrescens*, *C. merriami*) is sister to all *Cryptotis* except the *C. mexicanus* group, and

Table 6.—Scores on the first factor axis from principal component analysis (PCA) of nine morphological indices from 19 taxa of soricine shrews. The score is interpreted as representing relative adaptation of species for more ambulatory behavior (lower scores) versus more fossorial behavior (higher scores) (see Fig. 5).

Taxon	Factor 1 score
<i>C. merus</i>	-1.36
<i>C. tropicalis</i>	-1.28
<i>C. merriami</i>	-1.21
<i>C. nigrescens</i>	-1.08
<i>C. parvus</i>	-1.04
<i>C. meridensis</i>	-0.61
<i>Bl. quadricaudata</i>	-0.52
<i>C. gracilis</i>	-0.32
<i>B. peninsulæ</i>	-0.18
<i>B. b. jerryrhoatei</i>	-0.13
<i>B. b. talpoides</i>	-0.12
<i>B. carolinensis</i>	-0.07
<i>C. mexicanus</i>	0.26
<i>C. celaque</i>	1.04
<i>C. mccarthyi</i>	1.17
<i>C. mam</i>	1.25
<i>C. cavorculus</i>	1.28
<i>C. oreoryctes</i>	1.44
<i>C. lacertosus</i>	1.49

the *C. parvus* group (*C. parvus*, *C. tropicalis*) is sister to the *C. goldmani* group. Both the *C. nigrescens* group and the *C. parvus* group exhibit ambulatory morphologies. The *C. goldmani* group is expanded to show all of its resolved relationships. Within this group, semifossorial *C. gracilis* is sister to all other species. The next branching event divides members of the Honduran subclade (*C. cavorculus*, *C. celaque*, *C. mccarthyi*) from those of the Guatemalan subclade (*C. mam*, *C. lacertosus*, *C. oreoryctes*). All six of these species exhibit fossorial morphologies. The genetic relationships of the *C. thomasi* group relative to the rest of the genus remain unresolved. All three species of the *C. thomasi* group (*C. endersi*, *C. meridensis*, *C. thomasi*) exhibit intermediate morphologies, generally similar to that of *Bl. quadricaudata*.

DISCUSSION

Morphological trends.—In addressing locomotor functionality in the Blarinellini–Blarinini clade, we discuss morphologies and functional modes as though the typical

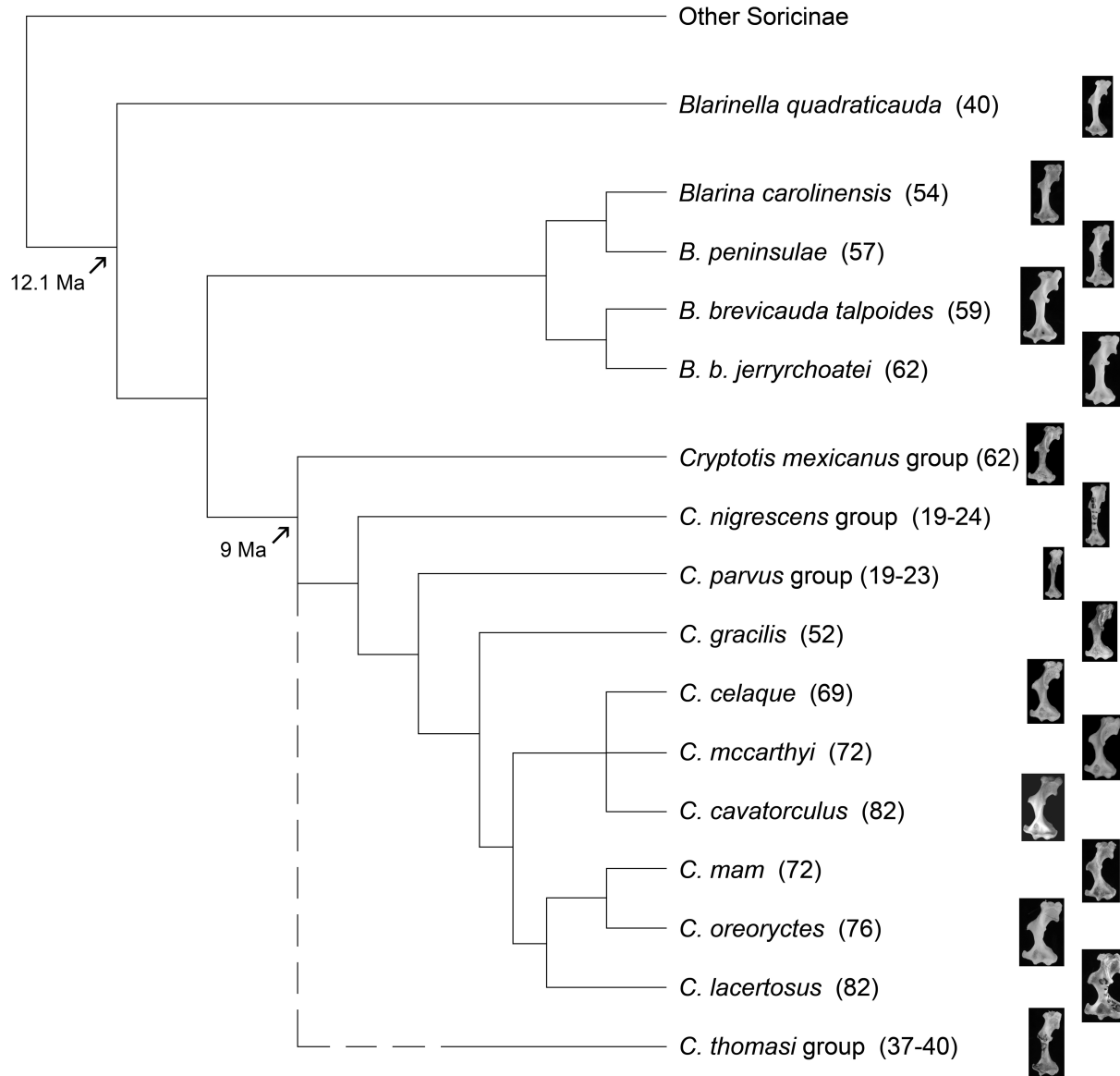


Fig. 7.—Phylogenetic tree of Blarinellini and Blarinini adapted from Reilly et al. (2005), Dubey et al. (2007), Chen et al. (2012), Baird et al. (2017), and Zeballos et al. (2018). Numbers in parentheses are mean percentile ranks. Time calibrations are from Harris (1998) and Dubey et al. (2007). The relationships of the *Cryptotis thomasi* group remain unresolved. Abbreviation: Ma, million years ago.

pattern represented unidirectional transitions from ambulatory to intermediate to semifossorial to fossorial. As we note in a subsequent section, however, transitions among functional locomotor modes in the Soricidae appear to be neither simple nor unidirectional. Much of our discussion of morphological trends in the group relates to indices and other results presented in Tables 1, 2, 8, and 9.

Body size.—There appears to be a slight trend of increasing body size with increased fossoriality among the Blarinellini and Blarinini (Fig. 8; Table 8; Supplementary Data SD1). This pattern is not as strong as that observable among the myosoricines (Woodman and Stabile 2015b). Moreover, the soricine trend is strongly influenced by the marked difference in body size between ambulatory species (HB = 60–69 mm) and the other three locomotor modes. There is little differentiation in the ranges of body sizes among intermediate (HB = 72–88 mm), semifossorial (HB = 67–89 mm), and fossorial (HB = 74–82 mm) functional

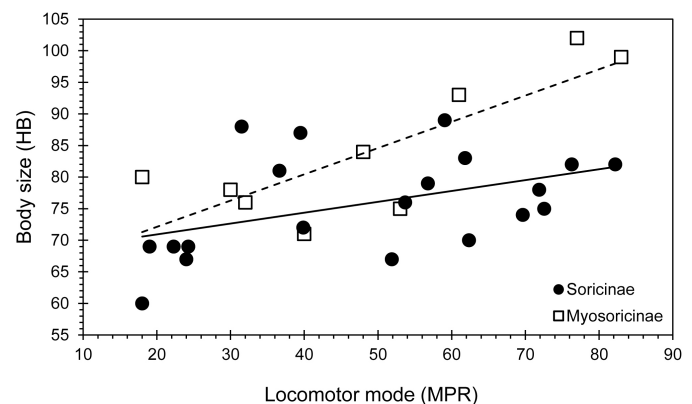


Fig. 8.—Relationship between body size (HB) and locomotor mode (MPR). Soricines: solid dots; solid regression line ($y = 1.1787x - 40.744$; $R^2 = 0.2026$); myosoricines: open squares; dashed regression line ($y = 1.5838x - 84.281$; $R^2 = 0.6584$). Data for myosoricines from Woodman and Stabile (2015b).

Table 7.—Percentile ranks calculated for 23 functional indices from 23 soricine shrews. Mean percentile ranks (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 to 100 (see Fig. 6). Taxa are listed in order by MPR. Abbreviations are explained in Table 1.

Taxon	CLAW	CLI	SHI	SMI	HRI	HTI	TTP	HEB	RDW	OLI	OCI	URI	%DPL
<i>C. parvus</i>	21	21	32	5	12	10	17	20	20	10	10	13	20
<i>C. merus</i>	14	12	8	79	12	2	2	20	—	—	—	—	5
<i>C. tropicalis</i>	2	21	42	62	31	21	26	3	20	3	10	13	5
<i>C. nigrescens</i>	7	5	8	17	12	21	12	10	20	20	37	50	20
<i>C. merriami</i>	33	5	8	38	12	10	7	10	3	20	30	50	13
<i>C. meridensis</i>	26	33	24	38	31	21	43	33	43	30	23	13	30
<i>C. endersi</i>	64	93	18	5	12	36	21	38	—	—	—	—	—
<i>C. thomasi</i>	33	40	42	38	45	62	31	—	—	—	—	—	30
<i>Bl. quadricaudata</i>	40	33	32	17	31	45	62	28	20	37	10	13	38
<i>C. gracilis</i>	14	21	53	79	45	45	62	53	—	—	—	—	43
<i>B. carolinensis</i>	50	55	66	88	62	45	43	63	43	63	43	50	63
<i>B. peninsulae</i>	64	79	61	93	62	31	43	53	63	83	50	83	53
<i>B. b. talpoides</i>	55	64	53	62	62	55	43	43	90	97	77	83	53
<i>B. b. jerrychoatei</i>	45	50	74	62	83	62	62	53	90	83	83	50	53
<i>C. mexicanus</i>	74	60	74	38	45	69	81	68	—	—	—	—	68
<i>C. celaque</i>	79	88	82	62	83	79	81	75	43	50	60	83	73
<i>C. mccarthyi</i>	64	45	—	17	83	74	62	75	—	—	—	—	80
<i>C. mam</i>	93	74	87	79	83	86	93	85	77	43	60	50	80
<i>C. oreoryctes</i>	88	83	92	38	83	98	93	93	63	83	90	50	90
<i>C. cavatorculus</i>	98	98	—	98	62	86	74	85	63	63	70	50	98
<i>C. lacertosus</i>	83	69	97	38	98	93	93	98	90	63	97	97	90

Taxon	%CL	%CLS	MW3	MANUS	PES	FRI	FEB	%hDPL	%hCL	%hCLS	MPR
<i>C. parvus</i>	23	7	3	15	72	6	26	19	26	7	18
<i>C. merus</i>	10	14	13	38	56	35	15	7	17	2	19
<i>C. tropicalis</i>	10	2	13	80	81	6	3	19	10	29	22
<i>C. nigrescens</i>	18	40	38	65	22	35	15	26	26	29	24
<i>C. merriami</i>	3	50	13	98	34	79	15	7	10	12	24
<i>C. meridensis</i>	28	24	25	3	—	35	47	50	64	29	32
<i>C. endersi</i>	—	14	—	—	81	35	79	7	2	43	37
<i>C. thomasi</i>	38	24	38	8	56	79	32	36	50	29	39
<i>Bl. quadricaudata</i>	33	40	25	80	91	79	47	36	64	17	40
<i>C. gracilis</i>	45	31	38	53	97	79	79	50	50	50	52
<i>B. carolinensis</i>	63	57	50	93	9	35	47	50	38	60	54
<i>B. peninsulae</i>	58	40	50	38	—	—	—	36	26	71	57
<i>B. b. talpoides</i>	53	57	60	15	9	79	65	64	50	71	59
<i>B. b. jerrychoatei</i>	45	67	60	28	56	79	47	64	38	88	62
<i>C. mexicanus</i>	68	67	68	38	—	—	—	64	64	55	62
<i>C. celaque</i>	73	83	78	23	34	35	94	76	76	93	70
<i>C. mccarthyi</i>	85	83	90	65	—	—	—	90	93	71	72
<i>C. mam</i>	85	74	78	80	56	35	65	76	88	43	73
<i>C. oreoryctes</i>	98	83	78	53	34	35	79	83	83	83	76
<i>C. cavatorculus</i>	78	98	90	80	—	—	—	90	76	98	82
<i>C. lacertosus</i>	93	93	98	53	9	79	94	98	98	71	82

groups, ultimately rendering body size a poor indicator of locomotor mode among soricines.

Fore limb versus hind limb.—Adaptations for fossoriality in mammals can include shortening of the overall lengths of the limbs (Shimer 1903; Reed 1951; Samuels and Van Valkenburgh 2008), as well as shortening of the hind limbs relative to the fore limbs so that they become more similar in length. Among the limited sample of three *Blarina*, *Bl. quadricaudata*, and seven *Cryptotis* for which complete suites of fore limb and hind limb bones were available (Table 8), fore limbs range 26–31% of head-and-body length (HB), and hind limbs from 36–41%. As observed among mysoricine shrews (Woodman and Stabile 2015b), there is no trend toward shortening of either the fore limb or the hind limb with increasing fossorial functionality, nor is there a tendency for lengths of the fore limb and

hind limb to move closer to parity. However, the three genera of soricine shrews in our study have relatively shorter fore limbs and hind limbs than mysoricines (range: 32–37%, 44–48% of HB, respectively). Despite the shorter limbs of soricines, the lengths of their fore limbs relative to the hind limbs (71–79%) generally accord with those of mysoricines (74–77%).

There is no indication of variation in relative lengths of individual long bones between the fore limb and hind limb. Neither proportional length of the humerus relative to the femur (84–92%) nor of the radius to the tibiofibula (56–62%) exhibit any pattern relative to locomotor mode.

In contrast to the long bones of the limbs, however, there are subtle differences between the bones of the manus and the pes that relate to fossoriality. As would be expected, the distal phalanges and claws of both the manus and pes increase in length

Table 8.—Proportional contributions of limb bones to the total length of the limb skeleton (not including the claw) and proportional lengths of the limbs. Abbreviations are explained in Figs. 2 and 3; calculations are explained in “Materials and Methods.” Species are ordered by mean percentile rank (see Table 7).

Species	Fore limb									Fore limb length/HB (%)
	HB (mm)	Fore limb length (mm)	HL (%)	RL (%)	3ML (%)	3PPL (%)	3MPL (%)	3DPL (%)	3CL (%)	
<i>C. parvus</i>	60	17.5	35	36	13	7	5	4	9	29
<i>C. tropicalis</i>	69	19.4	35	36	13	8	5	3	8	28
<i>C. nigrescens</i>	67	20.8	38	33	13	8	4	4	8	31
<i>C. merriami</i>	69	20.7	37	35	12	7	4	4	7	30
<i>C. meridensis</i>	88	24.3	35	36	14	7	4	5	10	28
<i>Bl. quadricaudata</i>	72	21.7	33	36	13	8	6	5	10	30
<i>B. carolinensis</i>	76	20.0	37	35	11	7	4	5	10	26
<i>B. b. talpoides</i>	89	24.9	37	34	13	7	4	6	10	28
<i>B. b. jerrychoatei</i>	83	23.5	36	33	13	8	4	6	10	28
<i>C. mam</i>	75	22.9	34	36	11	7	4	8	14	31
<i>C. oreoryctes</i>	82	24.0	35	36	11	7	4	8	14	29
<i>C. lacertosus</i>	82	24.9	35	36	11	6	4	8	13	30

Species	Hind limb									Hind limb length/HB (%)	Fore limb/hind limb (%)
	HB (mm)	Hind limb length (mm)	FL (%)	TL (%)	3hML (%)	3hPPL (%)	3hMPL (%)	3hDPL (%)	3hCL (%)		
<i>C. parvus</i>	60	24.0	30	44	14	6	3	3	6	40	73
<i>C. tropicalis</i>	69	26.3	30	44	14	6	3	3	5	38	74
<i>C. nigrescens</i>	67	27.7	31	42	13	6	3	3	6	41	75
<i>C. merriami</i>	69	27.7	31	44	13	6	3	3	5	40	75
<i>C. meridensis</i>	88	33.5	28	46	13	6	3	3	6	38	73
<i>Bl. quadricaudata</i>	72	28.3	28	44	14	6	4	4	7	39	77
<i>B. carolinensis</i>	76	27.2	32	43	13	6	3	3	6	36	73
<i>B. b. talpoides</i>	89	32.8	32	43	13	6	3	4	6	37	76
<i>B. b. jerrychoatei</i>	83	31.0	31	41	14	6	4	4	6	37	76
<i>C. mam</i>	75	30.3	29	45	13	5	3	4	8	40	76
<i>C. oreoryctes</i>	82	33.8	29	46	13	5	3	4	7	41	71
<i>C. lacertosus</i>	82	31.7	30	44	12	5	3	5	8	39	79

with increasing adaptation for fossoriality. However, the distal phalanges and claws of the manus elongate more than those of the pes (Table 2: CLAW, CLI).

Fore limb.—Some bones of the fore limb exhibit considerable variation related to locomotor mode. Most of the fore limb bones—humerus (HRI), radius (RDW), ulna (URI), and metacarpals and phalanges (MW3)—become more robust with increasing fossoriality to better withstand bending and shearing forces associated with digging. However, such character transitions do not always accompany transitions between locomotor modes. For example, width of the radius generally increases from ambulatory species to intermediate species and from intermediate species to semifossorial species, but there is little difference between semifossorial species and fossorial species.

As in myosoricines and talpids, the scapula increases in length with increasing fossoriality (Table 2: SHI; Reed 1951; Woodman and Gaffney 2014). Within the Blarinellini–Blarinini clade, there is little difference in scapular length between ambulatory and intermediate species, but there is a distinct increase in length in the transition to semifossorial and fossorial taxa (Table 2: SHI).

The humerus exhibits many of the most profound and obvious changes among locomotor modes (Fig. 1). The relative length of the delto-pectoral crest, represented by the index SMI (Table

2), gauges the size and importance of the deltoid and pectoral muscles that are involved in movement of humerus (Reed 1951; Woodman and Stabile 2015b). This index varies little between ambulatory and intermediate taxa, but tends to increase in size in both semifossorial and fossorial species. A teres tubercle, which acts as the insertion for the latissimus dorsi and teres major muscles, is a feature of the humerus unique to talpids, soricids, tachyglossids, and a few early mammals (Reed 1951; Hildebrand 1985b; Martin 2005; Woodman and Gaffney 2014). As in the myosoricines, the teres tubercle is longer and broader (Table 2: HTI), and it is more distally positioned (Table 2: TTP) with increasing fossoriality. Its prominence indicates that, as in talpids, the digging stroke of more fossorial soricids involves some degree of humeral rotation (Reed 1951; Hildebrand 1985b; Woodman and Gaffney 2014; Woodman and Stabile 2015b). The distal end of the humerus serves as the origin for fore arm flexor, pronator, and supinator muscles. It is expanded in more fossorial species (Table 2: HEB) to accommodate the larger muscles used in digging.

The ulna acts as a lever powered by the triceps brachii muscle, which inserts on the olecranon process of the proximal ulna. A longer olecranon process (input lever) is interpreted as signifying a larger, more powerful triceps brachii and greater input force. A shorter distal functional arm of the ulna (output lever) provides greater efficiency in transmitting muscular force to provide a more powerful digging stroke. Hence, the relative

Table 9.—Proportional contributions of the bones and claw of ray III to the total length of ray III (not including the claw) for the manus and pes. Abbreviations are explained in Fig. 3; calculations are explained in “Materials and Methods.” Species are ordered by mean percentile rank (see Table 7).

Species	Ray III length (mm)	Manus					3CL (%)
		3ML (%)	3PPL (%)	3MPL (%)	3DPL (%)		
<i>C. parvus</i>	5.0	45	24	17	13	30	
<i>C. merus</i>	6.0	46	26	16	12	26	
<i>C. tropicalis</i>	5.5	45	27	17	11	27	
<i>C. merriami</i>	5.7	44	27	16	13	25	
<i>C. nigrescens</i>	6.1	45	26	15	14	27	
<i>C. meridensis</i>	7.1	47	23	14	16	32	
<i>C. thomasi</i>	6.8	46	24	14	16	33	
<i>Bl. quadricaudata</i>	6.7	41	25	18	16	32	
<i>C. gracilis</i>	5.9	43	25	14	17	34	
<i>B. carolinensis</i>	5.5	41	25	15	19	36	
<i>B. peninsulæ</i>	6.7	43	24	15	18	36	
<i>B. b. talpoides</i>	7.4	43	23	15	19	35	
<i>B. b. jerrychoatei</i>	7.2	43	24	14	18	34	
<i>C. celaque</i>	6.6	41	23	12	25	44	
<i>C. mccarthyi</i>	6.3	39	23	13	26	46	
<i>C. mam</i>	6.8	38	23	14	26	46	
<i>C. oreoryctes</i>	7.1	38	22	13	27	47	
<i>C. cavatorculus</i>	7.2	38	23	13	27	44	
<i>C. lacertosus</i>	7.1	37	22	14	26	46	

Species	Ray III length (mm)	Pes					Manus/pes (%)
		3hML (%)	3hPPL (%)	3hMPL (%)	3hDPL (%)	3hCL (%)	
<i>C. parvus</i>	6.3	53	23	13	11	23	79
<i>C. merus</i>	7.3	53	24	12	10	22	83
<i>C. tropicalis</i>	6.9	54	23	11	11	21	81
<i>C. merriami</i>	7.2	51	25	13	10	21	79
<i>C. nigrescens</i>	7.4	50	24	13	13	23	82
<i>C. meridensis</i>	8.6	51	22	13	14	25	83
<i>C. thomasi</i>	8.3	53	21	12	13	24	82
<i>Bl. quadricaudata</i>	7.9	49	23	15	13	25	85
<i>C. gracilis</i>	8.0	51	23	13	14	24	74
<i>B. carolinensis</i>	6.9	51	23	13	14	23	80
<i>B. peninsulæ</i>	7.9	51	23	13	13	22	84
<i>B. b. talpoides</i>	8.4	51	22	12	14	24	88
<i>B. b. jerrychoatei</i>	8.6	50	22	13	14	23	84
<i>C. celaque</i>	7.9	50	23	10	17	26	84
<i>C. mccarthyi</i>	7.7	49	22	11	18	30	81
<i>C. mam</i>	7.9	51	21	11	17	30	86
<i>C. oreoryctes</i>	8.5	51	20	11	18	28	84
<i>C. cavatorculus</i>	8.1	49	21	12	18	26	89
<i>C. lacertosus</i>	8.1	49	21	12	19	31	88

size of the olecranon process in proportion to the length of the functional arm of the ulna provides a convenient means of assessing digging ability (Hildebrand 1985a, 1985b; Hildebrand and Goslow 2001). As among talpids, myosoricines, and rodents (Shimer 1903; Reed 1951; Hildebrand 1985b; Samuels and Van Valkenburgh 2008), the olecranon process generally enlarges with increasing fossoriality, although semifossorial *Blarina* have values similar to the most fossorial *Cryptotis* (Table 2: OLI, OCI).

In myosoricines and talpids, the radius becomes relatively longer relative to the humerus with increasing fossoriality (Reed 1951; Woodman and Stabile 2015b). In the Blarinellini–Blarinini clade, there is little variation in radial length that corresponds with locomotor mode (Table 2: BI), but there is some phylogenetic variation. Species and subspecies of *Blarina* and members of the *C. nigrescens* group have a relatively short radius. In contrast, the

radius of *Bl. quadraticauda* is relatively longer, closer in length to that in most other species groups of *Cryptotis*.

The total length of ray III of the manus remains stable relative to body size regardless of locomotor mode. However, the relative lengths of the bones composing ray III vary considerably (Table 9). Metacarpal III, proximal phalanx III, and middle phalanx III decrease in length with increasing fossoriality. In contrast, the relative lengths of distal phalanx III and its claw increase in length, with the distal phalanx lengthening proportionally more than the claw, thereby providing greater support for the claw in more fossorial taxa (Table 2: %CLS). These trends, also observed among the Myosoricinae (Woodman and Stabile 2015a), represent typical fossorial adaptations for scratch-digging mammals (Shimer 1903; Reed 1951; Hildebrand 1985b; Samuels and Van Valkenburgh 2008).

Hind limb.—There is generally less variation in the hind limb with locomotor mode than there is in the fore limb. Bones of the hind limb in intermediate, semifossorial, and fossorial species generally are more robust than those of ambulatory species (Table 2: FRI), but the increase in robusticity is less than that observed in the fore limb. There is little variation in the relative lengths of the femur, tibia, and metatarsal III related to locomotor mode (Table 2: PES).

Bones of the pes exhibit patterns of variation similar to those of the manus, but at a lower magnitude. The total length of ray III remains stable relative to body size regardless of locomotor mode, whereas the relative lengths of the bones composing the ray vary (Table 9). As in the manus, the proportional lengths of metatarsal III, proximal phalanx III, and middle phalanx III decrease with increasing fossoriality. In contrast, the distal phalanx and claw increase in length (Table 2: %hDPL, %hCL), with the distal phalanx increasing proportionally more (Table 2: %hCLS). Similar trends were observed among the Myosoricinae (Woodman and Stabile 2015a).

Phylogenetic patterns of functionality.—Intermediate and semifossorial locomotor morphologies are more widespread across the three genera in the Blarinellini–Blarinini clade, whereas ambulatory and fossorial morphologies occur only among species of *Cryptotis*, which includes all four locomotor modes. Lacking a well-supported phylogeny of the clade, we are as yet unable to formally estimate ancestral states using phylogenetic correlation analyses. However, based on the distribution of locomotor modes at the generic level, we can speculate that the last common ancestor of the Blarinellini–Blarinini clade had either an intermediate or a semifossorial locomotor morphology and the ancestor of the Blarinini was semifossorial. Regardless of the functional modes of these ancestral forms, species groups of *Cryptotis* evolved both ambulatory and fossorial morphologies. This suggests that both ambulatory and fossorial morphologies are apomorphic within the Blarinellini–Blarinini clade, and both suites of morphologies are under selection.

As documented previously for myosoricines (Woodman and Stabile 2015b), morphological variation associated with locomotor behavior in the soricine tribes Blarinellini and Blarinini has the superficial appearance of a graded series of generalized adaptive morphologies ranging from mostly ambulatory to mostly fossorial. The character suites comprising these morphologies have been viewed as unidirectional transition series that represent the evolution of complex structures from simpler structures and of more fossorial species with enhanced digging abilities from more ambulatory species (Woodman and Timm 1999, 2000; Woodman 2005; Woodman and Morgan 2005). Rather than being grades of variation sampled at temporally distinct intervals from a single lineage, the locomotor morphologies described by our analyses represent the extant tips of a series of independent, evolutionarily divergent lineages (Woodman and Stabile 2015b). All represent variations of a number of optimal morphologies. The complex scenario presented by our analyses of evolutionary patterns of locomotor morphology in the Blarinellini–Blarinini clade suggest directionality is less constrained. Selection for ambulatory

morphology is as likely as selection for fossorial morphology. Moreover, adaptive trends toward more fossorial morphology and toward more ambulatory morphology are likely to have occurred repeatedly. Recent work on the phylogeny of the Myosoricinae (J. A. Esselstyn, Louisiana State University, pers. comm., 16 July 2018) suggests similar repetitive trends in locomotor adaptations also occurred in that clade of the Soricidae (Woodman and Stabile 2015b).

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Mean measurements used to calculate functional indices.

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APPENDIX I

Specimens Examined

Specimens examined for this study are deposited National Museum of Natural History, Washington (USNM).

Blarina brevicauda talpoides ($n = 35$).—USA: PENNSYLVANIA: Allegheny Co. (USNM 288258, 288481, 288483); Beaver Co. (USNM 288482); Bucks Co. (USNM 568283, 568286–568288, 568290–568298, 568329, 568645, 568650, 568651, 568653, 568654); Monroe Co. (USNM 568340–568343); Northampton Co. (USNM 568402); Schuylkill Co. (USNM 568398, 568400); Somerset Co. (USNM 282767–282769); Westmoreland Co. (USNM 568396, 568397).

Blarina brevicauda jerrychoatei ($n = 9$).—USA: KANSAS: Douglas Co. (USNM 297183, 297184, 568976, 568982); Jefferson Co. (USNM 568207, 568983–568985, 569836).

Blarina carolinensis carolinensis ($n = 27$).—USA: GEORGIA: Liberty Co. (USNM 45155). NORTH CAROLINA: Brunswick Co. (USNM 268978); Chatham Co. (USNM 360549, 360550, 360553); Dare Co. (USNM 318991); Person Co. (USNM 360543); Wake Co. (USNM 344967, 344968); Warren Co. (USNM 360545); Washington Co. (USNM 334813). SOUTH CAROLINA: Charleston Co. (USNM 574143, 574146); Dorchester Co. (USNM 269928); Georgetown Co. (USNM 71468, 222890, 222891); Richland Co. (USNM 71471–71473, 71476); Williamsburg Co. (USNM 71470). TENNESSEE: Brunswick Co. (USNM 267175); Madison Co. (USNM 462501, 462502).

Blarina peninsulæ ($n = 11$).—USA: FLORIDA: Collier Co. (USNM 231462–231464); Everglades National Park (USNM 71482, 231465); Miami-Dade Co. (USNM 70875, 70876); Osceola Co. (USNM 111196, 568086); Orange Co. (USNM 568067–568068).

Blarinella quadricaudata ($n = 13$).—CHINA: SICHUAN (USNM 259368, 260754, 260755, 574288–574293, 574383–574386).