Skeletal indicators of locomotor adaptations in shrews

Neal Woodman[1, 2]*

[1] U.S. Geological Survey, Eastern Ecological Science Center, Laurel, MD 20708, USA. E-mail: woodmann@si.edu.
[2] Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC-108, Washington, DC 20013, USA.
*Corresponding author: https://orcid.org/0000-0003-2689-7373.

The Soricidae (Mammalia: Eulypotyphla) comprises more than 450 species inhabiting a variety of habitats on five continents. As a family, shrews employ a variety of locomotor modes that incorporate ambulatory, fossorial, aquatic, and scansorial behaviors, illustrating an ability to exploit a variety of natural substrates and their associated resources. In this study, the association of skeletal morphology and three of the dominant locomotor modes in the family—ambulatory, semi-fossorial, and semi-aquatic behaviors—was investigated in up to 52 species of 12 genera representing all three subfamilies of Soricidae. From skeletal measures, 34 morphological indices were calculated, most of which have been used previously to characterize substrate use among shrews, rodents, and other mammals, and analyzed for their individual effectiveness for discriminating the three locomotory modes. To assess their effectiveness in combination, subsets of locomotor indices were analyzed using 1) mean percentile ranks, 2) the first principal component from principal components analysis, and 3) plots and classifications from discriminant function analyses. In general, the three methods effectively identified and grouped the three locomotor modes and identified smaller subsets. Additional analyses were then used to classify the locomotor behaviors of five species whose locomotor modes were unknown or ambiguous. The analyses reinforce and broaden the scope of a previously identified observation of the wide range of grades of morphological variation that may permit an equally diverse range of locomotor abilities among the Soricidae.

La familia Soricidae (Mammalia: Eulypotyphla) comprende más de 450 especies que habitan varios hábitats en los cinco continentes. Como familia, las musarañas emplean una variedad de modos de locomoción que incorporan comportamientos ambulatorios, fosoriales, acuáticos y escansoriales (arborícolas), lo que ilustra su capacidad de explotar diferentes variedades de sustratos y sus recursos asociados. En este estudio, se investigó la asociación de la morfología esquelética y tres de los modos locomotores dominantes en la familia (ambulatorios, semifosoriales y semiacuáticos) en 52 especies de 12 géneros que representan las tres subfamilias de Soricidae. A partir de medidas esqueléticas, se calcularon 34 índices morfológicos, la mayoría de los cuales se han utilizado previamente para caracterizar el uso de sustrato entre musarañas, roedores y otros mamíferos. Se analizaron en cuanto a su eficacia individual para discriminar entre los tres modos de locomoción. Para evaluar su eficacia en combinación, se analizaron subconjuntos de índices locomotores usando 1) intervalos de percentiles medios, 2) el primer componente principal del análisis de componentes principales y 3) gráficas y clasificaciones del análisis de función discriminante. En general, los tres métodos identificaron y agruparon de manera efectiva los tres modos locomotores e identificaron subconjuntos más pequeños. Se usaron análisis adicionales para clasificar los comportamientos locomotores de cinco especies cuyos modos locomotores eran desconocidos o ambiguos. Los análisis refuerzan y amplían el alcance de una observación previamente identificada del intervalo en el grado de variación morfológica que pueden permitir una gama igualmente diversa de habilidades locomotoras entre los Soricidae.

Keywords: Ambulatory; anatomy; aquatic; ecomorphology; fossorial; functional morphology; Soricomorpha; substrate use; terrestrial.

Introduction

The locomotor behaviors of small, cryptic species of mammals have been studied directly for only a relatively few species. Instead, external and internal morphological characters are typically interpreted to provide insight into how individual species use available substrates, particularly while foraging (Shimer 1903; Reed 1951; Hildebrand 1985a, 1985b; Hutterer 1985; Price 1993; Samuels and Van Valkenburgh 2008; Hopkins and Davis 2009; Nations *et al.* 2019).

The typical external morphology of shrews (Mammalia: Eulypotyphla: Soricidae) can be generalized as a long cylindrical body, short legs, and simple feet with five digits used in a plantigrade-to-digitigrade posture, a body plan that is typical of ambulatory small mammals that make use of the ground surface as their primary locomotor substrate (Hutterer 1985; Churchfield 1990; Woodman and Morgan 2005).

In contrast, the relatively short dense fur, small pinnae, and small eyes of soricids are common mammalian adaptations for fossoriality (Shimer 1903; Eisenberg 1981). Although ambulation and semi-fossoriality are the two dominant locomotor modes among soricids, members of the family exhibit a range of other locomotor behaviors that assist in exploiting additional substrates. Based on a large sample of 266 species in 20 genera (the recognized diversity of Soricidae at that time), Hutterer (1985) estimated that almost 77 % of soricid species are primarily ambulatory (terrestrial), nearly 11 % are adapted for semi-fossoriality, about 5 % are scansorial, more than 4 % are semi-aquatic, 2 % are anthrophilic, and one species is psammophilic. In a related study based on a similar sample, Churchfield (1990:100) estimated that 82 % of soricid species have a dominantly epigeal foraging mode, 11 % are hypogeal, 5 % are aquatic,

and 3 % are scansorial, illustrating the seemingly close correspondence of primary locomotor mode and resource use.

Previous studies of soricid skeletal adaptations related to locomotor behavior have focused primarily on understanding morphological variation as it relates to ambulation and semi-fossoriality. Ambulatory and semi-fossorial species are distributed among all three subfamilies of the Soricidae (Hutterer 1985; Churchfield 1990), and they exhibit considerable intra-modal variation in morphological characteristics related to substrate use (Woodman and Gaffney 2014; Woodman and Stabile 2015b; Woodman and Wilken 2019). Herein, I explore skeletal variation as it relates to three of the four dominant locomotory modes identified for shrews by testing the discriminatory power of 34 common locomotor indices, mostly calculated from postcranial measurements. Although ambulatory and semi-fossorial locomotor modes occur in all three subfamilies of Soricidae, semi-aquatic-modes are confined to a smaller number of species in four genera representing two taxonomic tribes of the subfamily Soricinae: *Chimarrogale*, *Nectogale*, *Neomys*, and *Sorex* (This number increases to five genera if *Crossogale* is recognized as distinct from *Chimarrogale*: Wahab *et al.* 2020).

Materials and methods

The primary goal of this paper is to better understand skeletal variation among soricids in relation to a traditional, stereotyped classification of locomotor modes. This study of the association between morphology and locomotor behavior is admittedly incomplete, in part because locomotor modes of many soricids are based on inference rather than direct observation. Moreover, phylogeny is a potential primary driver of morphological variation, behavioral variation, or both, but genetic relationships among clades in the Soricidae remain poorly supported at nodes that appear to be crucial to understanding the evolution of locomotor morphology in the family (*e. g.*, He *et al.* 2015, 2021) and cannot yet be controlled for.

For the purposes of this paper, the word "ambulatory" refers to terrestrial shrews that use the ground surface as their primary locomotor substrate, and lack morphological characters linked to aquatic, fossorial, or scansorial adaptations or behaviors.

In this study, I used measurements and indices from 41 species and subspecies of soricids previously reported by Woodman and Gaffney (2014), Woodman and Stabile (2015a, 2015b), Woodman and Stabile (2015a, 2015b), and Woodman *et al.* (2019). To these, I added measurements from 180 individuals representing 11 additional species from the mammal collections of the Field Museum of Natural History, Chicago, IL (FMNH), and the National Museum of Natural History, Washington, DC (USNM; Appendix 1). All 52 species were classified *a priori* into one of five locomotor groupings based on reported behaviors and suites of external characteristics: ambulatory (*n* = 16); semi-aquatic (*n* = 7); semi-fossorial (*n* = 19); fossorial (*n* = 2); unknown (*n* = 5). Semi-fossorial and fossorial taxa tend

to have large body size, short tails, small pinnae hidden by the fur, enlarged forefeet, and long, broad foreclaws (Hildebrand 1985b; Hutterer 1985). Semi-aquatic shrews tend to have large body size, long tails that may be laterally flattened or have one or more keels of stiff bristles, long hind feet, and digits and feet fringed with bristles; some have webbed hind feet (Howell 1930; Hutterer 1985). Ambulatory species exhibit the entire range of body size and lack fossorial or aquatic characters. A complete list of species and their *a priori* locomotor classifications is provided in Appendix 2.

Skeletal measurements. To assess relative locomotor adaptations, I followed procedures explained in detail by Woodman and Gaffney (2014; see also Woodman and Stabile 2015b; Woodman and Wilken 2019). Total length and tail length are the standard external measurements recorded from skin tags, and head-and-body length was calculated by subtracting tail length from total length. Forty measurements (Table 1) were obtained from the manus, pes, and long bones of the appendicular skeletons. The scapula, humerus, ulna, radius, femur, and tibiofibula were digitally photographed, and the bones of the manus and pes were digitally x-rayed using a Kevex X-Ray Source 4.1.3 (Kevex, Palo Alto, CA) with Varian Image Viewing and Acquisition 2.0 software (VIVA, Waltham, MA) in the Division of Fishes, National Museum of Natural History, Washington, DC. The resulting digital images from both sources were imported into Adobe Photoshop CS3 Extended 10.0.1 (Adobe Systems, San Jose, CA) and variables (Supplementary Table S1) measured using the Custom Measuring Scale in the Analysis menu following Woodman and Gaffney (2014; see also Woodman and Morgan 2005; Woodman and Stephens 2010; Sargis et al. 2013a, 2013b; Woodman and Stabile 2015b; Woodman and Wilken 2019).

Locomotor indices. Skeletal measurements were used to calculate 34 osteological indices previously employed to characterize locomotor mode and identify potential adaptations for substrate use among soricids (Woodman and Gaffney 2014; Woodman and Stabile 2015a, b; Woodman and Wilken 2019; Woodman *et al.* 2019), rodents (Price 1993; Samuels and Van Valkenburgh 2008; Elissamburu and De Santis 2011; Nations *et al.* 2019), and other mammals (Sargis 2002; Hopkins and Davis 2009). To overcome the problem of missing elements, and thereby, missing data, indices (Table 2) were calculated from mean values of variables for each species (Supplementary material Table S1). Abbreviations of measurements used to calculate indices are explained in Table 1.

1. Intermembral index (IM = [HL+RL]/[FL+TL]) compares the lengths of the forelimbs and hind limbs (Sargis 2002).

2. Humerofemoral index (HFI = HL/FL) represents the length of the humerus as a proportion of the length of the femur (Sargis 2002).

3. Metapodial index (FOOT = ML/hML) indicates the relative sizes of the forefeet and hind feet by comparing the length of metacarpal III to that of metatarsal III.

Table 1. Measurements used for calculating locomotor indices (see Woodman and Morgan 2005; Woodman and Stephens 2010; Woodman and Gaffney 2014; Woodman and Stabile 2015a, 2015b; Woodman and Wilken 2019; Woodman *et al.* 2019). See Supplementary material Table S1 for mean measurements.

1. HAR: axis of rotation of the humerus.	21. UPC: width of proximal crest of the ulna.
2. HL: length of the humerus.	22. 3CL: length of claw of manus ray III.
3. HDPC: length of deltopectoral crest of the humerus.	23. 3CW: width of claw of manus ray III.
4. HDW: distal width (epicondylar breadth) of the humerus.	24. 3DPL: length of distal phalanx of manus ray III.
5. HLD: least mediolateral diameter of humerus.	25. 3DPW: width of distal phalanx of manus ray III.
6. HTT: length from head of humerus to distal edge of teres tubercle.	26. 3ML: length of metacarpal of manus ray III.
7. HTTR: breadth of teres tubercle, input lever for rotation of the humerus (measured at a right angle to HAR).	27. 3MPL: length of middle phalanx of manus ray III.
8. RDW: distal width of radius.	28. 3MPW: width of middle phalanx of manus ray III.
9. RL: length of radius.	29. 3PPL: length of proximal phalanx of manus ray III.
10. FDW: distal width (epicondylar breadth) of the femur.	30. 3PPW: width of proximal phalanx of manus ray III.
11. FL: length of the femur.	31. 3hCL: length of claw of pes ray III.
12. FLD: least mediolateral diameter of the femur.	32. 3hCW: width of claw of pes ray III.
13. SL: greatest length of scapula.	33. 3hDPL: length of distal phalanx of pes ray III.
14. TDA: width of the distal articular surface of the tibiofibula.	34. 3hDPW: width of distal phalanx of pes ray III.
15. TDW: distal width of the tibiofibula.	35. 3hML: length of metatarsal of pes ray III.
16. TL: length of the tibiofibula.	36. 3hMW: width of metacarpal of pes ray III.
17. UFL: functional length (output lever arm) of the ulna.	37. 3hMPL: length of middle phalanx of pes ray III.
18. UL: total length of the ulna.	38. 3hMPW: width of middle phalanx of pes ray III.
19. ULD: least mediolateral diameter of the ulna.	39. 3hPPL: length of proximal phalanx of pes ray III.
20. UOP: length of olecranon process (input lever arm) of the ulna.	40. 3hPPW: width of proximal phalanx of pes ray III.

4. Distal phalanx length index (CLAW = DPL/hDPL) compares the relative size of distal phalanx III of the manus to distal phalanx III of the pes.

5. Claw length index (CLI = CL/hCL) gauges the relative size of claw III of the manus to claw III of the pes.

6. Scapulohumeral index (SHI = SL/HL) indicates relative lengths of the scapula and humerus.

7. Brachial index (BI = RL/HL) shows the relative proportions of the proximal (humerus) and distal (radius) elements of the forelimb.

8. Shoulder moment index (SMI = HDPC/HL) is equivalent to the delto-pectoral crest length index (Sargis 2002). It measures the length of the deltopectoral crest of the humerus relative to the length of the humerus, thereby gauging the size and mechanical advantage of the deltoid and pectoral muscle groups, which are important in the movement, rotation, and counter-rotation of the humerus (Reed 1951).

9. Humeral robustness index (HRI = HLD/HL) indicates the robustness of the humerus and its ability to resist bending and shearing stresses.

10. Humeral rotation lever index (HTI = HTTR/HAR) shows the relative length of the teres tubercle measured at right angles to the longitudinal axis of rotation of the humerus. The teres tubercle is an elongate process unique to the humerus of talpids, soricids, tachyglossids, and a few early mammals (Reed 1951; Hildebrand 1985b). It serves as the insertion for the latissimus dorsi and teres major muscles and as a lever for rotating the humerus (Reed 1951).

11. Teres tubercle position index (TTP = HTT/HAR) represents the relative position of the teres tubercle along the axis of rotation of the humerus (HAR). In more robust, more fossorially adapted humeri with larger muscle attachment surfaces, the teres tubercle is often more distally positioned (Woodman and Gaffney 2014; Woodman and Stabile 2015).

12. Humeral epicondylar index (HEB = HDW/HL) measures the width of the distal humerus relative to the length of the humerus and represents the area available for the origins of muscles involved in flexing, pronating, and supinating the forearm.

13. Radial distal width index (RDW = RDW/RL) measures the relative width of the proximal end of the radius, providing a gauge of its robustness and its resistance to stress.

14. Olecranon length index (OLI = UOP/UFL) is one of several variations on the index of fossorial ability of Hildebrand (1985a). The ulna acts as a lever that pivots at the trochlear notch, and OLI gauges the force exerted by the triceps brachii muscle on the olecranon process that is transmitted to the functional arm of the ulna. Semi-fossorial and fossorial mammals generally have a longer olecranon process to accommodate a larger triceps brachii, resulting in larger OLI (Reed 1951; Vizcaino and Milne 2002; Samuels and Van Valkenburgh 2008; Woodman and Gaffney 2014).

15. Triceps metacarpal outforce index (TMO = UOP/[UFL+ML]), a variant of Hildebrand's (1985a) index of fossorial ability (OLI), gives the length of the olecranon process as a proportion of the functional arm provided by the ulna and metacarpal III together. This index measures the amount of force input on the olecranon process that is transmitted to the tip of the metacarpal of ray III (Price 1993).

16. Triceps claw outforce index (TCO = UOP/[UFL+ML+PPL+MPL+CL]) expresses the length of the olecranon process relative to the combined functional lengths of the ulna and the four bones comprising ray III of the

manus. An extension of Hildebrand's (1985b) index of fossorial ability (OLI) and Price's (1993) triceps metacarpal out-force index (TMO), TCO represents the proportion of force input on the olecranon process by the triceps muscle that is transmitted to the tip of the claw of ray III, which is the initial point of contact with the soil.

17. Olecranon crest index (OCI = UPC/UFL) is a measure of the relative length of the olecranon crest on the olecranon process. It serves as the insertion for much of the triceps brachii. OCI is an approximate gauge of muscle size, and, therefore, another measure of the relative input force on the ulna (Woodman and Gaffney 2014).

18. Ulnar robustness index (URI = ULD/UFL) measures the robustness of the ulna and its ability to resist bending and shearing stresses.

19. Manual distal phalanx index [%DPL = DPL/(ML+PPL+MPL)] is the length of distal phalanx III of the manus relative to the combined length of the proximal three bones of ray III.

20. Manual claw index [%CL = CL/(ML+PPL+MPL)] is the length of claw III of the manus relative to the combined length of the proximal three bones of ray III.

21. Manual claw support index (%CLS = DPL/CL) represents the proportion of claw III of the manus that is supported by the underlying distal phalanx III.

22. Metacarpal width index (MW3 = MW/ML) measures the robustness of metacarpal III of the manus in relation to its length.

23. Phalangeal index (PI = (PPL+MPL)/ML) shows the lengths of the proximal and middle phalanges relative to the metacarpal. This index reflects the degree to which the hand is prehensile and used for grasping (higher index value) versus walking on the ground (lower index value), and it has been used mainly for distinguishing arboreal and scansorial species from ambulatory species. PI varies considerably among rays of an individual, so ray III is typically used for comparisons among species (Lemelin 1999; Kirk *et al.* 2008). No arboreal or scansorial shrews were included in the present study.

24. Manus proportions index (MANUS = PPL/ML) measures the size of the proximal phalanx relative to the metacarpal of manual ray III (Samuels and Van Valkenburgh 2008), and it is the same as Kirk *et al.*'s (2008) proximal phalangeal index. There appears to be a large phylogenetic component to this index across mammalian orders (Kirk *et al.* 2008), but not within rodent families (Nations *et al.* 2019), and it is useful for distinguishing arboreally adapted species (larger indices) from ambulatory species (smaller indices).

25. Crural index (CI = TL/FL) measures the relative lengths of proximal (femur) and distal (tibiofibula) long bones of the hind limb.

26. Pes length index (PES = hML/FL) represents the length of metatarsal III relative to femur length and is used to indicate the relative size of the hind foot.

27. Femoral robustness index (FRI = FLD/FL) quantifies the robustness of the femur and its ability to resist bending and shearing stresses.

28. Femoral epicondylar index (FEB = FDW/FL) approximates the area available for the origins of the gastrocnemius and soleus muscles involved in extension of the knee and plantar-flexion of the pes in rodents (Samuels and Van Valkenburgh 2008). In shrews and talpids, this region is the origin for the plantaris, which flexes the toes, the gastrocnemius, which extends the pes, and the extensor digitorum longus, which extends and adducts the digits and dorsoflexes the foot. It is also the insertion for the caudofemoralis, which retracts the femur, and the adductor longis, which adducts the femur (Reed 1951).

29. Distal tibiofibular articulation index (DTA = TDA/TDW) measures the width of the articular region for the astragalus between the lateral and medial malleolus relative to the distal width of the tibia (Woodman and Gaffney 2014; Woodman and Stabile 2015).

30. Pedal distal phalanx index [%hDPL = hDPL/(hML+hPPL+hMPL)] is the length of the distal phalanx of ray III of the pes relative to the combined length of the proximal three bones of that ray.

31. Pedal claw index [%hCL = hCL/(hML+hPPL+hMPL)] is the length of the claw of ray III of the pes relative to the combined length of the proximal three bones of that ray.

32. Pedal claw support index (%hCLS = hDPL/hCL) is the proportion of the claw of ray III of the pes supported by the distal phalanx.

33. Tail length index (%TAIL = tail length/head-and-body length) measures the length of the tail relative to head-and-body length. This index was effective for distinguishing between arboreal and terrestrial species of murid rodents (Nations *et al.* 2019).

34. Relative robustness index (RR = HLD/FLD) measures the least breadth of the humerus relative to the least breadth of the femur.

Analyses of locomotor indices. The effectiveness of the 34 indices for distinguishing locomotor mode was initially evaluated by calculating standard univariate statistics (mean, SD, range) in Excel (Microsoft Corporation, Redmond, Washington) for each locomotor group and plotting as box-and-whisker plots (Supplementary material Figure 1). To provide overviews of interspecific variation and to determine relative grades of locomotor modes among taxa, analyses of percentile ranks and multivariate analyses were employed to combine multiple indices. Percentile ranks were calculated for each taxon for each of 23 locomotor indices (IM, HFI, FOOT, CLAW, CLI, SMI, HRI, HTI, TTP, HEB, TCO, OCI, URI, %DPL, %CL, MW3, CI, PES, FEB, %hDPL, %hCL, RR, %TAIL) using the percentile rank calculator at Statisticshelper.com (https://statisticshelper.com/percentile-rank-calculator/). A mean percentile rank was then calculated for each taxon from all indices for which it could be scored. Mean percentile ranks provide a

Table 2. Locomotor indices. See Materials and methods for abbreviations.

ID	Mode	IM	HFI	FOOT	CLAW	CLI	SHI	BI	SMI	HRI	HTI	TTP	HEB	RDW	OLI	TMO	TCO	OCI	URI	%DPL	%CL	%CLS	MW3	PI	MANUS	CI	PES	FRI	FEB	DTA	%hDPL	%hCL	%hCLS	%TAIL	RR	No. of indices
Chimarrogale himalayaca	SA			56	92	88	94		45	8	9	42	34							15	24	65	10	93	61						11	17	62	82		19
Nectogale elegans	SA	68	92	50	89	85	108	109	42	12	13	37	48	15	24	17		26	5			64	8		48	182	88	12	35	51	10	16	61	51	93	30
Neomys fodiens	SA	64	86	56	86	85	103	103	44	9	17	42	41	12	21	15	10	23	5	14	27	53	9	89	55	171	71	9	26	46	11	21	53	71	89	34
Sorex albibarbis	SA	68	94	51	85	84	93	105	39	9	13	37	35	11	19	14	10	26	5	14	27	54	9	89	56	184	75	10	28	42	10	19	53	89	86	34
Sorex bendirii	SA	68	91	53	87	88	99	106	40	10	17	42	38	12	23	17	12	28	6	17	33	51	9	85	53	178	67	10	28	52	12	23	52	82	89	34
Sorex navigator	SA	67	92	51	90	90	95	108	38	9	16	39	37	12	21	15	11	25	5	17	31	54	9	91	57	185	77	10	29	49	11	21	54	96	80	34
Sorex palustris	SA	68	93	55	88	90	96	102	39	8	13	37	34	12	22	15	11	26	5	15	30	50	9	84	52	177	71	10	29	**52**	11	21	51	79	55	34
Sorex cinereus	Am	67	90	54	79	86	94	105	38	8	13	35	32	10	20	14	10	23	5	14	27	52	8	90	55	177	64	9	25	55	11	20	57	72	82	34
Sorex hoyi	Am	67	90	62	89	102	91	102	40	8	15	38	33	11	20	15	10	25	5	15	30	49	8	94	55	169	57	7	26	53	11	20	56	57	94	34
Sorex sonomae	Am	68	90	59	99	99	97	108	39	10	14	39	37	11	20	15	10	26	6	17	35	49	10	93	55	175	64	9	27	51	12	24	50	73	96	34
Suncus hututsi	Am			69	74	81														10	19	53	10	86	55						11	19	59	53		13
Cryptotis parvus	Am	71	86	67	94	105	100	103	42	9	17	40	36	13	18	13	9	24	6	16	35	44	9	91	54	145	46	8	23	41	13	26	49	28	91	34
Cryptotis tropicalis	Am	71	87	66	81	105	101	102	45	10	18	42	34	13	17	13	9	24	6	13	30	43	10	98	60	148	48	8	21	43	12	23	55	33	108	34
Cryptotis merriami	Am	73	92	68	99	96	94	93	44	9	17	38	35	12	20	15	11	27	7	15	29	52	10	98	62	143	44	10	22	43	12	23	50	41	89	34
Cryptotis merus	Am		88	71	93	98	94		46	9	12	37	36							13	30	45	10	92	57	139	45	9	22	41	12	25	48	39	84	26
Cryptotis nigrescens	Am	73	92	73	89	96	94	87	43	9	18	39	35	13	20	14	10	29	7	16	31	51	12	94	59	136	43	9	22	46	14	26	55	43	88	34
Blarinella quadricaudata	Am	74	92	71	106	108	100	108	43	10	21	46	39	13	22	16	11	24	6	20	39	51	11	103	60	159	50	10	25	48	15	29	52	52	94	34
Crocidura olivieri	Am		85				90		50	9	8	37	27															10	21					58	85	11
Crocidura religiosa	Am		91				89		52	7	6	36	28															9	21					64	72	11
Crocidura suaveolens	Am	70	87				93	99	47	8	11	35	31	10	18			22	6							146		8	21	32				65	84	19
Myosorex cafer	Am		88	71	100	114	92		46	10	15	36	32							19	36	51	11	91	55		48	8	21		15	26	58	45	101	24
Myosorex geata	Am		91	72	93	116	94		47	9	16	39	35							21	42	50	13	90	54		46	10	23		19	31	62	55	84	24
Myosorex kihaulei	Am		90	70	97	117	94		46	9	16	40	35							23	46	49	12	88	53		47	10	23		19	32	59	47	87	24
Blarina brevicauda talpoides	SF	72	88	74	114	130	106	92	45	12	23	45	43	17	32	23	16	35	8	23	43	53	14	89	54	136	41	10	26	52	17	28	60	28	105	34
B. brevicauda jerryrchoatei	SF	73	88	73	108	125	110	92	45	13	24	46	44	17	29	21	14	36	7	23	41	55	14	88	56	133	45	10	25	56	17	27	63	27	110	34
Blarina carolinensis	SF	71	86	65	112	126	109	95	48	12	21	45	45	14	28	21	15	30	7	24	45	53	13	98	61	137	41	9	25	34	16	27	59	26	109	34
Blarina hylophaga	SF																			24	45	53	14	93	58						17	29	58	27		10
Blarina peninsulae	SF			70	117	136	107	94	49	12	19	45	44	15	29	21	14	32	8	23	44	51	13	92	57					44	15	26	60	27		27
Blarina shermani	SF			67	106	121														21	44	48	13	99	59						16	28	55	27		13
B. brevicauda jknoxjonesi	SF																			23	46	50	13	89	55						15	25	61	26		10
Cryptotis mexicanus	SF					110			44	11	25	49	46							26	48	55	15	89	57										39	13
Cryptotis phillipsii	SF								42	11	23	42	42																							46	6
Cryptotis eckerlini	SF		85	61	140	144	113	104	50	12	29	49	55	16	42	29	17	48	11	34	63	55	19	105	61		45	10	28		19	33	56	38	107	31
Cryptotis matsoni	SF		80	60	120	139	121		49	13	33	53	55							34	59	56		94	51		46	10	27		20	31	65	31	105	23
Cryptotis cavatorculus	SF			69	134	153		97	50	12	32	48	52	15	28	21	14	34	7	37	60	61	19	93	60						22	31	69			24
Cryptotis celaque	SF		88	68	123	142	112	107	45	13	31	49	51	14	26	20	13	33	8	33	58	57	17	84	55		44	9	28		20	31	66	36	119	31
Cryptotis mam	SF	72	88	64	133	134	113	106	46	13	32	51	52	16	25	19	12	33	7	35	62	56	17	97	60	153	45	9	26	44	20	36	56	38	129	34
Cryptotis magnimanus	SF								43	13	30	50	54																							31	6
Cryptotis mccarthyi	SF			64	117	124			43	13	30	46	51							35	62	57	19	91	59						22	37	60	30		18
Congosorex phillipsorum	SF		90	76	113	107	104		50	11	20	39	42							23	39	59	13	87	55		46	10	24		18	32	56	58	103	24
Myosorex blarina	SF	72	89	77	107	128	100	96	50	9	19	41	39	15	24	18	12	31	8	28	57	49	15	84	50	142	40	10	24	46	23	39	59	41	81	34
Myosorex varius	SF	70	86	69	109	126	99	103	48	10	18	43	35	13	19	14	10	30	5	27	52	52	14	88	52	149	44	9	22	45	20	34	60	40	99	34
Myosorex zinki	SF		82	75	120	152	108		47	13	18	42	47							29	61	48	16	86	51		42	11	25		21	34	60	39	99	24
Cryptotis lacertosus	SF	75	92	67	125	131	123	102	44	15	33	51	58	17	28	21	14	40	9	36	63	58	20	97	58	147	41	10	28	48	23	38	60	34	140	34
Cryptotis oreoryctes	SF	67	84	62	127	138	116	104	44	13	34	51	54	15	29	22	14	37	7	36	64	57	17	92	58	155	44	9	27	49	21	34	62	38	120	34
Surdisorex norae	F	70	81	71	143	166	120	103	62	17	35	51	60	17	31	23	14	40	9	46	78	60	20	84	50	135	42	11	25	44	27	38	69	38	125	34
Surdisorex polulus	F		84	79	162	174	113		62	17	39	55	58							45	76	59	20	83	49		42	10	24		25	39	64	40	135	24
Cryptotis gracilis	UN		91	63	93	105	106		46	11	21	46	44							21	41	50	12	91	58	175	53	10	27	43	16	28	57	55	95	26
Cryptotis endersi	UN		90		117	145	96		42	9	20	41	42												45		48	9	27		12	21	56	52	87	18
Cryptotis meridensis	UN	69	90		86	111	97	103	44	10	18	45	40	14	21	15	11	26	6	19	37	50	11	78	47	165		9	25	44			65	38	102	30
Cryptotis monteverdensis	UN								43	10	18	46	43																							58	6
Cryptotis thomasi	UN		90	70	99	113	101		44	11	24	44								19	40	49	12	83	52		45	10	24		15	28	55	29	100	23
Number of species		27	42	43	45	45	45	31	50	50	50	50	49	31	31	30	29	31	31	46	46	48	46	46	47	29	38	42	42	30	46	46	47	53	42	

convenient means of comparing all 52 taxa on a possible scale from 0 to 100. This permits broader taxonomic coverage, but the lack of data for some taxa means that morphological comparisons are not even across all taxa.

The largest complete dataset (*i. e.*, no missing data) that I could compile included 17 indices (CLI, CLAW, %CL, %DPL, SHI, HEB, HTI, %hCL, FOOT, TTP, SMI, %hDPL, MW3, HRI, PI, MANUS, %TAIL) from six semi-aquatic, 12 ambulatory, 13 semi-fossorial, and two fossorial species. To test the ability of this dataset to discriminate locomotor modes, I carried out both principal components analyses (PCAs) and discriminant function analyses (DFAs) in Past4.03 (Hammer *et al.* 2001).

To investigate the possible locomotory modes of four species (*Cryptotis gracilis, C. endersi, C. meridensis, C. thomasi*) for which locomotory mode was uncertain, I carried out PCA and DFA on a subset of 10 indices (CLAW, CLI, SHI, SMI, HRI, HTI, TTP, %CLS, FEB, %TAIL) from these species and 33 species of known locomotory mode. All four unknown species lacked sufficient data to be included in the 17-variable model (Table S1).

Results

Effectiveness of individual indices. Most of the indices tested individually show identifiable patterns of variation among locomotor modes in soricids, most typically either ascending or descending in mean values from semi-aquatic to ambulatory to semi-fossorial to fossorial. Only a few indices, however, exhibit ranges of variation that are sufficiently constrained to be useful for clearly distinguishing one or more modes.

Individual locomotor indices that appear to be the most reliable for distinguishing semi-aquatic species are PES (*n* =

37 species), FOOT (*n* = 46), CLI (*n* = 44), CI (*n* = 28), %TAIL (*n* = 52), and %hCL (*n* = 45). All but PES have ranges that overlap in value with one or more ambulatory species (Figure 1). The indices CLAW, OCI, MW3, %DPL, %CL, HTI, and CLI are useful for differentiating semi-aquatic and semi-fossorial species.

The ranges of individual locomotor indices of ambulatory species most commonly group with those of semi-aquatic species and often overlap the ranges of some semi-fossorial species. The most reliable indices for distinguishing ambulatory species from semi-aquatic species are PES, FOOT, CLI, FEB (*n* = 41), and %TAIL. The most efficient indices for distinguishing ambulatory species from semi-fossorial species are CLAW (*n* = 43), OCI (*n* = 30), and RDW (*n* = 30), followed by MW3 (*n* = 45), %DPL (*n* = 44), %CL (*n* = 45), HRI (*n* = 49), HTI (*n* = 49), SHI (*n* = 44), CLI, HEB (*n* = 48), TTP (*n* = 49), OLI (*n* = 30), TMO (*n* = 29), and TCO (*n* = 28).

The combination of semi-fossorial and fossorial species can be distinguished most effectively from the other two locomotory modes by OCI and CLAW, followed by MW3, %DPL, CLI, TMO, TCO, HTI, HRI, TTP, RDW, and %CL. The most useful indices for differentiating semi-fossorial from fossorial shrews are %DPL, %CL, %hDPL (*n* = 45), CLI, SMI (*n* = 49), HRI, and HTI, followed by CLAW, HEB, PI (*n* = 45), MANUS (*n* = 46), and %hCL.

1. Intermembral index (IM), which compares the lengths of the forelimbs and hind limbs, typically increases in rodents from semi-aquatic species to ambulatory, to semi-fossorial, and to fossorial species ([Samuels and Van Valkenburgh 2008](#)). The index shows a similar pattern with soricids (Supplementary material Figure 1a), indicating a tendency for semi-aquatic species to have relatively longer hind limbs (and/or shorter fore limbs) and for more fossorial forms to have relatively shorter hind limbs. Overlap
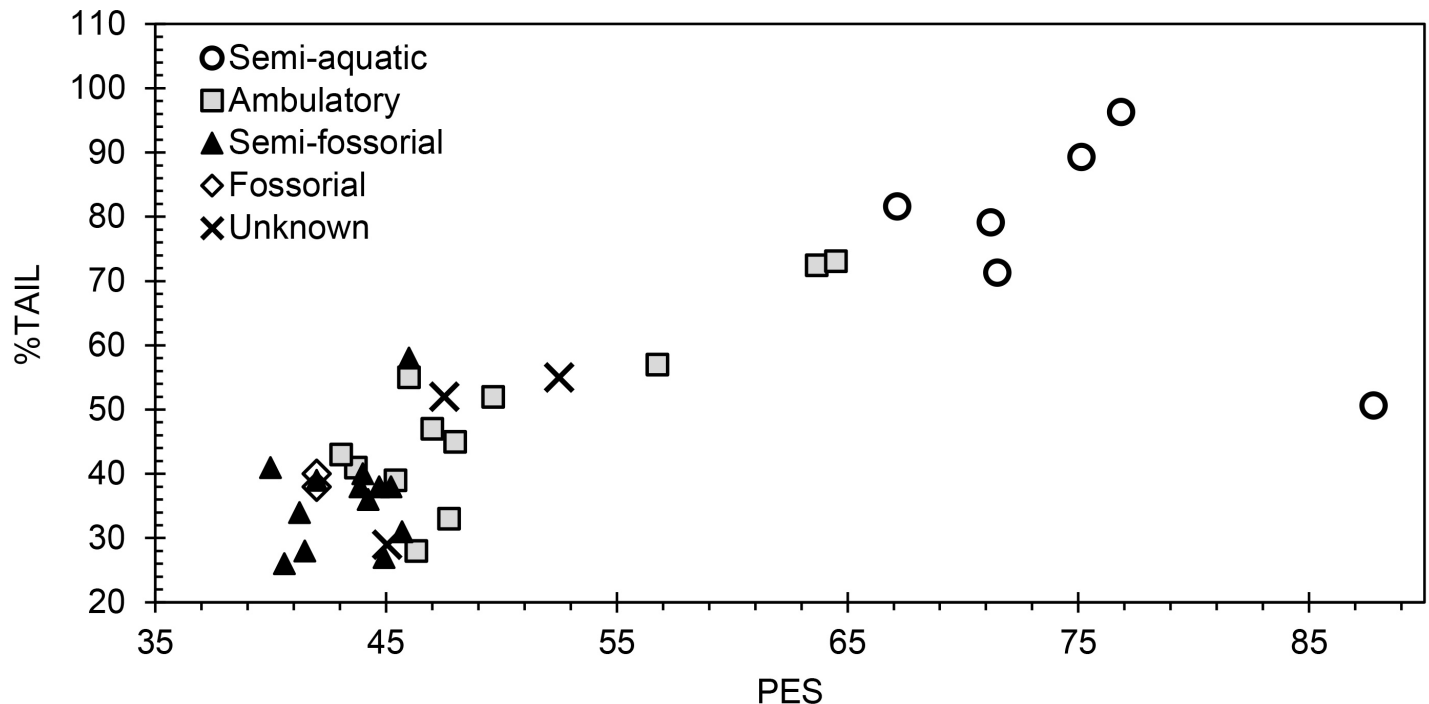
Figure 1. Plot of the indices PES and %TAIL showing separation between semi-aquatic and ambulatory species. The three species of unknown locomotor mode (*C. gracilis, C. endersi, C. thomasi*) plot with ambulatory and semi-fossorial taxa.

among most locomotor groups, however, limits the usefulness of this index for determining locomotory mode for any one species.

2. Humerofemoral index (HFI) represents the length of the humerus as a proportion of the length of the femur. Among soricids, this index decreases from semi-aquatic species to ambulatory, to semi-fossorial, and to fossorial species (Supplementary material Figure 1b), indicating that semi-aquatic species have a longer humerus relative to the femur, whereas more fossorial species have a shorter humerus. This pattern seems counterintuitive in light of the pattern displayed by the IM, but the longer hind limb in semi-aquatic shrews is a result of their relatively longer tibiofibula (see #25, crural index). Overlap among most locomotor groups makes this index most useful for distinguishing semi-aquatic species from semi-fossorial and fossorial species.

3. Metapodial index (FOOT) indicates the relative sizes of the forefeet and hind feet by comparing the lengths of metacarpal III and metatarsal III. Soricids exhibit an increase in the index from semi-aquatic species to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1c), indicating that semi-aquatic species have a relatively longer hind foot (metatarsal III) than other species, particularly the most fossorial species. This index is useful for distinguishing semi-aquatic (low values) and the most fossorial species (high values) from most other species.

4. Distal phalanx length index (CLAW) compares the relative lengths of manual distal phalanx III and pedal distal phalanx III. It increases with increasing fossoriality in rodents (Samuels and Van Valkenburgh 2008), indicating a relatively longer foreclaw than hind claw in more fossorial groups. Among soricids, CLAW clearly distinguishes most semi-fossorial and fossorial species from each other and from other locomotor modes (Supplementary material Figure 1d).

5. Claw length index (CLI) gauges the relative lengths of manual claw III and pedal claw III. CLI increases from semi-aquatic species to ambulatory to semi-fossorial to fossorial species with only minor overlap among locomotor modes (Supplementary material Figure 1e). It clearly distinguishes semi-fossorial and fossorial species from each other and from other locomotor modes, and it also distinguishes semi-aquatic species from most ambulatory species. In this study, only ambulatory *Suncus hututsi* (CLI = 81) and *Sorex cinereus* (86) overlapped with semi-aquatic species, and only semi-fossorial *Congosorex phillipsorum* (107) overlapped with the ambulatory species.

6. Scapulohumeral index (SHI) shows the relative lengths of the scapula and humerus (Supplementary material Figure 1f). This index is typically greater (relatively shorter humerus) for more semi-fossorial and fossorial soricids and lower for ambulatory and aquatic species (Woodman and Gaffney 2014), but its ability to distinguish individual locomotor modes is limited.

7. Brachial index (BI) shows the relative lengths of the humerus and radius. Mean values of this index decrease (relatively shorter radius) among rodents from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Samuels and Van Valkenburgh 2008). The pattern is less apparent among soricids, and ranges of the four modes overlap too extensively for this to be a useful index (Supplementary material Figure 1g).

8. Shoulder moment index (SMI) measures the length of the deltopectoral crest relative to humerus length. In rodents, the index increases from ambulatory to semi-fossorial to semi-aquatic to fossorial species (Samuels and Van Valkenburgh 2008). In contrast, in soricids there is a tendency to increase from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1h). Extensive overlap among groups makes the index useful only for distinguishing some semi-aquatic and some of the most fossorial species.

9. Humeral robustness index (HRI) indicates the relative thickness of the humerus, which increases (more robust humerus) from ambulatory to semi-fossorial to semi-aquatic to fossorial species among rodents (Samuels and Van Valkenburgh 2008). Among soricids, mean values increase from ambulatory to semi-aquatic to semi-fossorial to fossorial species (Supplementary material Figure 1i). Indices for ambulatory and semi-aquatic species overlap extensively, but most semi-fossorial and fossorial species are distinct. Two exceptions are semi-fossorial *Myosorex blarina* (HRI = 9), which has a lower index than expected, and *Nectogale elegans* (12), which has a higher index than is typical for a semi-aquatic species.

10. Humeral rotation lever index (HTI) shows the relative length of the teres tubercle of the humerus. HTI exhibits little difference between semi-aquatic and ambulatory soricids (Supplementary material Figure 1j), but increases substantially with increased semi-fossoriality and fossoriality (Woodman and Gaffney 2014; Woodman and Stabile 2015). Exceptions are *Myosorex varius* (HTI = 18) and *M. zinki* (18), which have lower index values than is typical for semi-fossorial soricids, and *Blarinella quadricaudata* (21), which has a higher index than expected for an ambulatory species.

11. Teres tubercle position index (TTP) measures the position of the teres tubercle along the humerus. TTP exhibits little difference between semi-aquatic and ambulatory soricids, but increases substantially with increased semi-fossoriality and fossoriality (Supplementary material Figure 1k). Exceptions are include *Congosorex phillipsorum* (TTP = 39) and *Myosorex blarina* (41), which have lower index values than expected for semi-fossorial shrews, and ambulatory *Blarinella quadricaudata* (46), with a higher index than expected.

12. Humeral epicondylar index (HEB) is the width of the distal humerus relative to its length. The index typically increases (greater relative width) in mammals with increasing fossoriality (Hildebrand 1985b), and among rodents

HEB increases (broader distal humerus) from ambulatory to semi-fossorial to semi-aquatic to fossorial species ([Samuels and Van Valkenburgh 2008](#)). Among soricids, mean values increase from ambulatory to semi-aquatic to semi-fossorial to fossorial species (Supplementary material Figure 1l). There is extensive overlap in index values among ambulatory, semi-aquatic, and semi-fossorial groups, making this index useful for distinguishing only the more fossorial species.

13. Radial distal width index (RDW) measures the relative width of the proximal end of the radius. Ambulatory and semiaquatic soricids tend to have lower RDW (narrower proximal radius), whereas semi-fossorial and fossorial species tend to have larger RDW (Supplementary material Figure 1m). There is extensive overlap, however, between terrestrial and semiaquatic species and between semi-fossorial and fossorial species.

14. Olecranon length index (OLI) represents the relative length of the olecranon process of the ulna. Semi-fossorial and fossorial mammals generally have a longer olecranon process to accommodate a larger triceps brachii, resulting in larger OLI ([Reed 1951](#); Vizcaino and Milne 2002; [Samuels and Van Valkenburgh 2008](#); [Woodman and Gaffney 2014](#)). Among rodents, OLI increases from ambulatory to semi-fossorial to semi-aquatic to fossorial species ([Samuels and Van Valkenburgh 2008](#)). Among soricids, mean values for this index increase from ambulatory to semi-aquatic to semi-fossorial to fossorial species (Supplementary material Figure 1n). Overlap among groups, however, limits the usefulness of this index for identifying locomotor modes for individual species.

15. Triceps metacarpal outforce index (TMO), like OLI, measures the relative length of the olecranon process. As for OLI, mean values among soricids increase from ambulatory to semi-aquatic to semi-fossorial to fossorial species (Supplementary material Figure 1o), but there is greater separation between semi-aquatic and semi-fossorial species. The one outlier causing overlap between these two groups is semi-fossorial *Myosorex varius* (TMO = 14), which has a lower index than is typical.

16. Triceps claw outforce index (TCO), like OLI and TMO, expresses the relative length of the olecranon process, and it exhibits a pattern similar to those shown by these two indices. Mean values increase from ambulatory to semi-aquatic to semi-fossorial to fossorial species (Supplementary material Figure 1p). Overlap between semi-aquatic and semi-fossorial species is again a result of a lower-than-expected index for semi-fossorial *Myosorex varius* (TMO = 10).

17. Olecranon crest index (OCI) measure of the relative length of the olecranon crest on the olecranon process. Among soricids, there is little difference in TCO between ambulatory and semi-aquatic species, but semi-fossorial and fossorial species exhibit a noticeable increase in the length of the olecranon crest and, therefore, in the index (Supplementary material Figure 1q).

18. Ulnar robustness index (URI) measures the robustness of the ulna. Among rodents, URI increases from ambulatory to semi-fossorial to semi-aquatic to fossorial species ([Samuels and Van Valkenburgh 2008](#)). In soricids, this index exhibits a clear pattern of increasing mean values from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1r). Overlap among groups, however, limits the usefulness of this index for identifying locomotor modes for most individual species. The semi-fossorial *Myosorex varius* (URI = 5), in particular, has a much lower URI than would be predicted.

19. Manual distal phalanx index (%DPL) gauges the length of the manual distal phalanx III. There is little difference in this index between ambulatory and semi-aquatic species, but there are clear distinctions among those two locomotor groups combined, and the semi-fossorial and fossorial species (Supplementary material Figure 1s). The overlap in ranges between ambulatory and semi-fossorial groups results from a lower-than-expected %DPL (and shorter distal phalanx) of semi-fossorial *Blarina shermani* (%DPL = 21) and greater-than-expected index of ambulatory *Myosorex kihaulei* (23).

20. Manual claw index (%CL) is the relative length of manual claw III. Among soricids, %CL shows increases in mean length from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1t). Overlap between the ranges for semi-aquatic and ambulatory species precludes its use for distinguishing individual species having those locomotor modes. In contrast, the ranges for semi-fossorial and fossorial species are distinct from each other and mostly from the other two modes. Exceptions are greater indices than expected for ambulatory *Myosorex geata* (%CL = 42) and *M. kihaulei* (46) and lower indices than expected for semi-fossorial *Congosorex phillipsorum* (39) and *Blarina brevicauda jerryrchoatei* (41).

21. Manual claw support index (%CLS) represents the proportion of manual claw III supported by underlying distal phalanx III. Mean values of this index increase from ambulatory to semifossorial to semi-aquatic to fossorial species (Supplementary material Figure 1u), but the great range of variation among semi-aquatic species and the consequent overlap with other locomotor groups prevents this index from being useful for identifying locomotor modes for individual species.

22. Metacarpal width index (MW3) represents the relative robustness of manual metacarpal III. There is a clear pattern of increase in this index, indicating relatively more robust bones of the manus, from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1v). Overlaps in values between semi-aquatic and ambulatory species and between semi-fossorial and fossorial species limit the usefulness of this index for distinguishing individual modes, but there is clear separation of most species with adaptations for digging.

23. Phalangeal index (PI) shows the relative lengths of the proximal and middle phalanges of manual ray III. Among the soricid species tested, mean indices increased from fossorial to semi-aquatic species to semi-fossorial species to ambulatory species (Supplementary material Figure 1w). The ranges in values of semi-aquatic, semi-fossorial, and ambulatory species overlap extensively. Fossorial species, however, have extremely low PI.

24. Manus proportions index (MANUS) measures the relative length of the proximal phalanx of manual ray III. Among rodents, mean MANUS increases from fossorial to semi-aquatic to semi-fossorial to ambulatory to arboreal and gliding species (Samuels and Van Valkenburgh 2008; Nations *et al.* 2019). In the Soricidae tested, values for MANUS overlap extensively among semi-aquatic, ambulatory, and semi-fossorial modes (Supplementary material Figure 1x). Fossorial species (*i. e.*, *Surdisorex*) exhibit particularly low MANUS values and are distinct from all other species except semi-aquatic *Nectogale elegans* (MANUS = 48) and semi-fossorial *Myosorex blarina* (50).

25. Crural index (CI) measures the relative lengths of the femur and tibiofibula. Among rodents, this index decreases (longer femur, shorter tibiofibula) with increasing fossoriality, but increases in semi-aquatic species (Samuels and Van Valkenburgh 2008). Although shrews have a relatively longer tibiofibula to begin with, they show a similar pattern, with mean values increasing from fossorial to semi-fossorial to ambulatory to semi-aquatic species (Supplementary material Figure 1y). Overlap in range among fossorial, semi-fossorial, and ambulatory modes is relatively large, making locomotor mode difficult to determine for most individual species. Semi-aquatic species are mostly distinct, overlapping only with *Sorex sonomae* (CI = 175) and *S. cinereus* (177), which have large indices for ambulatory species.

26. Pes length index (PES) represents the relative length of the hind foot. Among rodents, this index increases (relatively longer foot) from fossorial to semi-fossorial to ambulatory to semi-aquatic species (Samuels and Van Valkenburgh 2008). Soricids exhibit a similar pattern, and PES is particularly good for distinguishing semi-aquatic species (Supplementary material Figure 1z).

27. Femoral robustness index (FRI) quantifies the breadth of the femur shaft. Among rodents, this index increases (more robust femur) from ambulatory to semi-fossorial to fossorial to semi-aquatic species (Samuels and Van Valkenburgh 2008). Among rodents, mean values for FRI increase from ambulatory to semi-fossorial to semi-aquatic to fossorial species (Supplementary material Figure 1 α). In both groups, there is considerable overlap among locomotor groups, making it difficult to distinguish locomotor mode for a particular species.

28. Femoral epicondylar index (FEB) is the relative distal breadth of the femur. Among rodents, mean FEB is lowest (relatively smaller muscle attachment area) in ambulatory species and is sequentially larger in semi-fossorial, fossorial, and semi-aquatic species (Samuels and Van Valkenburgh 2008). FEB exhibits a slightly different pattern in soricids, increasing from ambulatory to fossorial to semi-fossorial to semi-aquatic species (Supplementary material Figure 1β). There is extensive overlap among groups, but some ambulatory species and some semi-aquatic species are distinguishable.

29. Distal tibiofibular articulation index (DTA) measures the relative width of the articular region for the astragalus. The ranges of this index overlap extensively among groups, rendering this index essentially useless (Supplementary material Figure 1γ).

30. Pedal distal phalanx index (%hDPL) is the relative length of the pedal distal phalanx III. This index shows a clear pattern of increasing (relatively longer distal phalanx) from semi-aquatic to ambulatory to semi-fossorial to fossorial species. Although this index clearly separates semi-fossorial and fossorial locomotor modes. there is considerable overlap between the ranges of semi-aquatic and ambulatory modes (Supplementary material Figure 1δ).

31. Pedal claw index (%hCL) is the relative length of the claw of pedal ray III. Like the pedal distal phalanx index (%hDPL), %hCL shows a clear pattern of increasing (longer claw) mean values from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1ε). Although there is greater overlap among the ranges of the four locomotory modes, there is greater separation of some semi-aquatic species from ambulatory species.

32. Pedal claw support index (%hCLS) is the proportion of the claw of pedal ray III supported by the distal phalanx. Values of this index for ambulatory and semi-aquatic species overlap nearly completely but show higher values (relatively greater support) in semi-fossorial and fossorial species (Supplementary material Figure 1ζ).

33. Tail length index (%TAIL) measures the relative length of the tail. Among shrews, there is a clear pattern of increase in the mean index (greater relative tail length) from fossorial and semi-fossorial species to ambulatory species to semi-aquatic species. There is considerable overlap in ranges among groups, but most semi-aquatic species have longer tails than those in other locomotor modes (Supplementary material Figure 1 η). The longer tail of semi-aquatic species may be used to provide added thrust and to prevent yaw rotation while swimming (Fish 1982, 2000). Overlap in the ranges of tail lengths between ambulatory and semi-aquatic shrews is mostly a result of the relatively short tail of semi-aquatic *Nectogale elegans* (%TAIL = 51) and the relatively long tails of ambulatory *Sorex cinereus* (72) and *S. sonomae* (73). As expected (Shimer 1903), semi-fossorial and fossorial species have the shortest tails, with the exception of semi-fossorial *Congosorex phillipsorum*, which has an unexpectedly long tail (58).

34. Relative robustness index (RR) compares the breadths of the humerus and femur. This index exhibits a

progressive increase in mean values (increasing robustness of the humerus) from semi-aquatic to ambulatory to semi-fossorial to fossorial species (Supplementary material Figure 1θ). There is considerable overlap among ranges of values, making it difficult to distinguish locomotor mode for a particular species.

Mean percentile ranks. A univariate plot of the mean percentile ranks calculated for each of the 52 soricid taxa is shown in Figure 2a. The four locomotor modes mostly form distinct groupings, although there is overlap among some of the modes. As in previous studies of locomotor mode in soricids (Woodman and Gaffney 2014; Woodman and Stabile 2015b; Woodman and Wilken 2019), there is a clear trend of increase in mean percentile rank from ambulatory to semi-fossorial to fossorial taxa. Semi-aquatic species all have relatively low mean ranks, and their range

overlaps that of the lower ranked ambulatory species (*Sorex cinereus, Suncus hututsi, Sorex hoyi*). There is also overlap of one semi-fossorial species (*Cryptotis phillipsii*) with the highest-ranked ambulatory species. In the latter case, the overlap may result from a lack of data, as *C. phillipsii* is represented by only six indices (Table 3). Among the five species of unknown locomotor mode, four species (*Cryptotis endersi, C. gracilis, C. meridensis, C. monteverdensis*) plot with the higher-ranked ambulatory species. The fifth species (*C. thomasi*) plots between the ambulatory species (and *Cryptotis phillipsii*) and the bulk of the semi-fossorial species, but is more closely allied to the latter.

PCA of locomotor indices. In the PCA of 17 locomotor indices, the first three principal components had high eigenvalues and together accounted for >94 % if the variation in the model. Fourteen indices contributed positively
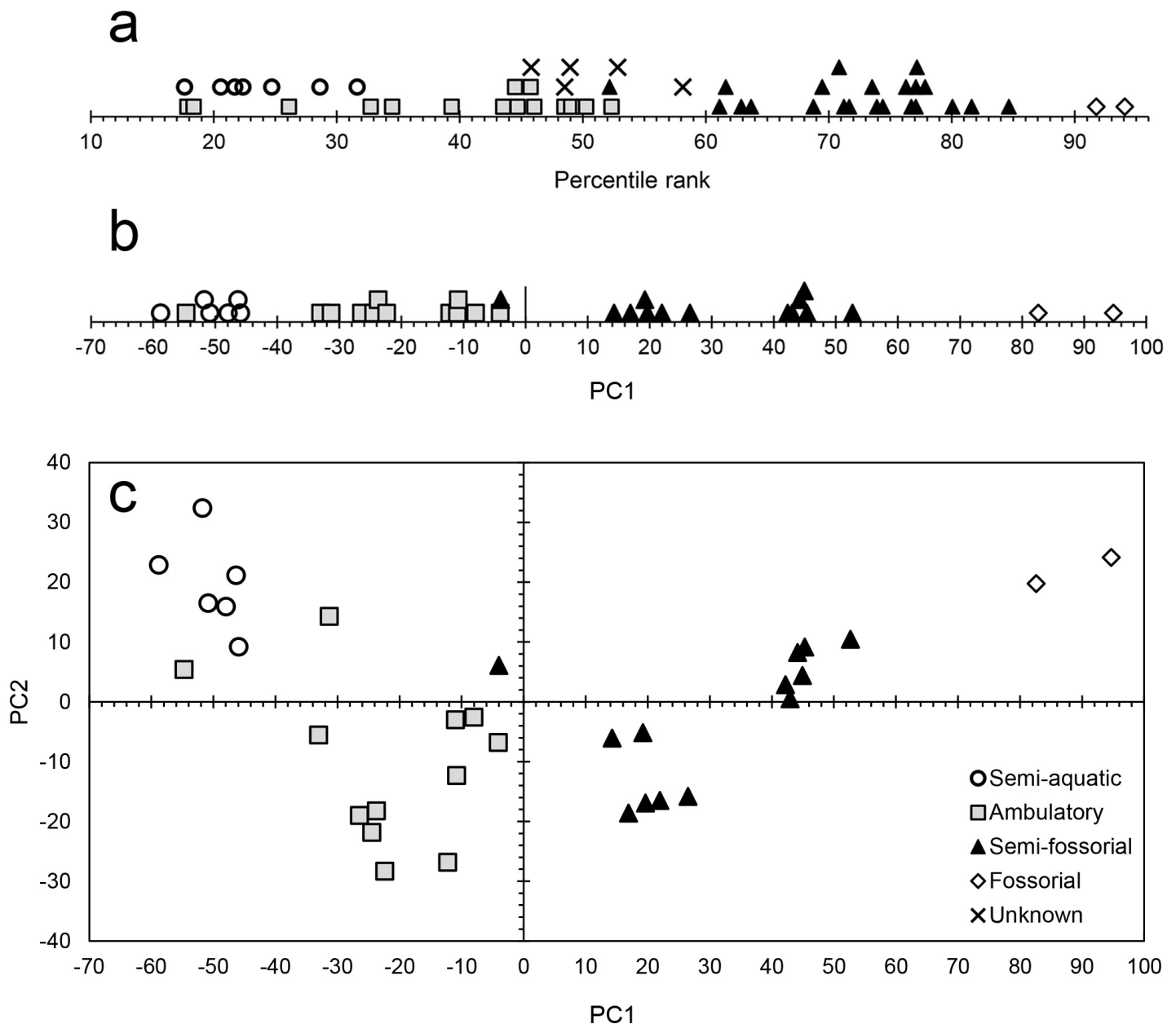

Figure 2. Scaling of locomotory modes: (a) Plot of mean percentile ranks calculated from up to 23 locomotor indices from 52 taxa of soricids, including species of unknown locomotor mode (Table 3). (b) Univariate plot of scores on PC1 (78.8% of variance) from PCA of 17 locomotor indices from 33 taxa (Table 4). (c) Bivariate plot of scores on PC1 and PC2 (12.2%) from a PCA of 17 locomotor indices from 33 taxa (Table 4). Species of unknown locomotor mode were not included in the PCA because of missing data. Key to all symbols is in Figure 2c.

Table 3. Percentile ranks for locomotor indices. See Materials and Methods for abbreviations. Taxa are ordered by increasing mean percentile rank within each *a priori* locomotor mode.

ID	Mode	IM	HFI	FOOT	CLAW	CLI	SMI	HRI	HTI	TTP	HEB	TCO	OCI	URI	%DPL	%CL	MW3	CI	PES	FEB	%hDPL	%hCL	RR	%TAIL	Sum of indices	Number of indices	Mean rank
Sorex albibarbis	SA	40	3	7	9	5	10	38	19	19	32	33	45	28	14	11	20	7	8	20	5	9	19	4	405	23	18
Sorex palustris	SA	40	5	15	19	21	10	13	19	19	19	52	45	28	23	23	20	22	14	8	20	23	3	12	473	23	21
Sorex navigator	SA	20	20	7	28	21	4	38	31	33	40	52	28	28	34	27	20	4	6	8	20	23	5	2	499	23	22
Chimarrogale himalayaca	SA	-	-	20	30	16	58	13	6	54	19	-	-	-	23	5	34	-	-	-	20	5		10	313	14	22
Nectogale elegans	SA	40	20	2	26	9	23	77	19	19	77	-	45	28	-	-	7	11	3	3	5	2	41	37	494	20	25
Neomys fodiens	SA	4	80	20	14	9	48	38	40	54	51	33	10	28	14	11	20	33	14	43	20	23	35	16	658	23	29
Sorex bendirii	SA	40	30	10	16	16	15	54	40	54	43	63	52	52	34	30	20	15	17	20	32	30	35	10	728	23	32
Sorex cinereus	Am	20	48	12	5	12	4	13	19	4	11	33	10	28	14	11	7	22	22	60	20	14	11	10	410	23	18
Suncus hututsi	Am	-	-	63	2	2	-	-	-	-	-	-	-	-	2	2	34	-	-	-	20	9		31	165	9	18
Sorex hoyi	Am	20	48	32	26	33	15	13	25	23	13	33	28	28	23	23	7	37	25	43	20	14	46	25	600	23	26
Crocidura religiosa	Am	-	30	-	-	-	96	2	2	8	4	-	-	-	-	-	-	-	-	-	100	-	-	20	262	8	33
Sorex sonomae	Am	40	48	22	49	30	10	54	21	33	40	33	45	52	34	34	34	30	22	33	32	32	51	14	793	23	34
Crocidura suaveolens	Am	56	70	-	-	-	75	13	8	4	6	-	3	52	-	-	-	67	-	100	-	-		18	472	12	39
Cryptotis merus	Am	-	65	80	37	28	69	38	10	19	36	-	-	-	7	23	34	81	67	88	32	36	16	61	827	19	44
Cryptotis parvus	Am	68	80	51	40	40	23	38	40	38	36	7	21	52	27	34	20	70	53	78	36	45	38	88	1023	23	44
Cryptotis tropicalis	Am	68	70	44	7	40	58	54	52	54	19	7	21	52	7	23	34	59	39	100	36	30	78	76	1028	23	45
Crocidura olivieri	Am	-	85	-	-	-	94	38	4	19	2	-	-	-	-	-	-	-	-	-	100	-	-	24	366	8	46
Cryptotis merriami	Am	92	20	56	49	26	48	38	40	23	32	52	48	76	23	14	34	74	78	88	32	30	35	51	1059	23	46
Myosorex cafer	Am	-	65	80	51	51	69	54	25	8	11	-	-	-	41	36	41	-	39	100	50	45	62	45	873	18	49
Cryptotis nigrescens	Am	92	20	88	26	26	33	38	52	33	32	33	55	76	27	27	50	93	81	88	39	45	27	47	1128	23	49
Myosorex geata	Am	-	30	83	37	53	75	38	31	33	32	-	-	-	50	52	64	-	53	78	73	73	16	29	900	18	50
Blarinella quadricaudata	Am	96	20	80	56	44	33	54	67	77	47	52	21	52	43	43	41	44	31	60	50	64	46	35	1156	23	50
Myosorex kihaulei	Am	-	48	71	42	56	69	38	31	38	32	-	-	-	64	68	50	-	42	78	73	77	24	41	942	18	52
Cryptotis phillipsii	SF	-	-	-	-	-	23	65	71	54	57	-	-	-	-	-	-	-	-	-	-	-		43	313	6	52
Blarina shermani	SF	-	-	51	56	58	-	-	-	-	-	-	-	-	50	59	64	-	-	-	57	59		96	550	9	61
Congosorex phillipsorum	SF	-	48	95	67	42	94	65	79	33	57	-	-	-	64	43	64	-	53	70	66	77	68	24	1109	18	62
Myosorex varius	SF	56	80	63	63	67	79	54	52	56	32	33	62	28	73	73	73	56	78	88	82	86	57	55	1446	23	63
Blarina brevicauda jknoxjonesi	SF	-	-	-	-	-	-	-	-	-	-	-	-	-	64	68	64	-	-	-	50	36		100	382	6	64
Myosorex blarina	SF	80	50	98	58	70	94	38	56	42	47	63	66	90	75	75	77	78	100	70	95	100	8	51	1581	23	69
Cryptotis mexicanus	SF	-	-	-	-	-	48	65	77	85	72	-	-	-	70	70	77	-	-	-	-	-		61	625	9	69
Blarina peninsulae	SF	-	-	71	77	79	83	77	56	67	68	89	69	90	64	59	64	-	-	-	50	45		96	1204	17	71
Blarina carolinensis	SF	68	80	41	65	67	79	77	67	67	70	93	62	76	68	64	64	85	97	60	57	50	81	100	1638	23	71
Blarina hylophaga	SF	-	-	-	-	-	-	-	-	-	-	-	-	-	68	64	73	-	-	-	65	64		96	430	6	72
Blarina brevicauda talpoides	SF	80	65	90	70	72	58	77	71	67	62	96	83	90	64	55	73	93	97	43	65	59	73	88	1691	23	74
Blarina brevicauda jerryrchoatei	SF	92	65	88	60	63	58	94	75	77	68	89	86	76	64	50	73	100	67	60	65	50	84	96	1700	23	74
Cryptotis celaque	SF	-	65	56	84	86	58	94	85	85	81	67	76	90	80	58	86	-	78	20	82	73	86	72	1562	21	74
Cryptotis oreoryctes	SF	20	90	32	88	81	48	94	96	96	89	89	90	76	93	95	86	48	78	33	86	86	89	71	1754	23	76
Cryptotis mam	SF	80	65	39	91	77	69	94	90	96	85	63	76	76	89	89	86	52	67	43	82	89	95	71	1764	23	77
Cryptotis matsoni	SF	-	100	24	81	84	83	94	94	98	94	-	-	-	84	80	-	-	53	33	82	73	73	80	1310	17	77
Cryptotis mccarthyi	SF	-	-	39	77	60	33	94	83	77	81	-	-	-	89	89	93	-	-	-	91	91		82	1079	14	77
Myosorex zinki	SF	-	93	93	81	93	75	94	52	54	74	-	-	-	77	84	80	-	89	60	86	86	57	61	1389	18	77
Cryptotis magnimanus	SF	-	-	-	-	-	33	94	83	88	89	-	-	-	-	-	-	-	-	-	-	-		80	467	6	78
Cryptotis eckerlini	SF	-	85	27	95	88	94	77	79	85	94	100	100	100	84	93	93	-	67	20	73	80	76	71	1681	21	80
Cryptotis lacertosus	SF	100	20	51	86	74	48	96	94	96	98	89	97	97	93	93	100	63	97	20	95	95	100	75	1877	23	82
Cryptotis cavatorculus	SF	-	-	63	93	95	94	77	90	79	85	89	79	76	95	82	93	-	-	-	91	73			1354	16	85
Surdisorex norae	F	56	98	80	98	98	100	100	98	96	100	89	97	97	100	100	100	96	89	60	100	95	92	71	2110	23	92
Surdisorex polulus	F	-	90	100	100	100	100	100	100	100	98	-	-	-	98	98	100	-	89	70	98	100	97	55	1693	18	94
Cryptotis endersi	UN	-	48	-	77	91	23	38	79	42	57	-	-	-	-	-	-	-	39	33	32	23	24	35	641	14	46
Cryptotis gracilis	UN	-	30	34	37	40	69	65	67	77	68	-	-	-	50	50	50	30	28	33	57	59	49	29	922	19	49
Cryptotis meridensis	UN	44	48	-	14	47	48	54	52	67	49	52	45	52	41	39	41	41		60	-	-	65	71	930	19	49
Cryptotis monteverdensis	UN	-	-	-	-	-	33	54	52	77	62	-	-	-	-	-	-	-	-	-	-	-		39	317	6	53
Cryptotis thomasi	UN	-	48	71	49	49	48	65	75	58	-	-	-	-	41	45	50	-	67	70	50	59	59	84	988	17	58

to the first principal component (PC1), which alone represented nearly 79 % of the variation. PC1 was most strongly influenced by four variables: CLI, CLAW, %CL, and negatively weighted %TAIL (Table 4). The second principal component (PC2) represented %TAIL and constituted about 12 % of variation. The third principal component (PC3), accounting for <4 % of the variation, was most influenced by PI, SHI, and negatively weighted FOOT.

In a plot of factor scores on PC1 (Figure 2b), *a priori* locomotory groups are mostly separated along PC1, with semi-aquatic species having the lowest scores, and ambulatory, semi-fossorial, and fossorial groups having increasingly greater scores, respectively. Ambulatory species exhibit two distinct clusters along this axis. The ambulatory group with the lower scores includes species of *Sorex* and *Cryptotis*, and the group with the larger scores includes *Cryptotis parvus*, *Blarinella quadricaudata*, and species of *Myosorex*. There are also two clusters of semi-fossorial species. The group with the lower scores includes species of *Myosorex* and *Blarina*, and that with the larger scores is comprised of *Myosorex zinki* and species of *Cryptotis*. The bimodal patterns within the ambulatory and semi-fossorial groups indicate that species in different genera have somewhat different suites of characters associated with a particular locomotor mode (Woodman and Wilken 2019).

One exception to the general pattern is ambulatory *Sorex cinereus*, which plotted with semi-aquatic species. Its low score on PC1 resulted from its low CLI and %CL (relatively short foreclaw) and high %TAIL (relatively long tail). Another exception is semi-fossorial *Congosorex phillipsorum*, which plotted with the ambulatory species. Its low score also resulted from its low CLI, %CL, and %DPL (short foreclaw and distal phalanx relative to other semi-fossorial species) and high %TAIL (long tail). The unique combination of ambulatory and semi-fossorial traits in *C. phillipsorum* previously was discussed in detail in Woodman and Stabile (2015b).

In a plot of factor scores on PC1 and PC2 (Figure 2c), the second factor axis separates fossorial species and most semi-aquatic species from ambulatory and semi-fossorial species. It also separates subgroupings of semi-fossorial shrews with semi-fossorial *Cryptotis* and *Myosorex zinki* plotting along the positive portion of PC2, whereas *Blarina* and other semi-fossorial *Myosorex* plot along the negative part of the axis.

The third factor axis (not shown) provides no discrimination among the *a priori* locomotor groupings. Within the ambulatory group, however, the low scores of the three species of *Myosorex* separate them from ambulatory taxa in other genera. Within the semi-fossorial group, PC3 separates three subgroupings that consist of three species of *Myosorex* (low scores); most taxa of *Blarina*, *Congosorex phillipsorum*, and *Cryptotis celaque* (intermediate scores); and *Blarina carolinensis* and four species of *Cryptotis*.

DFA of locomotor indices. Plots of scores from the DFA of 17 locomotor indices show clear separation of the four

Table 4. Variable loadings and taxon scores from a PCA of 17 locomotor indices from 33 taxa of soricids (*Figure* 2b, 2c).

Variable loadings			
Variable	PC 1	PC 2	PC 3
CLI	0.575	0.030	-0.359
CLAW	0.459	0.270	0.188
%CL	0.353	0.203	-0.103
%DPL	0.212	0.170	0.001
SHI	0.182	0.084	0.382
HEB	0.180	0.158	0.297
HTI	0.163	0.095	0.239
%hCL	0.135	0.014	-0.121
FOOT	0.120	-0.253	-0.359
TTP	0.108	0.068	0.204
SMI	0.106	0.011	-0.168
%hDPL	0.104	0.027	-0.112
MW3	0.086	0.036	0.026
HRI	0.054	0.028	0.038
PI	-0.009	-0.098	0.422
MANUS	-0.018	-0.055	0.301
%TAIL	-0.347	0.855	-0.192
Eigenvalue	1682.600	260.054	80.536
% variance	78.801	12.179	3.772

Taxon scores on PC1		
Taxon	Mode	PC 1
Sorex albibarbis	SA	-58.812
Sorex navigator	SA	-51.795
Chimarrogale himalayaca	SA	-50.854
Sorex palustris	SA	-47.955
Sorex bendirii	SA	-46.349
Neomys fodiens	SA	-45.918
Sorex cinereus	Am	-54.719
Sorex hoyi	Am	-33.033
Sorex sonomae	Am	-31.319
Cryptotis nigrescens	Am	-26.47
Cryptotis merus	Am	-24.479
Cryptotis merriami	Am	-23.749
Cryptotis tropicalis	Am	-22.373
Cryptotis parvus	Am	-12.229
Myosorex geata	Am	-10.973
Myosorex cafer	Am	-10.832
Blarinella quadricaudata	Am	-8.0403
Myosorex kihaulei	Am	-4.0992
Congosorex phillipsorum	SF	-3.981
Myosorex varius	SF	14.246
B. brevicauda jerryrchoatei	SF	16.908
Myosorex blarina	SF	19.219
Blarina carolinensis	SF	19.619
B. brevicauda talpoides	SF	21.945
Blarina peninsulae	SF	26.478
Cryptotis celaque	SF	42.205
Myosorex zinki	SF	42.961
Cryptotis mam	SF	44.161
Cryptotis lacertosus	SF	44.912
Cryptotis oreoryctes	SF	45.322
Cryptotis eckerlini	SF	52.677
Surdisorex norae	F	82.629
Surdisorex polulus	F	94.698

locomotor groups along combinations of the first three canonical variates (Table 5; Figure 3). Fossorial species are strongly separated along CV1, and the other three locomotor groups are separated from each other along CV2 (Figure 3a). Semi-aquatic and semi-fossorial species overlap along CV3, but are separated from both ambulatory and fossorial species (Figure 3b).

The *post hoc* classification matrix indicates that 100 % of taxa were correctly classified into their *a priori* locomotor groups by the DFA (Table 5). In the jack-knifed classification, five species were misclassified as belonging to a locomotor mode other than their *a priori* mode. Ambulatory *Sorex cinereus* and *Cryptotis tropicalis* were both misclassified as being semi-aquatic; ambulatory *Myosorex cafer* was misclas-
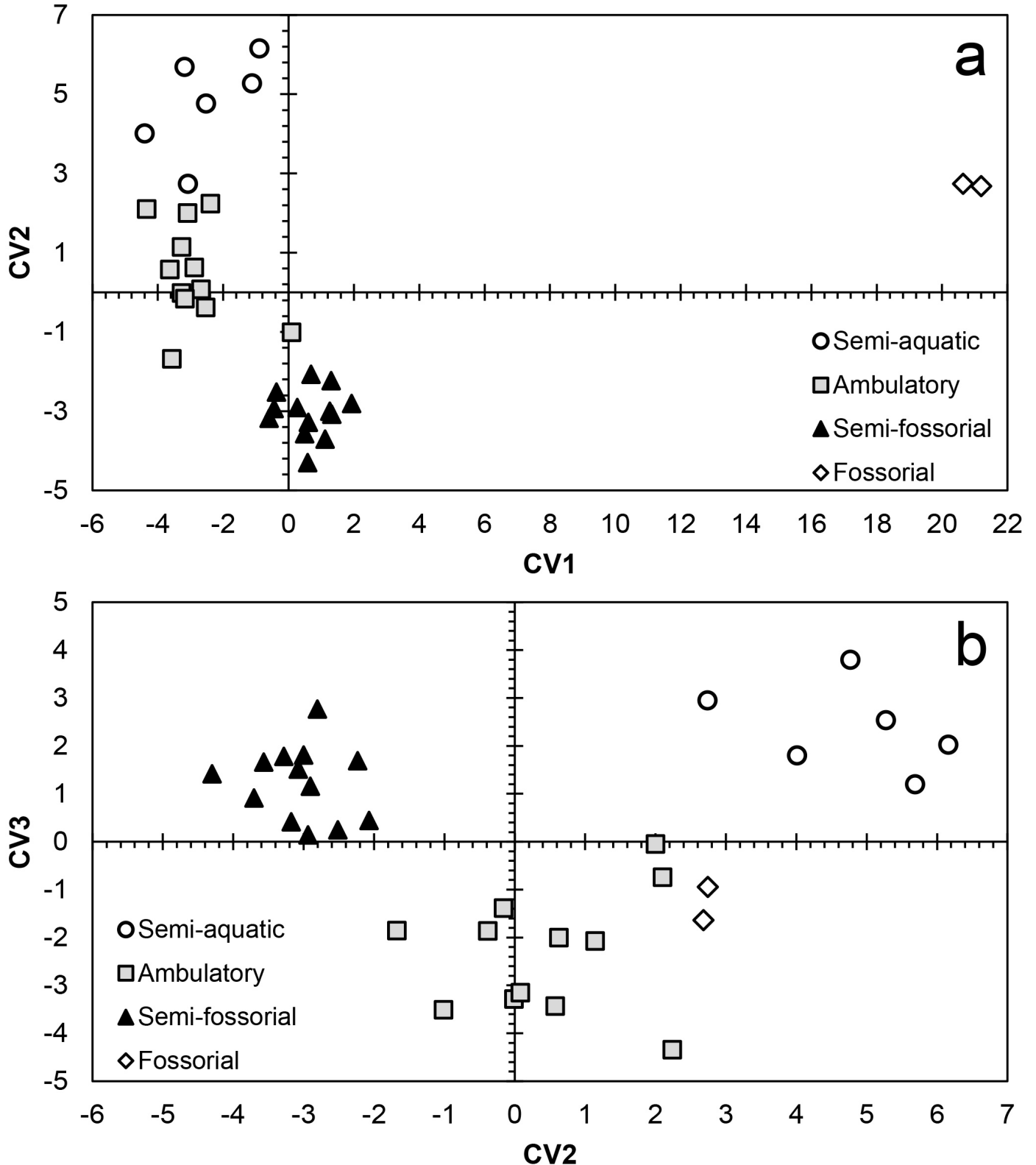
Figure 3. Plots of scores a) on CV1 and CV2 and b) on CV2 and CV3 from a DFA of 17 locomotor indices from 33 species (Table 5).

Table 5. Variable loadings of 17 locomotor indices and classification matrix. A and B classification matrices from a DFA of 17 locomotor indices from 33 taxa of soricids (Figure 3).

	Variable loadings		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
%hCL	-1.139	-0.730	0.569
MANUS	-0.576	-0.302	0.386
%hDPL	-0.373	0.184	-0.186
HEB	-0.345	0.158	-0.129
CLI	-0.281	-0.240	0.150
MW3	-0.162	0.000	0.522
TTP	-0.050	0.346	0.197
CLAW	-0.010	-0.057	0.098
%TAIL	0.031	0.050	0.060
SHI	0.103	-0.354	0.360
PI	0.176	0.069	-0.420
HTI	0.235	0.106	-0.190
%DPL	0.340	-0.476	-0.223
FOOT	0.351	0.068	-0.266
%CL	0.687	0.579	-0.336
SMI	0.717	0.369	-0.023
HRI	1.096	0.754	-0.737

	SA	Am	SF	F	Total
A					
Classification matrix (100% correct classification)					
Semi-aquatic (SA)	6	0	0	0	6
Ambulatory (Am)	0	12	0	0	12
Semi-fossorial (SF)	0	0	13	0	13
Fossorial (F)	0	0	0	2	2
Total	6	12	13	2	33
B					
Jackknifed classification matrix (81.8% correct classification)					
Semi-aquatic (SA)	6	0	0	0	6
Ambulatory (Am)	3	8	1	0	12
Semi-fossorial (SF)	0	2	11	0	13
Fossorial (F)	0	0	0	2	2
Total	9	10	12	2	33

sified as semi-fossorial; and semi-fossorial *Myosorex blarina* and *M. varius* were misclassified as being ambulatory.

PCA of species having unknown locomotor mode. In the PCA carried out in an attempt to classify four species whose locomotor mode was unknown, eight of 10 locomotor indices contributed positively to the first principal component (PC1). PC1 accounted for more than 77 % of the variation in the model (Table 6), and it was most strongly influenced by three variables: CLI, CLAW, and negatively weighted %TAIL. As in the 17-variable model, *a priori* locomotory groups are mostly separated along this axis, from semi-aquatic spe-

cies with the lowest scores to ambulatory to semi-fossorial to fossorial groups having increasingly higher scores (Figure 4). As in the 17-variable model, semi-fossorial species plotted in two primary clusters with the same compositions as in that model. In contrast, ambulatory species were more cohesive. Ambulatory *Sorex cinereus*, which plotted with semi-aquatic species, and semi-fossorial *Congosorex phillipsorum*, which plotted with ambulatory species, again proved to be exceptions to the general pattern.

Among the species of uncertain locomotor mode, *Cryptotis gracilis* and *C. meridensis* plotted within the distribution of ambulatory species; *C. thomasi* occurred between the ambulatory species (and *Congosorex phillipsorum*) and semi-fossorial species; and *C. endersi* plotted with the *Blarina* grouping of semi-fossorial species rather than with the *Cryptotis* grouping of semi-fossorial species (Figure 4, Table 6).

DFA of species of unknown locomotor mode. Plots of scores from the DFA of 10 locomotor indices exhibit similar patterns as those from the 17-variable model, although the separations among locomotor groups are generally not as clear (Table 7; Figure 5). Fossorial species are again strongly separated along CV1, whereas the other three locomotor groups are separated from each other along a combination of CV1 and CV2 (Figure 5a). Semi-aquatic and semi-fossorial species overlap along CV3, but are separated from both ambulatory and fossorial species (Figure 6b).

The *post hoc* classification matrix had a correct classification rate of nearly 97 % (Table 7). The only misclassification was ambulatory *Sorex sonomae*, which was misclassified as semi-aquatic. Among the species of uncertain locomotor mode, *Cryptotis gracilis* was classified as semi-aquatic, *C. meridensis* and *C. thomasi* as ambulatory, and *C. endersi* as semi-fossorial (Figure 5; Table 7). In multivariate space, *C. gracilis* actually plots by itself away from the *a priori* locomotor groups, although it is physically closest to semi-aquatic species. Similarly, *C. endersi* plots in its own multivariate space between the ambulatory and semi-fossorial groups of species, but it is physically closest to the semi-fossorial group.

Discussion

As noted previously, there is considerable variation among soricids in skeletal characteristics that are typically associated with locomotion (Woodman and Gaffney 2014; Woodman and Stabile 2015b; Woodman and Wilken 2019). Such variation suggests that individual species' abilities to use various substrates are more nuanced and diverse (*e. g.*, Mendes-Soares and Rychlik 2009; Tapisso
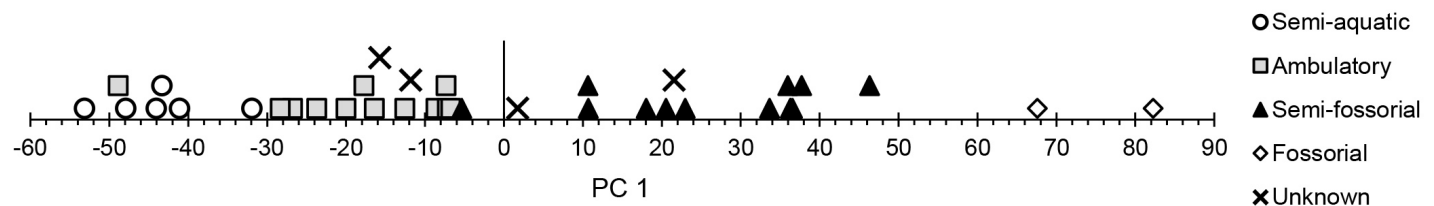
Figure 4. Plot of scores on PC1 from a PCA of 10 locomotor indices from 33 species of known locomotor mode and four species of uncertain locomotor mode (Table 6).
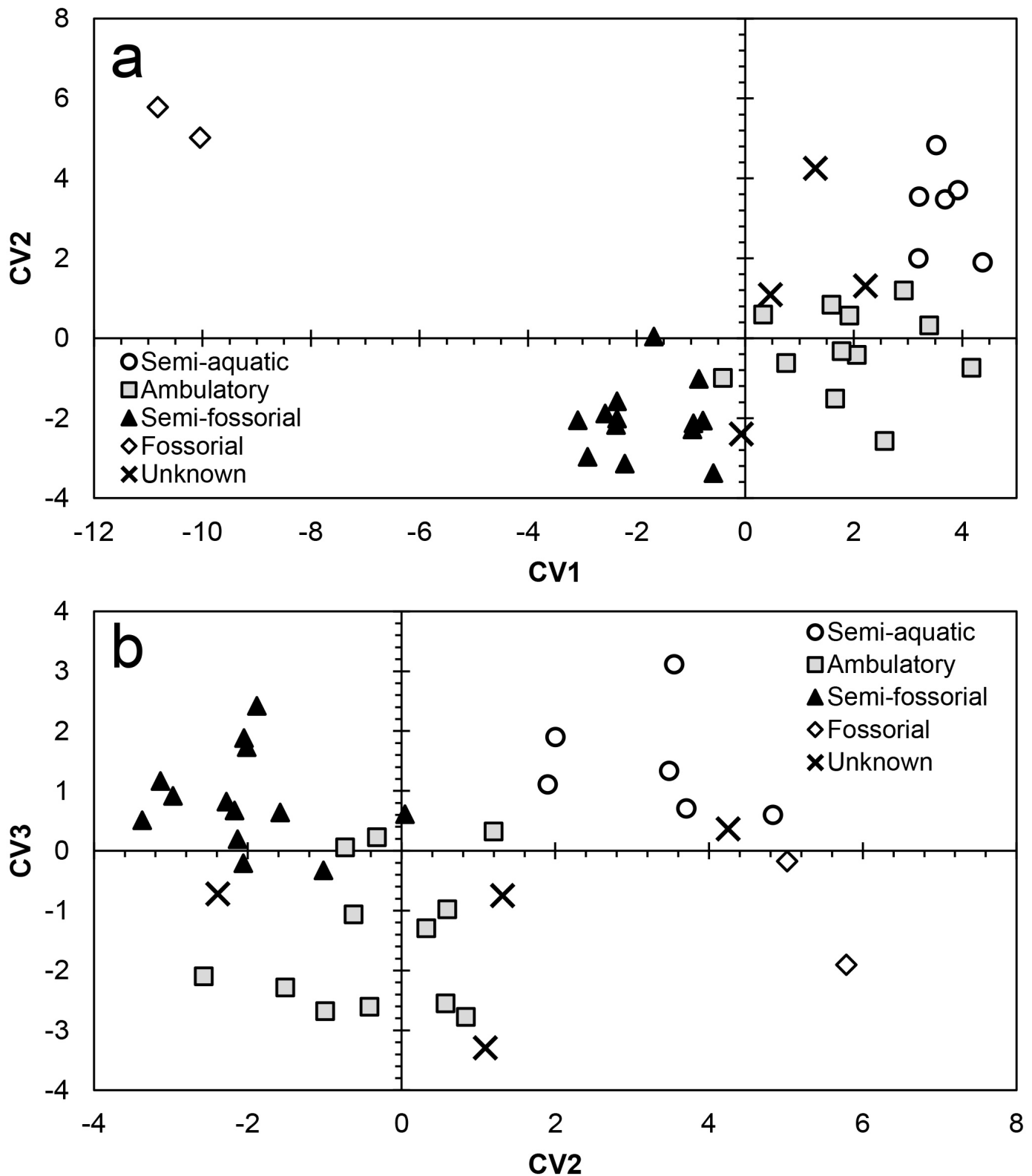
Figure 5. Plots of scores a) on CV1 and CV2 and b) on CV2 and CV3 from a DFA of 10 locomotor indices from 33 species of known locomotor mode and four species of uncertain locomotor mode (Table 7).

_et al._ 2013). Rather than representing discrete categories permitted by classification, locomotor modes exhibit diverse ranges in morphology that are not always easily defined or distinguished. This observation suggests that not all morphological traits associated with a particular locomotor mode—or the indices used to gauge them—

are necessarily adaptive. Instead, phylogeny may control or at least contribute to some traits. Hence, a morphological trait that varies among species or groups of species within a particular locomotor mode may not be employed, or may not be employed to the same extent or purpose, in each species.

Morphological diversity may also reflect the reality that individuals are not entirely restricted in their use of substrate or in their locomotor behavior by either the possession or lack of specialized traits. Morphological traits that are related to particular modes of locomotion may simply reflect enhanced abilities that permit a species to specialize to a greater extent in certain behaviors that, given a shrew's high metabolism, are most likely related to foraging strategies. This likely accounts for the close correspondence between the numbers of species that appear specialized for ambulatory, semi-fossorial, and semi-aquatic locomotor behaviors (Hutterer 1985) and those that specialize on foraging for epigeal, hypogeal, and aquatic prey (Churchfield 1990). Despite this, ambulatory species can be vigorous scratch-diggers despite the lighter bone structure of their arms and their relatively short foreclaws (Chamberlain 1929). Ambulatory *Cryptotis parvus*, *Sorex cinereus*, and *S. hoyi*, and the semi-aquatic *S. palustris* are reported to excavate subterranean tunnels of varying lengths, depths, and degrees of complexity (Cahn 1937; Davis and Joeris 1945; Sorenson 1962; Tuttle 1964; Beneski and Stinson 1987). Similarly, non-aquatic shrews, such as ambulatory *Sorex araneus*, *S. cinereus*, *S. fumeus*, and *S. minutus*, have been documented to be capable swimmers (Dagg and Windsor 1972; Hanski 1986). Based on the diversity of species and numbers of individuals that have been found in the digestive tracts of various freshwater fishes (*e. g.*, Huish and Hoffmeister 1947; Hodgson 1986; Moore and Kenagy 2004; Jung *et al.* 2011; Lisi *et al.* 2013), a number of additional ambulatory and semi-fossorial species readily take to water.

There is also no reason to assume that any particular species cannot possess traits that enhance its abilities for more than one locomotor mode. A ready example in the Talpidae is the *Condylura cristata*, which possesses numerous anatomical traits associated with fossorial locomotion, but which is also an active swimmer and may forage dominantly on hypogeal or aquatic prey, depending on where it lives (Petersen and Yates 1980).

Despite the foregoing caveats, a number of generalizations can be suggested regarding the external and skeletal morphological traits marking common, generalized locomotor modes in soricids.

Ambulatory shrews. Most species of shrews are ambulatory and have short legs and a moderately long tail (Hutterer 1985). The foreclaws and hind claws are short (%DPL, %CL, %hDPL, %hCL), the manual distal phalanges are typically somewhat shorter than the pedal distal phalanges (CLAW), although the claws on the fore feet and hind feet may be of approximately the same length (CLI). This means the foreclaw is less supported by the underlying distal phalanx (%CLS) than the hind claw (%hCLS). This relatively unspecialized body form is assumed to be the basic plan for soricids from which more specialized swimming, climbing, and digging forms evolved, but such singular directionality remains to be substantiated. Regardless, the generalized body morphology of ambulatory shrews represents the

Table 6. Variable loadings and taxon scores from a PCA of 10 locomotor indices from 33 taxa of known locomotor mode and four species for which locomotor mode is uncertain (Figure 4).

Variable loadings	
Variable	**PC 1**
CLI	0.674
CLAW	0.538
SHI	0.201
HTI	0.188
TTP	0.131
SMI	0.121
HRI	0.057
%CLS	0.049
FEB	-0.008
%TAIL	-0.378
Eigenvalue	1144.07
% variance	77.244

Taxon scores on PC1 with classification of unknowns

Taxon	**Mode**	**PC 1**
Sorex albibarbis	SA	-53.13
Sorex navigator	SA	-47.943
Sorex bendirii	SA	-44.065
Sorex palustris	SA	-43.347
Neomys fodiens	SA	-41.121
Nectogale elegans	SA	-31.949
Sorex cinereus	Am	-48.893
Sorex sonomae	Am	-28.365
Sorex hoyi	Am	-26.805
Cryptotis nigrescens	Am	-23.709
Cryptotis merus	Am	-20.019
Cryptotis merriami	Am	-17.725
Cryptotis tropicalis	Am	-16.444
Myosorex geata	Am	-12.561
Cryptotis parvus	Am	-8.6015
Myosorex cafer	Am	-7.3472
Blarinella quadricaudata	Am	-7.1599
Myosorex kihaulei	Am	-6.7505
Congosorex phillipsorum	SF	-5.3339
Myosorex varius	SF	10.644
Myosorex blarina	SF	10.691
Blarina brevicauda jerryrchoatei	SF	18.017
Blarina carolinensis	SF	20.531
Blarina brevicauda talpoides	SF	22.948
Cryptotis lacertosus	SF	33.638
Myosorex zinki	SF	35.979
Cryptotis mam	SF	36.293
Cryptotis celaque	SF	36.328
Cryptotis oreoryctes	SF	36.544
Cryptotis matsoni	SF	37.737
Cryptotis eckerlini	SF	46.334
Surdisorex norae	F	67.586
Surdisorex polulus	F	82.263
Cryptotis gracilis	unknown	-15.742
Cryptotis meridensis	unknown	-11.824
Cryptotis thomasi	unknown	1.7374
Cryptotis endersi	unknown	21.566

model to which more specialized shrews are compared and contrasted ([Woodman and Gaffney 2014](); [Woodman and Stabile 2015b](); [Woodman and Wilken 2019]()).

Semi-aquatic shrews. Externally, semi-aquatic shrews typically possess long tails relative to other shrews, and there may be a dorsal; dorsal and ventral; or dorsal, ventral, and lateral keels of stiff hairs. The tail probably functions like that of a muskrat (*Ondatra zibethicus*) tail, by providing a small amount of forward thrust, but more importantly, by preventing the animal from yawing ([Fish 1982]()). In contrast with the muskrat, which swims with just the hind limbs ([Fish 1984]()), however, semi-aquatic and terrestrial shrews typically paddle by alternately stroking the front and hind limbs ([Jackson 1928](); [Dagg and Windsor 1972](); [Mendes-Soares and Rychlik 2009]()). There is also a fringe of stiff hairs on the lateral edges of the digits of the hands and feet. In some species, notably *Nectogale*, the digits are partly webbed ([Hutterer 1985]()). The foreclaws and hind claws are generally short (%DPL, %CL, %hDPL, %hCL), the foreclaws and manual distal phalanges typically are somewhat shorter than the hind claws and pedal distal phalanges (CLI, CLAW). The underlying manual distal phalanx, however, supports a greater proportion of the foreclaw than is typical in, for example, ambulatory shrews (%CLS). Semi-aquatic shrews typically have long hind limbs and hind feet relative to other shrews. Proportionally, the femur averages 28 % (range 27 to 29 %, $n = 6$ species), tibiofibula 50 % (44 to 52), and metacarpal III 22 % (19–26) of their combined length. This is in contrast to ambulatory shrews in which the femur averages 33 % (range 29 to 36 %, $n = 9$ species), tibiofibula 50 % (49 to 52), and metacarpal III 17 % (15 to 19) of their combined length, and to semi-fossorial and fossorial shrews, in which the femur averages 35 % (range 33 to 36 %, $n = 9$ species), tibiofibula 50 % (48 to –52), and metacarpal III 15 % (14 to 16) of their combined length. Moreover, the humerus of semi-aquatic shrews tends to be long in proportion to the femur (HFI), so much of the length of hind limb is a result of the proportionally longer tibiofibula (CI) and hind foot (PES).

Skeletally, the emphasis on the hind limbs in semi-aquatic shrews may be further illustrated by the relatively broad epicondyles of the femur (FEB), from which the plantaris, gastrocnemius, and the extensor digitorum longus muscles originate. The long bones of the limbs and manus bones are not particularly robust (HRI, RDW, URI) and are generally similarly proportioned to those of ambulatory shrews, with the exception of the femur (FRI), which can be considerably more robust than those of ambulatory and even semi-fossorial shrews (RR). The humerus has relatively small muscle attachment areas in the short deltopectoral crest (SMI) and small teres tubercle of the humerus (HTI), but can have a relatively broad epicondylar region (HEB) relative to ambulatory shrews. The olecranon process of the ulna tends to be slightly longer than in ambulatory shrews (OLI, TMO, TCO), suggesting the transmission of greater force from the triceps brachii muscle, although the insertion for that muscle (OCI)

Table 7. Variable loadings from a DFA of 10 locomotor indices from 33 taxa of known locomotor mode and four species for which locomotor mode is uncertain (Figure 5).

Variable loadings			
Variable	Axis 1	Axis 2	Axis 3
TTP	0.177	-0.034	0.285
FEB	0.123	0.734	-0.021
SHI	0.006	-0.339	0.262
%TAIL	-0.016	0.060	0.041
CLAW	-0.016	-0.091	0.015
%CLS	-0.017	-0.338	0.238
CLI	-0.052	-0.102	0.045
HTI	-0.145	0.339	-0.388
SMI	-0.217	0.579	-0.086
HRI	-0.448	1.388	-0.681

	SA	Am	SF	F	Total	Unknowns
Classification matrix (96.97% correct classification)						
Semi-aquatic (SA)	6	0	0	0	6	1
Ambulatory (Am)	1	11	0	0	12	2
Semi-fossorial (SF)	0	0	13	0	13	1
Fossorial (F)	0	0	0	2	2	0
Total	7	11	13	2	33	4

is no larger than in ambulatory shrews and the ulna averages slightly less breadth, therefore rendering it somewhat less resistant to bending and shearing stresses.

Semi-fossorial and fossorial shrews. In contrast to semi-aquatic shrews, the emphasis in semi-fossorial and fossorial shrews is on the changes in the morphology of the forelimb, particularly the humerus, ulna, and manus ([Woodman and Morgan 2005](); [Woodman and Stephens 2010](); [Woodman and Gaffney 2014](); [Woodman and Stabile 2015a](), [2015b](); [Woodman and Timm 2016](); [Woodman and Wilken 2019](); [Woodman *et al.* 2019]()). Among species in these two locomotor groups, morphological changes can appear to be gradual and progressive (*e. g.*, Figs. 2, 3, 5), but traits do not necessarily co-vary in the same way or to the same degree (*e. g.*, Figs. 1, 4, 6).

Externally, semi-fossorial and fossorial shrews are typically characterized by having small (or absent) pinnae, short tails, broadened forefeet, and elongated and broadened foreclaws (%DPL, %CL). They also have elongated and broadened hind claws (%hDPL, %hCL), although not to the same degree as the foreclaws (CLI,CLAW), and there is increasing support from the underlying distal phalanx as the claws increase in size (%CLS, %hCLS). There may be a tendency to reduce the overall length of the hind limbs relative to the forelimbs (IM) and the hind feet relative to the fore feet (FOOT), but, in contrast, there is a definite trend toward reduction of the length of the humerus relative to that of the femur (HFI).

Skeletally, the long bones of the limbs and manus bones become increasingly robust (HRI, RDW, URI, FRI, RR), particularly relative to those of ambulatory shrews. The humerus shortens, but becomes much broadened with enlarged teres tubercle (HTI), deltopectoral crest (SMI), epicondyles (HEB), and other regions involved in muscle attachment.

The olecranon process of the ulna elongates and broadens relative to the functional arm (OLI, TMO, TCO), allowing for the transmission of much greater force from the triceps brachii muscle, and the insertion for that muscle on the olecranon process (OCI) greatly increases. In contrast, the breadth of the distal epicondyles of the femur (FEB) are only slightly enlarged relative to those of ambulatory shrews, and they are generally smaller than those of semi-aquatic shrews.

Locomotory modes of the "unknowns". *Cryptotis gracilis* and members of the *C. thomasi* group of species (*C. endersi, C. meridensis, C. monteverdensis, C. thomasi*) have defied easy characterization of their locomotory modes based on external and skeletal characters (Supplementary material Figure 1). These shrews all have relatively long foreclaws and hind claws and associated distal phalanges, like semi-fossorial shrews, but the claws are not particularly broad, and their tails in some cases (*e. g.*, *C. gracilis*, *C. endersi*, *C. monteverdensis*) are rather long, as in ambulatory shrews. Previous analyses of these species showed most of them to plot between the ambulatory and semi-fossorial shrews, with *C. gracilis* somewhat more semi-fossorial (Woodman and Timm 2016; Woodman 2019; Woodman and Wilken 2019).

In the current analyses, most of these species remain ambiguous, in part because of a continued lack of data regarding relevant characters, particularly for the rare *C. endersi* and *C. monteverdensis* (Pine *et al.* 2002; Woodman and Timm 2016). *Cryptotis gracilis* plots out as ambulatory based on mean percentile ranks (Figure 1; Table 2) and PCA (Figure 5; Table 5), but it was classified by DFA (Figure 6; Table 6) as semi-aquatic. In reality, it is separate from all other species in multivariate space between the ambulatory and semi-aquatic groups of species. It is unlikely to be truly semi-aquatic, as it plots as an ambulatory species for two of the more relevant characteristics of semi-aquatic species, represented by the locomotor indices PES and %TAIL (Figure 1; Table 2), and because it lacks more obvious external characteristics of typical semi-aquatic shrews, such as the fringes of short hairs lining the digits and tail.

The four members of the *C. thomasi* group all plot as ambulatory, semi-fossorial, or intermediate between those two modes. *Cryptotis meridensis* is consistently ambulatory, and *C. monteverdensis* plots as ambulatory based on mean percentile rank, the only analysis in which it could be included. *Cryptotis endersi* plots as ambulatory in the mean percentile rank analysis, and it is classified as semi-fossorial based on both PCA and DFA, but it really plots as somewhat intermediate between both groups (Figure 6; Table 6). In contrast, *C. thomasi* plots as intermediate between the ambulatory and semi-fossorial groupings in both the mean percentile rank analysis and the PCA, but was classified as ambulatory in the DFA.

All five of these species occupy high elevation habitats in southern Central America and Andean South America, and they may represent one or more unique locomotor adaptations or combinations of adaptations for foraging in high-elevation forests and páramo-like habitats.

1. Of 34 locomotor indices tested in this study, 23 (IM, HFI, FOOT, CLAW, CLI, SMI, HRI, HTI, TTP, HEB, TCO, OCI, URI, %DPL, %CL, MW3, CI, PES, FEB, %hDPL, %hCL, RR, %TAIL) proved effective for discriminating one or more of the four *a priori* locomotor groups (ambulatory, semi-aquatic, semi-fossorial, fossorial).

2. Among three analyses of locomotor indices, percentile ranking was the only analysis that permitted the inclusion of all 52 taxa, including species of unknown locomotor mode. The lack of data for some taxa, however, results in uneven morphological comparisons across taxa, and there was considerable overlap of some locomotor groups, particularly the semi-aquatic and ambulatory groups.

In contrast, PCA and DFA require complete datasets, and the largest sample I could compile was 17 indices from 33 taxa, which excluded the unknowns in this study. The first principal component (PC1) from PCA distinguished the major (and some minor) locomotor groupings, but there was overlap between locomotor groups that makes it difficult to identify locomotor mode for some species. Plotting PC1 and PC2 provided greater discrimination among groups, but some overlap remains.

DFA classification of *a priori* locomotor groups provided the best discrimination among locomotor groups, but requires complete datasets.

3. Classification of four species of unknown locomotor mode using PCA and DFA of 10 locomotor indices provided contrasting results. One species was classified as ambulatory by PCA and semi-aquatic by DFA; one species was classified as ambulatory by both analyses; one species was classified as intermediate between ambulatory and semi-fossorial by PCA and semi-fossorial by DFA; and one species was classified as semi-fossorial by both. The lack of complete datasets clearly hampered the analyses, but there is also strong indication that some of these species have unique combinations of morphological traits that are not easily explained by comparison with other shrews, even those in the same genus.

4. Results here confirm that variation in skeletal traits typically exists within defined locomotor modes. Such variation probably results in part from the reality that 1) most species (and individuals) are not restricted to a single mode, but engage in a variety of locomotor behaviors to varying degrees; 2) the traits that we can measure or otherwise gauge are not necessarily adaptive for a particular locomotor mode; and 3) seemingly similar traits may be employed in different ways by different species or populations.

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Literature cited

Beneski, J. T., Jr., and D.W. Stinson. 1987 . *Sorex palustris*. Mammalian Species 296:1–6.

Cahn, A. R. 1937. The mammals of Quetico Provincial Park of Ontario. Journal of Mammalogy 18:19–30.

Chamberlain, E. B. 1929. Behavior of the least shrew. Journal of Mammalogy 10:250–251.

Churchfield, S. 1990. The Natural History of Shrews. Comstock Publishing Associates. Ithaca, U.S.A.

Dagg, A. I., and E. E. Windsor. 1972. Swimming in northern terrestrial mammals. Canadian Journal of Zoology 50:117–139.

Davis, W. B., and L. Joeris. 1945. Notes on the life history of the little short-tailed shrew. Journal of Mammalogy 26:136–138.

Eisenberg, J. F. 1981. The Mammalian Radiations. The University of Chicago Press. Chicago, U.S.A.

Elissamburu, A., and L. De Santis. 2011. Forelimb proportions and fossorial adaptations in the scratch-digging rodent Ctenomys (Caviomorpha). Journal of Mammalogy 92:683–689.

Fish, F. E. 1982. Function of the compressed tail of surface swimming muskrats (*Ondatra zibethicus*). Journal of Mammalogy 63:591–597.

Fish, F. E. 1984. Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). Journal of Experimental Biology 110:183–201.

Fish, F. E. 2000. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches 73:683–698.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologica Electronica 4:1–9.

Hanski, I. 1986. Population dynamics of shrews on small islands accord with the equilibrium model. Biological Journal of the Linnean Society 28:23–36.

Hildebrand, M. 1985a. Walking and running. Pp. 38–57, *in* Functional Vertebrate Morphology (Hildebrand, M., D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, U.S.A.

Hildebrand, M. 1985b. Digging of quadrupeds. Pp. 89–109, *in* Functional Vertebrate Morphology (Hildebrand, M., D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). Belknap Press, Cambridge, U.S.A.

Hodgson, J. R. 1986. The occurrence of small mammals in the diets of largemouth bass (*Micropterus salmoides*). Jack-Pine Warbler 64:39–40.

Hopkins, S. S. B., and E. B. Davis. 2009. Quantitative morphological proxies for fossoriality in small mammals. Journal of Mammalogy 90:1449–1460.

Howell, H. B. 1930. Aquatic mammals. Their adaptations to life in the water. Charles C. Thomas. Springfield, USA.

He, K., et al. 2015. Molecular phylogeny supports repeated adaptation to burrowing within small-eared shrews, genus of *Cryptotis* (Eulipotyphla, Soricidae). Plos One DOI:10.1371/journal.pone.0140280 October 21.

He, K., et al. 2021. Mitogenome and comprehensive phylogenetic analyses support rapid diversifications among species groups of small eared shrews genus *Cryptotis* (Mammalia: Eulipotyphla: Soricidae). Zoological Research 42:739–745.

Huish, M. T., and D. F. Hoffmeister. 1947. The short-tailed shrew (*Blarina*) as a source of food for the green sunfish. Copeia 1947:198.

Hutterer, R. 1985. Anatomical adaptations of shrews. Mammal Review 15:43–55.

Jackson, H. H. T. 1928. A taxonomic review of the American long-tailed shrews (genera *Sorex* and *Microsorex*). North American Fauna 51:1–238.

Jung, T. S., et al. 2011. American pygmy shrew, *Sorex hoyi*, consumed by an arctic grayling, *Thymallus arcticus*. Canadian Field Naturalist 125:255–256.

Kirk E. C., P. 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.

Lemelin P. 1999. Morphological correlates of substrate use in didelphid marsupials: Implications for primate origins. Journal of Zoology 247:165–175.

Lisi, P. J., et al. 2013. Episodic predation of mammals by stream fishes in a boreal river basin. Ecology of Freshwater Fish 23:622–630

Mendes-Soares, H., and L. Rychlik. 2009. Differences in swimming and diving abilities between two sympatric species of water shrews: *Neomys anomalus* and *Neomys fodiens* (Soricidae). Journal of Ethology 27:317–325

Moore, J. W., and G. J. Kenagy. 2004. Consumption of shrews, *Sorex* spp., by Arctic grayling, *Thymallus arcticus*. The Canadian Field Naturalist 118:111–115.

Nations, J. A., et al. 2019. A simple skeletal measurement effectively predicts climbing behaviour in a diverse clade of small mammals. Biological Journal of the Linnean Society 128:323–336.

Petersen, K. E., and T. L. Yates. 1980. *Condylura cristata*. Mammalian Species 129:1–4.

Pine, R. H., N. Woodman, and R. M. Timm. 2002. Rediscovery of Enders's small-eared shrew, *Cryptotis endersi* (Insectivora: Soricidae), with a redescription of the species. Mammalian Biology 67:372 –377.

Price, M. V. 1993. A functional–morphometric analysis of forelimbs in bipedal and quadrupedal heteromyid rodents. Biological Journal of the Linnean Society 50:339–360.

Reed, C. A. 1951. Locomotion and appendicular anatomy in three soricoid insectivores. American Midland Naturalist 45:513–670.

Samuels, J. X., and B. Van Valkenburgh. 2008. Skeletal indicators of locomotor adaptations in living and extinct rodents. Journal of Morphology 269:1387–1411.

Sargis, E. J. 2002. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. Journal of Morphology 253:10–42.

Sargis, E. J., et al. 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., et al. 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.

Sorenson, M. W. 1962. Some aspects of water shrew behavior. American Midland Naturalist 68:445–462.

Tapisso, J. T., et al. 2013. Ecological release: swimming and diving behavior of an allopatric population of the Mediterranean water shrew. Journal of Mammalogy 94:29–39.

Tuttle, M. D. 1964. Observation of *Sorex cinereus*. Journal of Mammalogy 45:148.

Vizcaino, S. F., and N. Milne. 2002. Structure and function in armadillo limbs (Mammalia: Xenarthra: Dasypodidae). Journal of Zoology 257:117–127.

Wahab, M. F. A., et al. 2020. Taxonomic assessment of the Malayan water shrew *Chimarrogale hantu* Harrison, 1958 and reclassification to the genus *Crossogale*. Mammalian Biology 100:399–409.

Woodman, N. 2019. Three new species of small-eared shrews, genus *Cryptotis*, from El Salvador and Guatemala (Mammalia: Eulipotyphla: Soricidae). Special Publication of the Museum of Texas Tech University 72:1–46.

Woodman, N., and S. A. Gaffney. 2014. Can they dig it? Functional morphology and degrees of semi-fossoriality among some American shrews (Mammalia, Soricidae). Journal of Morphology 275:745–759.

Woodman, N., and J. P. J. 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 F. A. Stabile. 2015a. Variation in the myosoricine hand skeleton and its implications for locomotory behavior (Eulipotyphla: Soricidae). Journal of Mammalogy 96:159–171.

Woodman, N., and F. A. Stabile. 2015b. Functional skeletal morphology and its implications for locomotory behavior among three genera of mysoricine shrews (Eulipotyphla: Soricidae). Journal of Morphology 276:550–563.

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. 2016. A new species of small-eared shrew in the *Cryptotis thomasi* species group from Costa Rica (Mammalia: Eulipotyphla: Soricidae). Mammal Research 62:89–101 (published online 27 August 2016).

Woodman, N., and A. T. Wilken. 2019. Comparative functional skeletal morphology among three genera of shrews: implications for the evolution of locomotory behavior in the Soricinae (Eulipotyphla: Soricidae). Journal of Mammalogy 100:1750–1764.

Woodman, N., A. T. Wilken, and S. Ikram. 2019. See how they ran: morphological and functional aspects of skeletons from ancient Egyptian shrew mummies (Eulipotyphla: Soricidae: Crocidurinae). Journal of Mammalogy 100:1199–1210.

Appendix 1

New specimens examined and measured.

Specimens used for postcranial measurements (long bones of the appendicular skeleton).

Soricinae: Soricini

Sorex cinereus (*n* = 20).   New Hampshire: Carroll Co.: Bartlett Experimental Forest (USNM 600625, 600626, 600628, 600629, 600630, 600631, 600633, 600634, 600635, 600637, 600638, 600639, 600642, 600643, 600646, 600648, 600649, 600650, 600651, 600653).

Sorex hoyi (*n* = 8).   New Hampshire: Carroll Co.: Bartlett Experimental Forest (USNM 600742, 600743, 601995, 601996, 601999, 602000, 602001, 602001).

Sorex sonomae (*n* = 4). Oregon: Douglas Co.: 24.4 km S, 6 km W of Elkton (USNM 560070). Lane Co.: 0.4 km N, 18.5 km W Lorane (USNM 561167); 3 km N, 19.5 km W Lorane (USNM 561184); 1.6 km S, 5.2 km W McKenzie Bridge (USNM 556750).

Sorex bendirii (*n* = 19). California: 271162; Washington: (USNM 250616, 558133, 563996, 563997, 563998, 564000). Oregon: (USNM 556532, 556546, 556554, 556558, 556572, 556583, 557725, 557726, 557734, 561125, 561127, 563080).

Sorex navigator (*n* = 10). Colorado: (USNM 485409, 485411, 485413, 515058, 515059, 515060). Oregon: (USNM 556780). Washington: (USNM 241998, 241999, 242003).

Sorex albibarbis (*n* = 6). CANADA: Nova Scotia: 30 mi E of Trenton (USNM 530829). USA: New Hampshire: (USNM 515061, 515062, 600745); Maine: (USNM 600798). West Virginia: Pocahontas Co.: Allegheny Mountains (USNM 569120).

Sorex palustris (*n* = 4). CANADA: Ontario: Quetico Provincial Park, side Lake (FMNH 44529). USA: Michigan: Schoolcraft Co.: Seney National Wildlife Refuge (USNM 530501, 551769). Minnesota: Cook Co.: Greenwood Lake, 47° 59' 55" N, -90° 8' 30" W (FMNH 163321). Wisconsin: Douglas Co.: 13 mi W of Salon Springs (USNM 600003).

Soricinae: Nectogalini

Chimarrogale himalayica (*n* = 2). TAIWAN: 6.5 km S of Wu Sheh (USNM 358140); Mupin (USNM 358141).

Nectogale elegans (*n* = 2). CHINA: Sichuan: ca. 17 km SSE of Shimian (USNM 254812, 574296).

Neomys fodiens (*n* = 4). FRANCE: Bourgogne: Is-Sur-Tille (USNM 233967). SWEDEN: Lapland (USNM 1058). SPAIN: Cantabria: Camargo, Barrio El Juyo, Igollo, 60 m (FMNH 153665, 153666).

Specimens used for measurements of the manus and pes.

Soricinae: Soricini

Ambulatory/terrestrial:

Sorex cinereus (*n* = 25).   New Hampshire: Carroll Co.: Bartlett Experimental Forest (USNM 601840, 601841, 601842, 601843, 601846, 601847, 601849, 601850, 601855, 601858, 601859, 601862, 601863, 601925); Coos Co.: Lake Umbagog National Wildlife Refuge (USNM 568177, 568178, 568179, 568180, 568184, 568186, 568189, 568190, 568191, 568195); Strafford Co.:1 mi N, 7 mi W of Rochester (USNM 600627).

Sorex hoyi (*n* = 18). CANADA: New Brunswick: Mt. Carleton Provincial Park (USNM 553310, 553311, 553312, 553313, 553314, 553315, 553316, 553317, 553318, 553319, 553320, 553321). USA: New Hampshire: Carroll Co.: Bartlett Experimental Forest (USNM 601998, 602001, 602004); Coos Co.: Bretton Woods (USNM 294773); Lake Umbagog National Wildlife Refuge (USNM 568192, 568198)

Sorex sonomae (*n* = 8). USA: California: Del Norte Co.: Crescent City (USNM 68166, 68167); Gasquet (USNM 91551, 91552, 91553). Humboldt Co.: Eureka (USNM 47090, 63520, 63521).

Semi-aquatic:

Sorex bendirii (*n* = 39). California: Del Norte Co.: Crescent City (USNM 97601, 97603, 97604, 97605, 97606, 97607); Gasquet (USNM 91555, 91552, 91553). Oregon: Morrow Co.: Camas Prairie, Mount Hood, eastern base of Cascade Mountains (USNM 79964). Clatsop Co.: Astoria (USNM 89019). Lane Co.: 4.4 km N, 6.8 km E Blue River (USNM 556565); Eugene (USNM 204482); Vida (USNM 204480). Lincoln Co.: Otis (USNM 264398). Linn Co.: 9.2 km N, 1.2 km W McKenzie Bridge (USNM 556534, 556535, 557728). Multnomah Co.: Larch Mountain, T1N, R5E, sec. 36 (USNM 294066); Portland (USNM 140852). Washington: Grays Harbor Co.: Oakville (USNM 231022, 231024, 231025). Klickitat Co.: Trout Lake (USNM 230235). Lewis Co.: 8 mi W of Chehalis (USNM 230230, 230233, 230234, 230236); Toledo (USNM 231023). Pacific Co.: Ilwaco (USNM 230231, 230237). Pierce Co.: Mount Rainier, Ohanapecosh Springs (USNM 232844, 232845); Mount Rainier, 1 mi W Rainier Park, Meslers Ranch (USNM 233593, 233594, 233595); Pullalup (USNM 227155); 6 mi S of Tacoma (USNM 231019). Snohomish County: Oso (USNM 234503). Wahkiakum Co.: Cathlamet (USNM 230232). Yakima Co.: Yakima Indian Reservation (USNM 226862).

Sorex navigator (*n* = 22). Colorado: Boulder Co.: Boulder (USNM 112064); Gold Hill (USNM 35671, 73862, 73863). Gilpin Co.: Black Hawk, Dory Hill Pond (USNM 112048, 112049). Larimer Co.: Elkhorn (USNM 148154). Montrose Co.: Maverick Canyon, 2 mi N Coventry (USNM 149968, 149969, 149970, 149972). Washington: Pierce Co.: Mount Rainier (USNM 232843, 232846, 233093, 233222, 233590, 233591, 233592). Skamania Co.: Mount St. Helens (USNM 90751). Snohomish Co.: Suiattle River, Chiwawa Mountain Fork (USNM 229887). Yakima Co.: Yakima Indian Reservation (USNM 226860, 226861).

Sorex albibarbis (*n* = 24). CANADA: New Brunswick: 5.3 km N, 3.5 km N Riverside-Albert (USNM 528207); Mount Carleton Provincial Park (USNM 553303, 553304, 553305, 553306, 553307, 553308). Nova Scotia: Digby (USNM 150056, 150068); Halifax (USNM 288005). 30 km E of Tren-

ton (530829). Q<small>UEBEC</small>: St. Rose (USNM 150079). USA: M<small>AINE</small>: Mount Katahdin (USNM 117980, 117981). Somerset Co.: N shore of Russell Pond (USNM 569772). York Co.: Lyman, Massabesic Experimental Forest (USNM 600798). N<small>EW</small> H<small>AMP</small>-<small>SHIRE</small>: Coos Co.: Bretton Woods (USNM 294622, 294772); Lake Umbagog National Wildlife Refuge (USNM 568193). Carroll Co.: Bartlett Experimental Forest (USNM 600745). T<small>ENNESSEE</small>: Sevier Co.: Great Smoky Mountain National Park (USNM 294409). V<small>ERMONT</small>: Rutland Co.: Mondon (USNM 250165). V<small>IR</small>-<small>GINIA</small>: Bath Co.: Little Back Creek (USNM 512048).

Sorex palustris (*n* = 15). M<small>ICHIGAN</small>: Marquette Co.: Michigamme (USNM 243724, 243725); Schoolcraft Co.: Seney National Wildlife Refuge (USNM 514244, 514382, 524518, 524519, 530499, 530500, 530501, 551765, 551766, 551768, 551770, 551773). M<small>INNESOTA</small>: Cook Co.: Greenwood Lake, 47º 59' 55" N, - 90º 8' 30" W (FMNH 163321).

S<small>ORICINAE</small>: N<small>ECTOGALINI</small>

Semi-aquatic:

Chimarrogale himalayica (*n* = 4). CHINA: Yunnan: West Slope of Likiang (USNM 240167). Taiwan: Nan-T'Ou: Meichi (USNM 358139, 358140, 358141).

Nectogale elegans (*n* = 4). CHINA: Qinghai: Bei Zha Forestry Station (USNM 449155). Sichuan: Mupin (USNM 254812); ca. 17 km SSE Shimian (USNM 574296). INDIA: Sikkim: Lachung (USNM 260768).

Neomys fodiens (*n* = 20). FRANCE: B<small>OURGOGNE</small>: Cote-D'Or Department, Is-Sur-Tille (USNM 498756, 498757, 498759, 498760, 498761). SWEDEN: Lapland (USNM 1058); U<small>PPSALA</small>: Uppsala (USNM 84909). Locality unknown (USNM 12330). SWITZERLAND: B<small>ERN</small>: Meiringen (USNM 85938, 85939, 85941, 85942, 85943, 85944, 85946, 85947, 85949). N<small>EUCHATEL</small>: Neuchatel (USNM 12329). S<small>ANKT</small> G<small>ALLEN</small>: Sitterwald (USNM 86497). V<small>AUD</small>: Lausanne (USNM 104486).

C<small>ROCIDURINAE</small>:

Ambulatory/terrestrial:

Suncus hututsi (*n* = 1). BURUNDI: Bururi Province: Bururi Commune, 2170 m: Bururi Forest Reserve, Ruhinga Hill. (FMNH 155925).

Appendix 2

A priori locomotor classifications of soricid species.

C<small>ROCIDURINAE</small>:

<u>Ambulatory:</u>

Crocidura olivieri

Crocidura religiosa

Crocidura suaveolens

Suncus hututsi

M<small>YOSORICINAE</small>:

<u>Ambulatory:</u>

Myosorex cafer

Myosorex geata

Myosorex kihaulei

<u>Semi-fossorial:</u>

Congosorex phillipsorum

Myosorex blarina

Myosorex varius

Myosorex zinki

<u>Fossorial:</u>

Surdisorex norae

Surdisorex polulus

S<small>ORICINAE</small>: B<small>LARINELLINI</small>

<u>Ambulatory:</u>

Blarinella quadricaudata

S<small>ORICINAE</small>: B<small>LARININI</small>

<u>Ambulatory:</u>

Cryptotis parvus

Cryptotis tropicalis

Cryptotis merriami

Cryptotis merus

Cryptotis nigrescens

<u>Semi-fossorial:</u>

Blarina brevicauda jerryrchoatei

Blarina brevicauda jknoxjonesi

Blarina brevicauda talpoides

Blarina carolinensis

Blarina hylophaga

Blarina peninsulae

Blarina shermani

Cryptotis cavatorculus

Cryptotis celaque

Cryptotis eckerlini

Cryptotis lacertosus

Cryptotis magnimanus

Cryptotis mam

Cryptotis matsoni

Cryptotis mccarthyi

Cryptotis mexicanus

Cryptotis oreoryctes

Cryptotis phillipsii

Unknown:

Cryptotis endersi

Cryptotis gracilis

Cryptotis meridensis

Cryptotis monteverdensis

Cryptotis thomasi

SORICINAE: NECTOGALINI

Semi-aquatic:

Chimarrogale himalayica

Nectogale elegans

Neomys fodiens

Soricinae: Soricini

Ambulatory:

Sorex cinereus

Sorex hoyi

Sorex sonomae

Semi-aquatic:

Sorex albibarbis

Sorex bendirii

Sorex navigator

Sorex palustris