Functional Morphology of the Forelimb of North American Shrews

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Figure 1. The small bones of *Blarina* make it challenging to obtain accurate measurements.

Introduction

Shrews (Mammalia: Soricidae) occupy a wide range of locomotory behaviors including climbing, swimming, and burrowing. Within the sister genera *Blarina* and *Cryptotis*, primary locomotory behaviors are ambulatory (running) and fossorial (burrowing). These two locomotory modes are facilitated by anatomical specializations, such as broad, robust bones, reoriented muscle attachment sites, and rotational moments (Woodman and Stabile, 2015). Banfield (1974) stated *B. brevicauda* is the most fossorial North American shrew, but how does *B. brevicauda's* and other *Blarina* species' anatomical specializations compare to the skeletal modifications of other known burrowers like *Cryptotis*? To assess the degree of burrowing capability present in different shrew species we examined postcranial morphology with PCA and mean percentile ranking.

Materials and Methods

We measured 71 individuals representing 4 species of the genus Blarina. Due to their size (Fig. 1), individual bones are difficult to handle and precisely measure. We used photographs of postcrania (Fig. 2) and x-ray imaging (Fig. 3) to overcome this challenge. We used a Kevex X-Ray Source and Varian Image Viewing and Acquisition software (VIVA) in the Division of Fishes to obtain images of the fore and hind feet from skin specimens (Fig. 4). ImageJ scientific photo analysis software (Schneider et al., 2012) to measure the rays and postcranial bones (humerus, femur, tibiofibula, radius, ulna; Fig. 5). Measurements (mm) were recorded to the nearest 0.01 mm. These measurements were then used to create 33 indexes that describe different aspects of functional anatomy related to locomotory behavior. These indices were compared to similar measures from 14 species of *Cryptotis* reported by Woodman and Gaffney (2014). We combined these indices to analyze morphological variation related to digging ability in two ways: (1) we carried out principle component analysis (PCA) of the 33 indices and interpreted the first factor axis as a relative scale of fossorial adaptation (Fig. 6); (2) we calculated mean percentile ranks for each species and used those ranks as a scale of digging ability (Fig. 7).

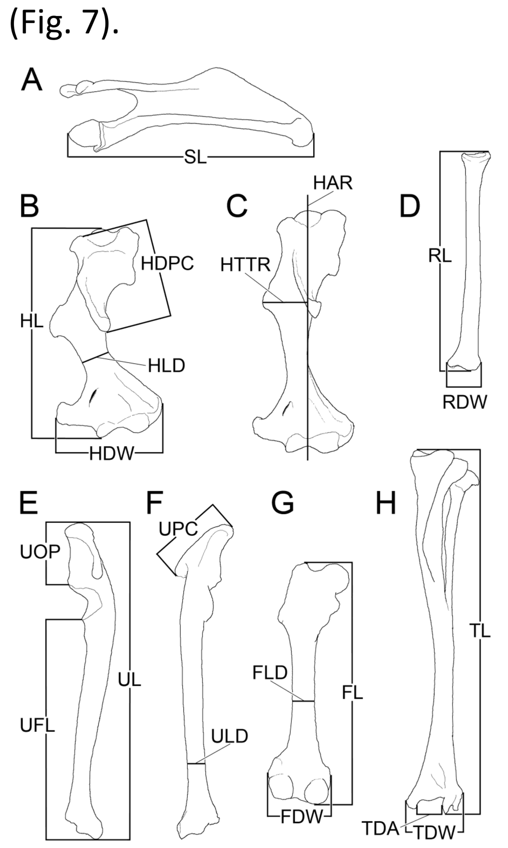
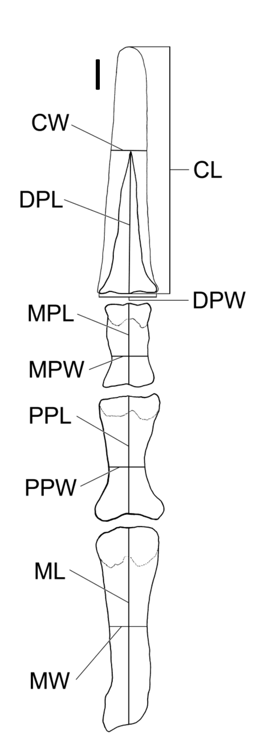


Figure 5. Measurements from digital photographs of postcrania and x-rays of feet: **a**, scapula; **b**, humerus; **c**, humerus; **d**, radius; **e**, ulna; **f**, ulna; **g**, femur; **h**, tibiofibular; **i**, ray.



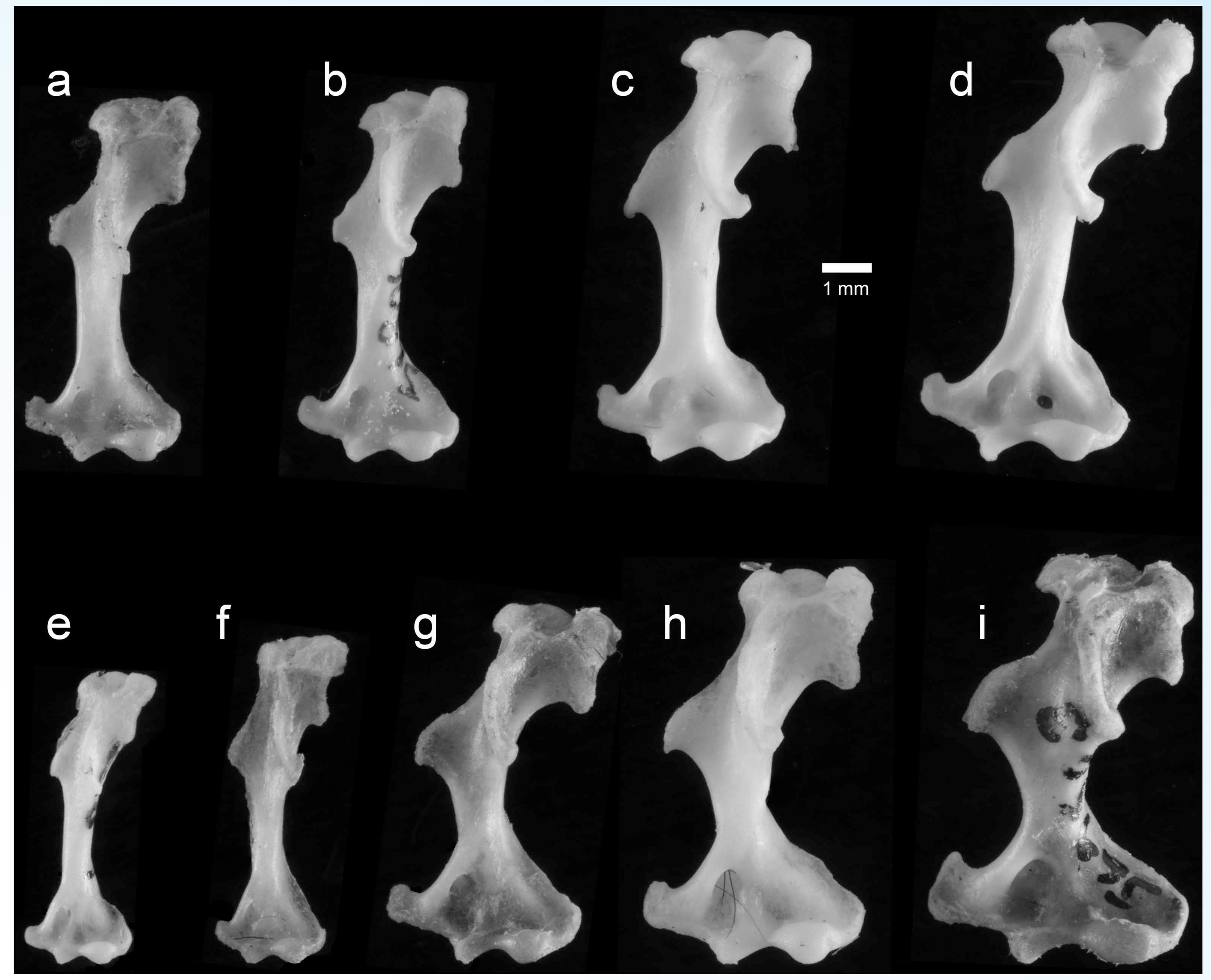


Figure 2. Left humeri of: **a**, *B. carolinensis;* **b**, *B. peninsulae;* **c,** *B. hylophaga;* **d**, *B. brevicauda;* **e,** *C. parvus;* **f,** *C. tropicalis;* **g,** *C. mam*; **h,** *C. oreorcytes;* **i,** *C. lacertosus*. These humeri reflect the animals' locomotory mode through muscle attachment sites and robusticity. Animals with locomotory modes such as burrowing require larger muscle attachment sites to create greater forces and leverage.

Figure 3. X-ray of right manus of *B. carolinensis.* These x-rays were used to obtain measurements of the forefeet and hindfeet.

Figure 4. Skin specimen of *Blarina hylophaga.* X-rays can provided measureable images of hand and foot bones.

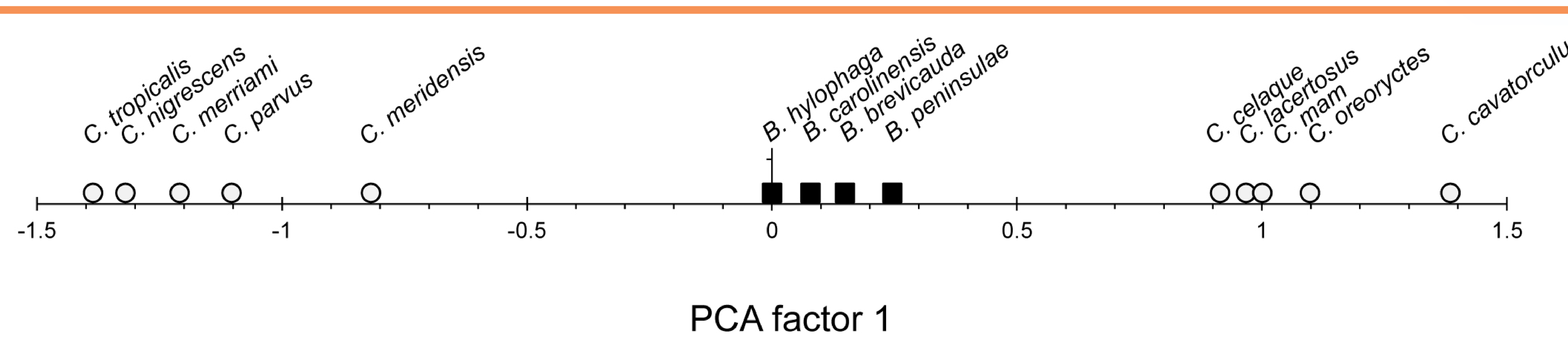


Figure 6. Principle component analysis factor 1 is interpreted as a scale of relative adaptation for more ambulatory (lower scores) to more fossorial (higher scores) behavior for *Blarina* and *Cryptotis*. Here, *Blarina* discretely groups together, separate from groupings of *Cryptotis*.

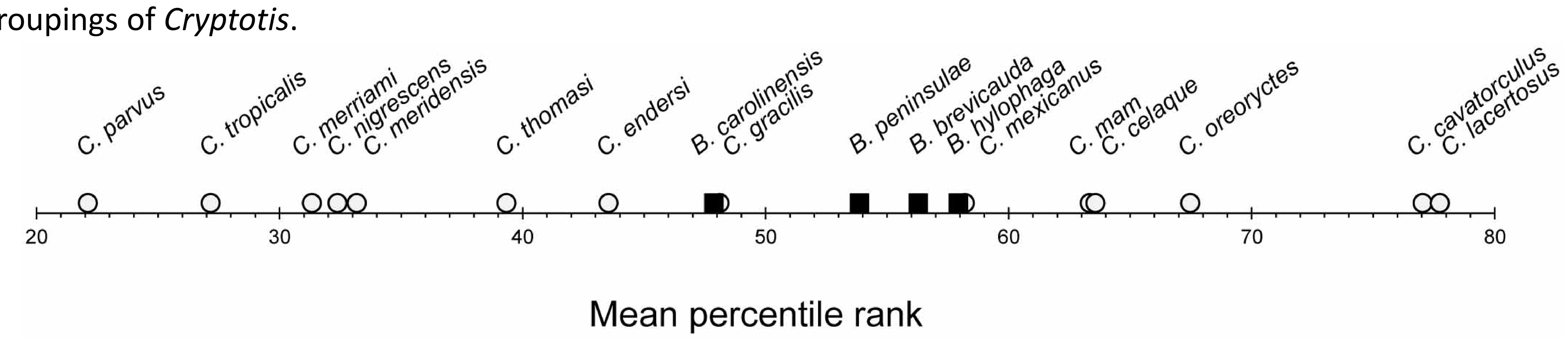


Figure 7. Mean percentile ranks serve as a scale of fossoriality (burrowing adaptation). Higher values indicate greater capacity for fossorial behavior. Additional taxa in this analysis show there is a functional gradient among species.

Results

Blarina and *Cryptotis* show varying degrees of morphological specialization and functional capacity. The mean percentile rank scale (Fig. 7) and the PCA Factor 1 scale (Fig. 6) show a gradient in burrowing modifications and provide superficially similar results. The 4 species of *Blarina* cluster tightly along both the percentile rank and PCA Factor 1 scales. In both graphs, *Blarina* is an intermediate between two functional groups of *Cryptotis*, a group that show considerable modifications for fossorial and ambulatory behaviors, respectively. Interestingly, the two spectra are not completely identical. While functional groups tend stay in fixed places along the two graphs, the order of individual species within these groups is less static.

Discussion

Our anatomical investigation of *Blarina* and *Cryptotis* postcrania revealed three discrete groupings based on the functionality of the humerus, manus, and other postcranial elements that facilitate fossoriality of North American shrews. Adding taxa to the mean percentile rankings creates a continuous spectrum of fossoriality. Broader, more robust humeri and rays are better modified for the mechanics of fossoriality, which requires greater bending resistance and larger muscle forces. Gross observations of *Blarina* humeri morphology and PCA of *Blarina* indicate its species are all very similar with no extreme modifications for either classical ambulatory behavior or fossorial bavior. This contrasts with the sample of *Cryptotis* (Fig. 3), some of which show broad, robust anatomical features that are hypothesized to aid in fossorial behavior, others of which align more closely with the functional modifications observed in *Blarina*, and others that appear to be more adapted for ambulatory behavior. We hypothesize the variation between the PCA Factor 1 graph and mean percentile rank graph suggests that species more modified for fossoriality are not obligated to perform this behavior and species less modified for fossoriality are still able to burrow, establishing gradients within the three different clusters and broader spectrum among all the sampled taxa.

Conclusions

- There is variation between features associated with fossoriality and mean percentile ranking of fossorial capacity. PCA illustrate isolated groupings of fossorial adaption, while mean percentile ranking demonstrates a continuum of fossorial ability.
- More postcranial anatomical variation is present within *Cryptotis* than between *Cryptotis* and *Blarina.*
- *Blarina* exhibits little morphological variation, but does show a slight morphological and functional gradient.
- *B. brevicauda* is not the most fossorial North American shrew.

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