

Skeletal Morphology of the Forefoot in Shrews (Mammalia: Soricidae) of the Genus *Cryptotis*, as Revealed by Digital X-rays

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ABSTRACT Variation in the forefoot skeleton of small-eared shrews (family Soricidae, genus *Cryptotis*) has been previously documented, but the paucity of available skeletons for most taxa makes assessment of the degrees of intraspecific and interspecific variation difficult. We used a digital X-ray system to extract images of the forefoot skeleton from 101 dried skins of eight taxa (seven species, including two subspecies of one species) of these shrews. Lengths and widths of each of the four bones of digit III were measured directly from the digital images, and we used these data to quantify variation within and among taxa. Analysis of the images and measurements showed that interspecific variation exceeds intraspecific variation. In fact, most taxa could be distinguished in multivariate and some bivariate plots. Our quantitative data helped us define a number of specific forefoot characters that we subsequently used to hypothesize evolutionary relationships among the taxa using the exhaustive search option in PAUP, a computer program for phylogenetic analysis. The resulting trees generally concur with previously published evolutionary hypotheses for small-eared shrews. *Cryptotis meridensis*, a taxon not previously examined in recent phylogenies, is rooted at the base of the branch leading to the *C. mexicana* group of species. The position of this species suggests that the mostly South American *C. thomasi* group shares an early ancestor with the *C. mexicana* group. *J. Morphol.* 266:60–73, 2005.

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Variation in the morphology of the forelimb and manus has long been recognized as being useful for distinguishing among higher taxonomic levels of mammals. Extensive structural modifications of the plesiomorphic mammalian plan (Romer, 1966; Lewis, 1989), for example, characterize the orders Artiodactyla, Cetacea, and Chiroptera (Owen, 1866; Vaughan, 1970; Carroll, 1988; Kardong, 1998). At lower taxonomic levels, patterns of variation in the forelimb skeleton—particularly that of the forefoot—have been documented even for orders characterized by generalized, less derived patterns of forelimb structure, such as within the rodent families Muridae (Musser, 1981; Voss, 1988; Carleton

and Musser, 1989) and Sciuridae (Long and Captain, 1974; Thorington and Darrow, 2000). Attempts have been made to infer ecological adaptations from particular limb morphologies (Long and Captain, 1974; Hutterer, 1985), but in many instances structural modifications of the extremities also exhibit phylogenetic signal (Choate, 1970; Voss, 1988; Woodman and Timm, 1999, 2000). Among shrews (Soricidae), external characteristics of the forefoot can be useful for distinguishing among genera and species (Goldman, 1912; Hutterer, 1985) and to infer phylogenetic relationships (Choate, 1970). Previously, forefoot morphology was investigated in some detail among small-eared shrews of the genus *Cryptotis*. Like other soricids, small-eared shrews employ both forefeet and hindfeet together in terrestrial, quadrupedal locomotion. In addition, they construct runways and burrows, using their forefeet for digging and pushing excavated soil aside (Whitaker, 1974). External variation in the forefoot among species of *Cryptotis* was revealed to be underlain by considerable osteological variation, and skeletal morphology of the manus provided characters that are potentially useful for understanding phylogenetic and ecological relationships (Woodman and Timm, 1999, 2000; Woodman, 2002; Woodman et al., 2003).

Unfortunately, few complete skeletons of soricids currently are available for study. Where skeletons are available, the minute bones of the manus and

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pes are among the elements most likely to be disarticulated and lost. Where they are present, these bones often are obscured by remaining soft tissue, they are difficult to observe adequately even at high magnification under a stereoscope, and they are difficult to handle. However, traditional methods of preparing skins of small mammals for systematic museum collections typically leave articulated bones of the feet within the dried skins. We investigated the use of a digital X-ray system to reveal the bones of the forefeet preserved in dried skins and found that we typically could record usable digital images. Among the better-prepared specimens, the digits are flat and slightly spread, and the full length and breadth and general shape of the dorsal aspect of the metacarpals and phalanges are readily visible. Carpals are more difficult to discern clearly in X-ray images because their margins often overlap, and in some specimens they are partly hidden by wires inserted to support the legs of the specimens.

Herein, we use the digital X-ray images we recorded to illustrate the general structural pattern of the skeleton of the manus among species of small-eared shrews and to quantify intraspecific and interspecific variability. We were particularly interested in contrasting variability among the metatarsals and phalanges because these bones are more consistently visible in the X-rays and they exhibited the most obvious trends and patterns in previous studies of these shrews (Woodman and Timm, 1999, 2000). Our quantitative results assisted in evaluating and delineating specific characters of the forefoot that we then analyzed using PAUP, a computer program for hypothesizing phylogenetic relationships (Swofford, 1998). The resulting tree was then compared to previous hypotheses of phylogenetic relationships among species in the genus.

MATERIALS AND METHODS

In this study, we used digital X-rays to investigate the osteology of the forefoot of eight taxa of shrews of the genus *Cryptotis*. Numerous names have been assigned to the individual mammalian carpals (e.g., Owen, 1866; Flower, 1870; Edwards, 1937; Reed, 1951; Lewis, 1989; Stafford and Thorington, 1998; Thorington and Darrow, 2000; Vaughan et al., 2000; Martin et al., 2001). We employ the following terms for these bones, providing alternative names for each in parentheses: capitate (carpale 3, magnum); centrale (central; intermedium of Owen, 1866); falciform (prepollex); hamate (carpale 4+5, unciform); lunate (intermedium, lunar, semilunar); pisiform; scaphoid (navicular, naviculare, radiale); scapholunate (fused scaphoid and lunate); trapezium (greater multangular, carpale 1); trapezoid (lesser multangular, carpale 2); triquetrum (cuneiform, pyramidale, triquetral, triangular, ulnare). The bones in the forefoot of *Cryptotis* are illustrated in Figure 1.

Species of *Cryptotis* have been allocated to four species groups based primarily on external characteristics and cranial morphology. Although one or more of these groupings may represent clades, relationships among the groups are not fully resolved, and it is likely that some of the groups are paraphyletic with respect to each other and to species currently unassigned to groups (Woodman and Timm, 1999). Instead, these groups represent working hypotheses regarding relationships among species based

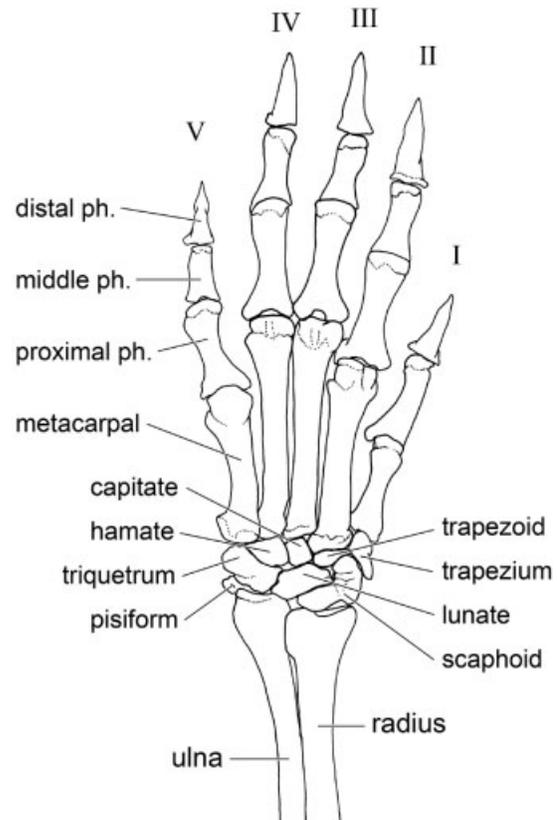


Fig. 1. Dorsal view of skeleton of left forefoot of *Cryptotis meridensis* illustrating terms used for bones of the manus. The falciform is not visible in this view. There is no scapholunate (scaphoid and lunate are individual elements) and no separate centrale. Roman numerals are formal designations for the digits. ph, phalanx.

on similar morphologies. Our choice of taxa to examine in this study was influenced by this partitioning, by previous studies of forelimb variation in *Cryptotis*, and by the specimens readily available to us. Our sample of dry skins for X-ray study included three species in the *C. mexicana* group (*C. goldmani*, *C. goodwini*, *C. mexicana*); two species from the *C. nigrescens* group (*C. mera*, *C. nigrescens*); two subspecies from the *C. parva* group (*C. parva parva*, *C. parva floridana*); and one species of the *C. thomasi* group (*C. meridensis*). A complete listing of the specimens examined and measured is provided in the Appendix. In addition, we inspected, but did not measure, a few cleaned skeletons each of the soricine shrews *Blarina brevicauda*, *Blarinella quadraticauda*, *C. parva floridana*, *C. parva parva*, and *Sorex haydeni*, and the crocidurine shrews *Crocidura cyanea*, *C. fuliginosa dracula*, *C. leucodon*, and *C. pullata*.

Digital images of the left manus of each specimen used in this study were produced using the Keven-Varian digital X-ray system at the Division of Fishes, National Museum of Natural History, Washington, DC. We transferred the images to Adobe PhotoShop (San Jose, CA), where they were trimmed, converted to positive images, and saved. To quantify intraspecific and interspecific variation in the metacarpals, phalanges, and keratinous claw sheath, we measured the images of these elements along the dorsal surface of left digit III of all individuals using the coordinate grid in the Info window of PhotoShop. To calibrate the grid units, we included a metal straight pin of known breadth (0.52 mm) in all images. Grid units were converted to millimeters (mm), and all measurements reported herein are in millimeters. Lengths were measured following the long axis of each individual

TABLE 1. Unbiased coefficients of variation (V^*) for each variable

Taxon of <i>Cryptotis</i>	N ^a	ML	PPL	MPL	DPL	CL	TDL	T3L	MW	PPW	MPW	DPW	HB
<i>floridana</i>	11	5.5	4.7	8.5	17.0	9.1	5.1	4.4	11.0	12.8	12.0	19.4	7.2
<i>parva</i>	10	6.7	5.2	8.6	12.9	10.0	3.9	3.9	11.0	7.3	7.8	16.1	6.1
<i>mexicana</i>	20	5.3	3.3	8.6	8.4	14.6	3.6	3.7	8.0	9.1	9.5	6.4	5.0
<i>mera</i>	2	5.3	7.5	7.1	2.2	0.9	3.0	3.7	15.5	4.8	0.7	22.4	8.0
<i>nigrescens</i>	16	7.1	8.2	13.6	12.6	12.0	8.1	8.0	14.8	13.1	10.6	27.6	7.4 ^b
<i>goldmani</i>	10	10.5	9.4	25.0	13.6	14.1	11.0	11.6	9.9	9.3	11.4	25.7	6.4 ^c
<i>goodwini</i>	12	4.8	5.3	11.7	4.8	6.3	4.0	4.7	8.9	9.5	8.5	17.0	5.6
<i>meridensis</i>	20	3.9	5.7	7.5	5.3	4.7	3.1	3.5	6.6	6.9	11.5	17.0	4.3
All taxa	101	12.5	9.2	16.0	39.7	31.5	12.4	10.2	28.6	32.3	35.6	31.9	13.4

^aExcept as noted.

^bn = 15.

^cn = 9.

bone from the proximal end to its distalmost point. Widths were taken at right angles to length exactly midway along the measured length of the bone. The following measurements were recorded: CL = length of claw; CW = width of claw; DPL = length of distal phalanx; DPW = width of distal phalanx; ML = length of metacarpal; MPL = length of middle phalanx; MPW = width of middle phalanx; MW = width of metacarpal; P3L = total length of proximal three bones of digit III (= ML + PPL + MPL); PPL = length of proximal phalanx; PPW = width of proximal phalanx; TDL = total length of digit III (= ML + PPL + MPL + DPL). We used length of head and body (HB) to represent body size for individual specimens and taxa. In most diagrams, figures, and tables, taxa are ordered by mean body size.

Tabled univariate statistics include mean \pm SD and total range. We calculated an unbiased coefficient of variation for each variable (V^* —Sokal and Rohlf, 1981; Table 1) to compare relative amounts of variation among populations. To account for differences in body size among taxa and determine proportional similarities and differences among elements of the digit, we calculated two different percentages. For the first, we divided individual lengths by the total length of the proximal three bones (P3L). We used total length of the proximal three bones rather than total length of the digit (TDL) because visual inspection indicated that the distal phalanx accounted for a large proportion of the total variation in length among species. To calculate the second percentage, we converted lengths by dividing by length of the proximal phalanx (PPL). We used this measure because the proximal phalanx generally exhibited the least amount of intraspecific and interspecific variation in length (Table 1). We did not attempt to calculate percentages using body size (HB) because of the large difference in accuracy with which this variable and the digit variables were measured. We did, however, employ body size in regression analyses used to investigate the possible relationship between size variation among forefoot variables and body size. Statistical significance throughout our study was considered to be $P < 0.05$.

Variation in most length and width variables was consistently greater among taxa than within an individual taxon, suggesting that some of these variables might be useful in distinguishing taxa or groups of taxa. Principal components analysis (PCA) is useful for investigating relationships in overall shape, and it is additionally helpful for identifying individual variables and groups of variables that distinguish or group taxa. We carried out a PCA among the eight taxa using a correlation matrix of five log-transformed forefoot variables (DPL, ML, MPL, MW, PPL).

To define individual characters from continuous variables, we plotted out variable means \pm 1 SD for each taxon. Taxa with overlapping intervals were scored the same; taxa with gaps between intervals were scored differently. Phylogenetic analysis of forefeet was carried out with the computer program PAUP 4.0b10 for Macintosh (see Swofford, 1998) using the exhaustive search option on nine ordered and equally weighted transition series derived from the eight taxa. Transition series were polarized by

comparison with the manus of the Prairie Shrew, *Sorex haydeni*. Character evolution on the resultant tree was analyzed using MCCLADE 3.0 (see Maddison and Maddison, 1992).

RESULTS

General Description of Forefoot Skeleton of *Cryptotis*

The morphology of the feet of soricids is generally plesiomorphic for mammals (Lewis, 1989; Hopson, 1995; Vaughan et al., 2000). The feet are pentadactyl and plantigrade, although shrews raise the metatarsals off the ground when running, essentially assuming a digitigrade posture of the hindfeet. The phalangeal formula is 2-3-3-3-3 (Fig. 1). All five digits are elongate and well developed on both manus and pes. The digits typically are of different lengths, the order of increasing length being I, V, II, IV, III on the forefeet for nearly all taxa, except the Elegant Water Shrew, *Nectogale elegans*, in which digits III, IV, and V are nearly equal in length. On the hindfoot, the order of increasing length is similar, except that either digit III or IV may be longer, or they may be equal in length. *Nectogale elegans* again provides an exception, the order being I, II, III, V, IV. Neither pollex nor hallux is opposable. Each digit bears a long, curved claw rather than a nail. The claw on digit II of the pes is notably asymmetrical. The ulnar (lateral) side of the claw is flared, widening the claw and creating a hollow on its ventral surface. This flaring also is present to a lesser extent on the claw of digit III. The function of this modification, if any, is not known. Asymmetrical flaring of the hind claws also is present in talpids, although the number of digits involved varies.

Our characterization of the skeleton of the forefoot in *Cryptotis* is based on our inspection of X-ray images and a few available skeletons. Some skeletal elements of the forefoot are difficult to discern clearly for some taxa, and our observations may not be representative of all species in the genus.

In general, the radius and ulna articulate distally with separate scaphoid, lunate, triquetrum, and

pisiform (Fig. 1). The proximal row of carpals in *Cryptotis* articulates distally with trapezium, trapezoid, capitate, and hamate. There is no separate centrale. The distal row of carpals articulates distally with the five metacarpals: trapezium primarily with metacarpal I, but also with the radio-proximal edge of metacarpal II; trapezoid with metacarpal II; capitate primarily with metacarpal III, but also with the ulno-proximal edge of metacarpal II; hamate primarily with metacarpal IV, but also with the ulno-proximal edge of metacarpal III and with the radio-proximal edge of metacarpal V. In addition, the triquetrum extends distally to articulate with metacarpal V. A long, thin, poorly ossified falciform is present in palmar view of the manus of one taxon (*C. p. parva*), for which we had some particularly well-prepared, well-preserved, articulated skeletons. This bone is likely to be present in other species of *Cryptotis*, but it was not visible in any of the X-ray images. Altogether, the manus of *Cryptotis* consists of 28 individual bones. The possession of entirely separate scaphoid and lunate is similar to the condition in the Sichuan Short-tailed Shrew, *Blarinella quadratacauda* (our observations) and in the White-toothed Shrew, *Crocidura russula* (Sánchez-Villagra and Menke, 2005). In the Northern Short-tailed Shrew, *Blarina brevicauda*, the two bones are fused, but there is a distinct suture that makes them appear to be separate bones (Sánchez-Villagra and Menke, 2005; our observations). Both conditions are unlike that documented for the Long-tailed Shrew, *Sorex* (Reed, 1951; Sánchez-Villagra and Menke, 2005; our observations of *S. haydeni*), other species of *Crocidura* (Haines, 1955—*C. “coerulea”*; our observations of *C. cyanea*, *C. fuliginosa dracula*, *C. leucodon*, *C. pullata*), the hedgehog, *Erinaceus* (Vaughan et al., 2000; Sánchez-Villagra and Menke, 2005), and many other mammals (Lewis, 1989; Stafford and Thorington, 1998); in all of these taxa the two bones are solidly fused into a single scapholunate.

Variation in the Forefoot Skeleton of *Cryptotis*

The X-ray images (Fig. 2) reveal considerable interspecific variation among the forefeet of the eight taxa that we investigated. These images support previous reports (Woodman and Timm, 1999, 2000; Woodman et al., 2003) of qualitative differences in the dimensions of the metacarpals and phalanges among species of *Cryptotis*, and they provide both a greater diversity of taxa and larger sample sizes per taxon than were available previously. Most notable are changes in the relative proportions and shapes of the individual elements comprising the digits. In particular, members of the *C. mexicana* group exhibit a tendency to have long distal phalanges and short, broad metacarpals and proximal and middle phalanges. This variation is reflected in our quanti-

tative analyses of the digits and their individual components.

The eight taxa range considerably in body size—mean length of head and body (HB) ranges from 59–86 mm (Table 2; $V^* = 13.4$). This variation in body size is reflected to a large extent in the forefeet as well. Mean total length of digit III (TDL) varies from 5.17–7.50 mm (Table 2, Fig. 3A; $V^* = 12.4$), and length of the proximal three bones of the digit (P3L) ranges from 4.53–5.49 mm ($V^* = 10.2$). Regression analyses of total length of digit III (Fig. 4A) and total length of the proximal three bones (Fig. 4B) on length of head and body indicate a significant positive interspecific trend of increasing digit length with increasing body size using either measure. Individual species, however, do not all conform exactly to this general trend. In the plot of the regression for total length of the proximal three bones (Fig. 4B), for example, individuals of *Cryptotis meridensis* and *C. p. floridana* tend to fall above the regression line, indicating that digit III is longer than would be predicted based on their body sizes. In contrast, the third digits of *C. mexicana* and *C. p. parva* tend to be shorter than expected. Regression analyses of total length of digit III and total length of the proximal three bones on length of head and body for individual species yielded only one instance in which there was a significant slope (*C. mexicana*: $TDL = 0.0307 HB + 3.99$; $F = 5.76$, $P = 0.027$, $R^2 = 24.2\%$). Hence, the positive interspecific relationship between length of digit and body size generally does not hold intraspecifically as well. To provide some measure of control for interspecific variation in body size, we transformed each length variable to percentages in relation to both total length of the proximal three bones (Table 3) and length of proximal phalanx (Table 4). The first relation emphasizes variation in the length of the distal phalanx (Fig. 3B). The second calculation shows variation in relation to the proximal phalanx, which is interspecifically the least variable bone of the digit (Fig. 3C).

Among the individual bones, the most variable element in terms of length is the distal phalanx (Tables 1–4; Fig. 3A–C). The total range of variation among taxon means for length of distal phalanx (DPL) is 1.38 mm (Table 2). Much of the variability in length of distal phalanx is a result of variation among the species of the *Cryptotis mexicana* group (*C. goldmani*, *C. goodwini*, *C. mexicana*) and *C. meridensis*. Among the remaining four taxa the range in mean lengths is only 0.17 mm. The intraspecific relationship between length of distal phalanx and body size is significant and positive ($DPL = 0.0239 HB + 0.586$; $F = 32.97$, $P = 0.000$, $R^2 = 25.4\%$, $n = 99$).

The other three bones of digit III are less variable in length among taxa (Tables 1–4), and all exhibit significant positive relationships of increasing length with increasing body size (middle phalanx: $MPL = 0.00576 HB + 0.547$; $F = 14.71$, $P = 0.000$,

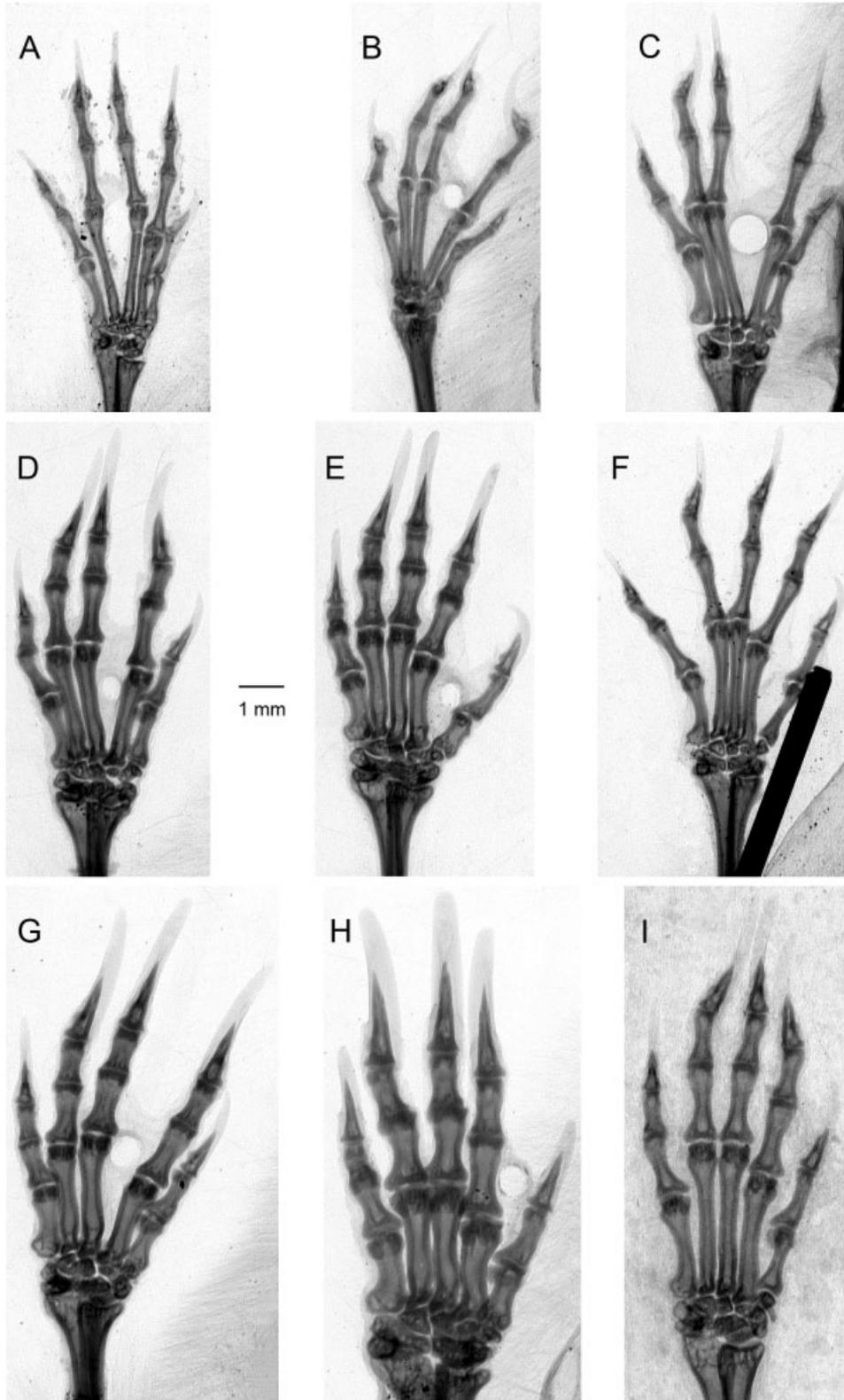


Fig. 2. Digital X-ray images of the left manus of *Cryptotis*. Original negatives have been converted to positive images. Taxa are in order of increasing body size. **A:** *C. parva floridana*. **B:** *C. parva parva*. **C:** *C. mera*. **D:** *C. mexicana*. **E:** *C. mexicana*. **F:** *C. nigrescens*. **G:** *C. goldmani*. **H:** *C. goodwini*. **I:** *C. meridensis*.

TABLE 2. Body size and length variables for bones of digit III (mm)

Taxon of <i>Cryptotis</i>	Body size (HB)	Metacarpal (ML)	Proximal phalanx (PPL)	Middle phalanx (MPL)	Distal phalanx (DPL)	Claw sheath (CL)	Three proximal bones (P3L)	Total length of Digit III (TDL)
<i>floridana</i> (n = 11)	59 ± 4 53–67	2.71 ± 0.15 2.43–2.93	1.50 ± 0.07 1.41–1.62	1.01 ± 0.08 0.91–1.14	0.71 ± 0.12 0.52–0.87	1.43 ± 0.13 1.23–1.62	5.22 ± 0.23 4.83–5.52	5.93 ± 0.30 5.39–6.39
<i>parva</i> (n = 10)	63 ± 4 57–69	2.36 ± 0.15 2.15–2.55	1.31 ± 0.07 1.17–1.43	0.86 ± 0.07 0.71–0.99	0.64 ± 0.08 0.53–0.78	1.73 ± 0.17 1.33–1.89	4.53 ± 0.17 4.26–4.78	5.17 ± 0.20 4.78–5.43
<i>mexicana</i> (n = 20)	70 ± 3 64–79	2.57 ± 0.13 2.25–2.79	1.47 ± 0.05 1.37–1.54	0.83 ± 0.07 0.72–1.02	1.28 ± 0.11 0.93–1.44	2.32 ± 0.34 1.34–2.82	4.86 ± 0.18 4.41–5.14	6.14 ± 0.22 5.72–6.51
<i>mera</i> (n = 2)	70 ± 5 66–73	2.72 ± 0.13 2.63–2.81	1.62 ± 0.11 1.54–1.69	0.97 ± 0.06 0.93–1.02	0.74 ± 0.01 0.73–0.75	1.57 ± 0.01 1.56–1.58	5.31 ± 0.18 5.19–5.44	6.05 ± 0.16 5.93–6.16
<i>nigrescens</i> (n = 16) ^a	74 ^b ± 5 65–83	2.66 ± 0.19 2.39–3.02	1.63 ± 0.14 1.52–1.91	0.97 ± 0.13 0.82–1.22	0.81 ± 0.10 0.62–1.02	1.57 ± 0.19 1.25–1.86	5.27 ± 0.42 4.77–6.11	6.08 ± 0.49 5.56–7.13
<i>goldmani</i> (n = 10) ^a	77 ^c ± 5 67–84	2.67 ± 0.28 2.12–3.00	1.56 ± 0.14 1.45–1.86	1.09 ± 0.27 0.86–1.54	1.81 ± 0.24 1.64–2.31	3.27 ± 0.45 2.50–3.97	5.32 ± 0.60 4.42–6.27	7.13 ± 0.77 6.10–8.58
<i>goodwini</i> (n = 12)	82 ± 4 75–87	2.70 ± 0.13 2.44–2.86	1.66 ± 0.09 1.46–1.76	1.13 ± 0.13 0.95–1.39	2.02 ± 0.10 1.79–2.12	3.39 ± 0.21 3.09–3.74	5.49 ± 0.25 5.15–6.02	7.50 ± 0.29 7.02–8.09
<i>meridensis</i> (n = 20)	86 ± 4 76–94	3.34 ± 0.13 3.13–3.57	1.66 ± 0.09 1.43–1.86	1.01 ± 0.07 0.85–1.14	1.13 ± 0.06 0.97–1.21	2.32 ± 0.11 2.11–2.48	6.01 ± 0.21 5.70–6.45	7.14 ± 0.22 6.80–7.64

Statistics are mean ± SD and range. Taxa are listed in increasing order of body size.

^aExcept as noted.

^bn = 15.

^cn = 9.

$R^2 = 13.2\%$; proximal phalanx: $PPL = 0.00863 HB + 0.916$; $F = 52.37$, $P = 0.000$, $R^2 = 35.1\%$; metacarpal: $ML = 0.0224 HB + 1.11$; $F = 65.95$, $P = 0.000$, $R^2 = 40.5\%$). Much of the variability in length of the metacarpal is attributable to the relatively longer metacarpal of *Cryptotis meridensis* (Tables 2–4). The difference in length of metacarpal in this species is offset by a correspondingly smaller middle phalanx. The different contributions of these bones to the length of digit III (relative to other taxa) are especially evident in Figure 3A–C.

As with length of distal phalanx, the length of the keratinous claw sheath (CL), which covers the distal phalanx, is quite variable. Because of the close physical association between these two elements, we considered that there might be a positive relationship between length of distal phalanx and length of the keratinous claw sheath. The correlation between the two variables is high ($r = 0.952$, $n = 101$), and regression analysis confirms a strong, positive interspecific trend of increasing claw length with increasing length of distal phalanx (Fig. 5). However, not all individual taxa correspond exactly to this interspecific trend. For example, *Cryptotis goodwini* tends to have a shorter claw relative to length of distal phalanx, whereas *C. p. parva* and *C. meridensis* tend to have longer claws. The magnitudes of the differences are not great, but they are sufficient to distinguish many of the taxa in Figure 5.

Variation in the mean widths of the bones of digit III is high (Table 5; Fig. 6). In fact, interspecific coefficients of variation for width are higher than for corresponding lengths (Table 1). Variation among the widths of individual elements appears to be more consistent than for lengths in that the magnitudes of the ranges of variation for metacarpals and

phalanges within a given taxon is similar, especially for the proximal three bones of the digit. In addition, taxon to taxon increases or decreases in the width of one bone generally are accompanied by more or less proportional changes in the other elements (Table 5).

Like the length measures for these elements, the width measures of the four bones making up digit III all show significant interspecific trends of increasing as body size increases (distal phalanx: $DPW = 0.00334 HB + 0.0123$; $F = 18.16$, $P = 0.000$, $R^2 = 15.8\%$; middle phalanx: $MPW = 0.00622 HB + 0.129$; $F = 35.45$, $P = 0.000$, $R^2 = 26.8\%$; proximal phalanx: $PPW = 0.00623 HB + 0.113$; $F = 41.22$, $P = 0.000$, $R^2 = 29.8\%$; metacarpal: $MW = 0.0772 HB + 0.00591$; $F = 45.69$, $P = 0.000$, $R^2 = 32.0\%$). However, inspection of the plots of the regressions against the individual points suggests that a single regression does not adequately explain the patterns of variation in the width variables with body size. For example, in the regression of width of proximal phalanx on length of head and body, species in the *Cryptotis mexicana* group tend to fall above the regression line (Fig. 7, line a), whereas the remaining taxa tend to fall below it. This pattern supports the hypothesis that members of the *C. mexicana* group exhibit an accelerated broadening of the digits relative to other members of the genus. To better define this pattern, we calculated two additional regressions, one based on just the three species in the *C. mexicana* group (Fig. 7, line b), the second using the remaining five taxa (Fig. 7, line c). If line c in Figure 7 represents the typical digit width to body size relationship in the genus, then the line b provides a visual representation of the divergence of the *C. mexicana* group from the typical pattern.

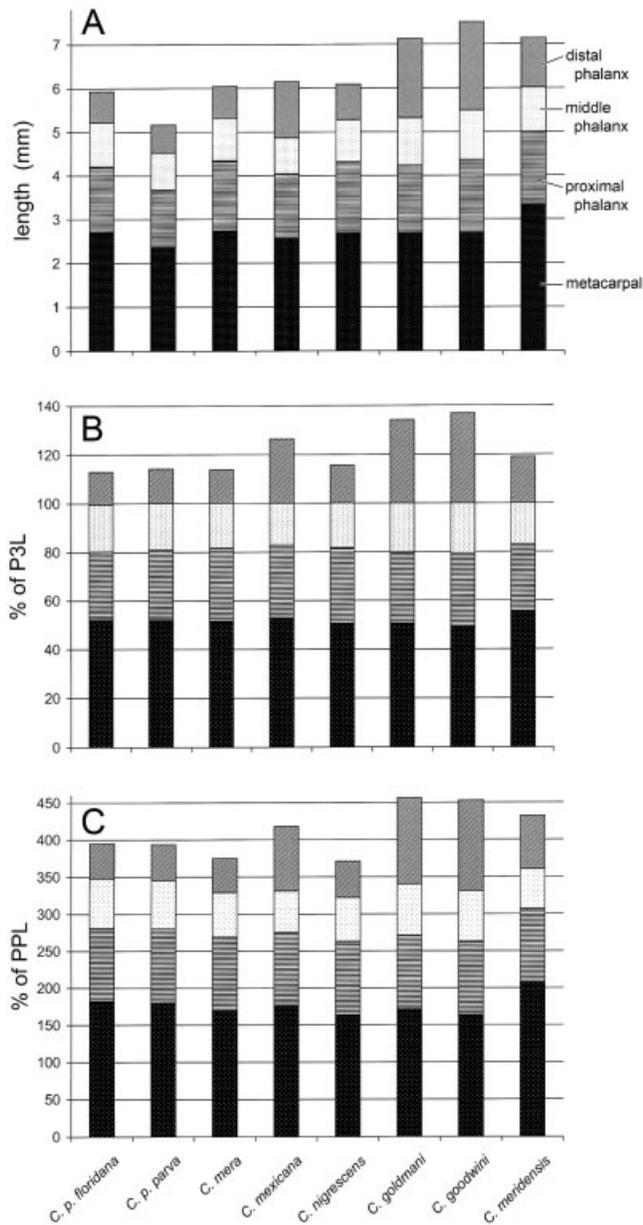


Fig. 3. Diagrammatic representations of the mean length values for the elements of digit III among the eight taxa of *Cryptotis*. Taxa are listed from left to right in order of increasing body size. **A:** Mean lengths of the individual elements from Table 2. **B:** Means as a percentages of total length of the proximal three bones from Table 3; the distal end of the each middle phalanx is at 100%. **C:** Means as percentages of length of proximal phalanx from Table 4; the length of the proximal phalanx equals 100% for each taxon.

As an additional index of width and length for each of the individual bones, we calculated a percentage by dividing the width of each bone by its length (Table 6). This provides a continuous range of values representing the combined length and width characteristics for the metacarpals and phalanges. High values may represent either relatively short or broad (but not both) elements, whereas low values

may be either relatively long or narrow elements. Comparison of the proportional values to the original X-ray images of the forefeet (Fig. 2) and to the mean values as represented in Figures 3 and 6 provides additional details regarding the case for each taxon. The middle phalanx shows the greatest range in mean values for this index, followed by proximal phalanx, distal phalanx, and metacarpal. The width/length proportion for the distal phalanx suggests two groupings. A group consisting of *Cryptotis p. floridana*, *C. p. parva*, and *C. nigrescens* exhibits high values, and all of these taxa have a short and narrow distal phalanx. The remaining species clump in a second, lower proportion group. Of these, *C. goldmani*, *C. goodwini*, and *C. mexicana* all have long and broad distal phalanges, *C. meridensis* has a moderately long and broad distal phalanx, and *C. mera* has a short, but very narrow distal phalanx. The width/length proportion for the middle phalanx likewise is suggestive of two groups of taxa: a high proportion group consisting of *C. goldmani*, *C. goodwini*, and *C. mexicana*, which all have a broad mid-

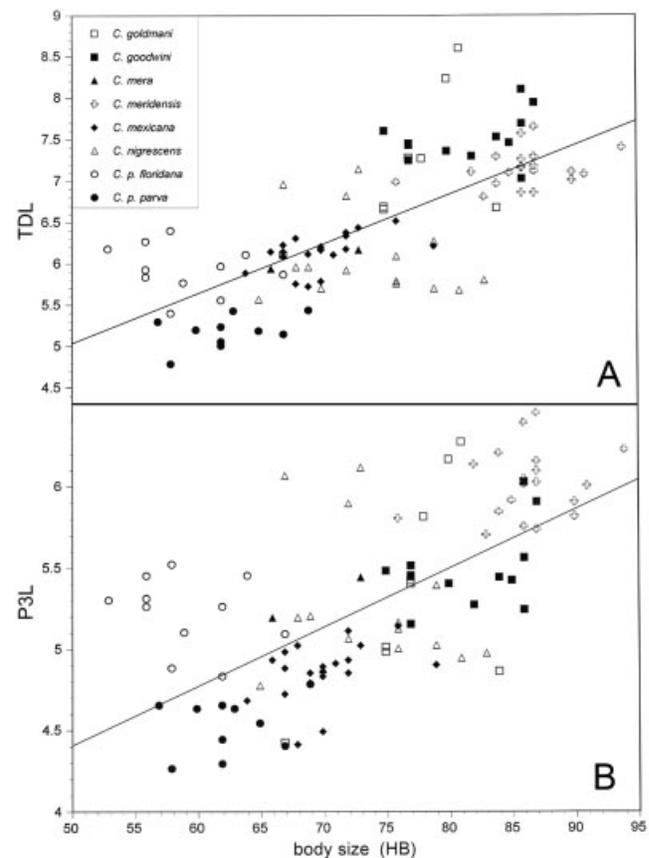


Fig. 4. Regressions showing the positive relationship between digit length and body size (HB). **A:** Regression of total length of digit III on length of head and body ($TDL = 0.0607 HB + 1.98$; $F = 116.65$, $P = 0.000$, $R^2 = 44.1\%$; $n = 99$). **B:** Regression of total length of the proximal three bones of digit III on length of head and body ($P3L = 0.0367 HB + 2.57$; $F = 76.54$, $P = 0.000$, $R^2 = 54.6\%$; $n = 99$).

TABLE 3. Relative lengths (%) of the bones and keratinous claw sheath of digit III relative to the combined lengths of the three most proximal bones (P3L)

Taxon of <i>Cryptotis</i>	n	Metacarpal (ML)	Proximal phalanx (PPL)	Middle phalanx (MPL)	Distal phalanx (DPL)	Claw sheath (CL)
<i>floridana</i>	11	52 ± 1 50–54	29 ± 1 27–30	19 ± 1 17–22	14 ± 2 11–16	27 ± 3 23–30
<i>parva</i>	10	52 ± 2 48–55	29 ± 1 28–31	19 ± 2 15–22	14 ± 2 12–17	38 ± 4 29–43
<i>mexicana</i>	20	53 ± 1 50–55	30 ± 1 29–32	17 ± 1 15–20	26 ± 2 19–30	48 ± 7 28–58
<i>mera</i>	2	51 ± 1 51–52	30 ± 1 30–31	18 ± 2 17–20	14 ± 1 13–14	30 ± 1 29–30
<i>nigrescens</i>	16	51 ± 1 49–54	31 ± 1 29–34	18 ± 1 17–20	15 ± 2 12–18	30 ± 3 24–34
<i>goldmani</i>	10	50 ± 3 46–54	29 ± 2 27–33	20 ± 3 16–25	34 ± 4 25–38	62 ± 8 43–72
<i>goodwini</i>	12	49 ± 2 47–54	30 ± 1 28–32	21 ± 2 18–23	37 ± 2 34–41	62 ± 4 57–71
<i>meridensis</i>	20	56 ± 1 53–57	28 ± 1 24–30	17 ± 1 15–19	19 ± 1 16–20	39 ± 2 34–43

Statistics are mean ± SD and range.

dle phalanx. *Cryptotis meridensis* also has a broad middle phalanx, but it is comparatively short, relegating it, with the remaining taxa, to a second group that otherwise possesses narrow middle phalanges. The width/length proportion for the proximal phalanx gives the impression of three groupings: a high value group with a broad proximal phalanx that includes *C. goldmani* and *C. goodwini*; a group comprised of *C. meridensis* and *C. mexicana*, which have moderately broad proximal phalanges; and a group consisting of the other four taxa, all of which have narrow proximal phalanges. The width/length proportion for the metacarpal hints at two groupings with the same membership as the groups defined by middle phalanx. The high proportion group consists of *C. goldmani*, *C. goodwini*, and *C. mexicana*, all

which all have a broad metacarpal. The remaining taxa have narrow metacarpals, except *C. meridensis*. This species has a metacarpal that is broad, but also very long, lumping with it other taxa that have lower values using this index.

Multivariate Analysis

Principal components analysis of five variables measured from digit III yielded a model that separated most of the individual taxa into distinct, coherent groups. All variables had strong loadings on PC 1, indicating that this axis represents overall “size” of digit III (Table 7). PC 2 is a contrast of length of distal phalanx and width of metacarpal with the lengths of the three proximal bones. In a plot of

TABLE 4. Relative lengths (%) of the bones and keratinous claw sheath of digit III relative to the length of the proximal phalanx (PPL)

Taxon of <i>Cryptotis</i>	n	Metacarpal (ML)	Proximal phalanx (PPL)	Middle phalanx (MPL)	Distal phalanx (DPL)	Claw sheath (CL)
<i>floridana</i>	11	181 ± 7 165–191	100	67 ± 6 58–80	47 ± 7 37–58	95 ± 9 77–106
<i>parva</i>	10	180 ± 12 162–193	100	65 ± 6 52–73	49 ± 5 44–57	132 ± 13 103–156
<i>mexicana</i>	20	175 ± 8 157–184	100	56 ± 5 48–67	87 ± 7 67–97	158 ± 22 96–197
<i>mera</i>	2	169 ± 3 166–171	100	60 ± 8 55–66	46 ± 4 43–48	97 ± 6 93–101
<i>nigrescens</i>	16	163 ± 9 143–183	100	59 ± 4 49–66	49 ± 4 41–57	96 ± 9 77–109
<i>goldmani</i>	10	171 ± 13 146–186	100	69 ± 13 53–88	116 ± 10 90–127	209 ± 22 155–234
<i>goodwini</i>	12	163 ± 10 154–192	100	68 ± 7 57–79	122 ± 7 115–136	205 ± 15 186–237
<i>meridensis</i>	20	202 ± 11 185–234	100	61 ± 5 49–74	68 ± 5 58–74	140 ± 11 126–167

Statistics are mean ± SD and range.

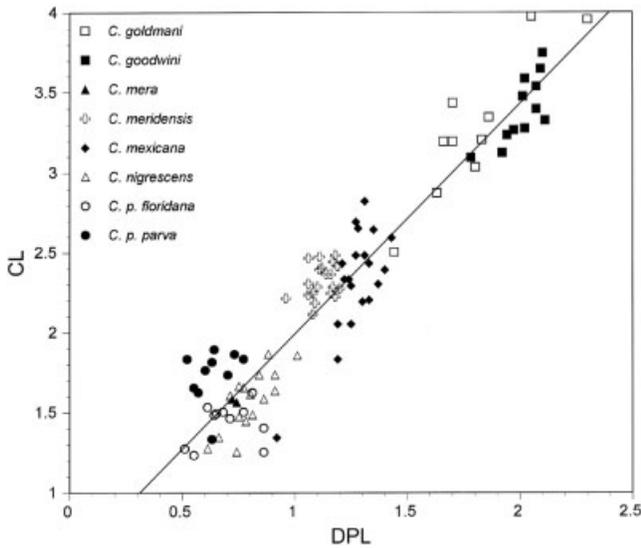


Fig. 5. Regression of length of keratinous claw (CL) on length of distal phalanx (DPL) showing a strong, positive interspecific relationship between these two variables ($CL = 1.44 DPL + 0.552$; $F = 962.78$, $P = 0.000$, $R^2 = 90.7\%$; $n = 101$).

factor scores on the two axes, the individual taxa form more or less discrete clusters (Fig. 8), showing that, surprisingly, five measurements from a single digit are sufficient to discriminate these eight taxa.

The eight taxa segregate into two larger groups. One of these groups consists of the three species in the *Cryptotis mexicana* group, the other comprises the remaining five taxa. This separation is primarily a result of the influence of PC 2, and it reflects the longer distal phalanges and broader metacarpals of species in the *C. mexicana* group, and the longer proximal three phalanges of the other five taxa (Table 7). Regression analyses indicate common positive trends of increasing PC 2 scores with increasing

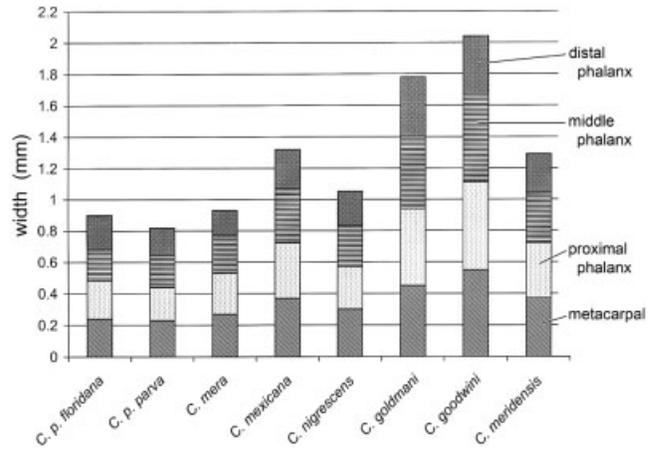


Fig. 6. Diagrammatic representations of the mean width values for the elements of digit III among the eight taxa of *Cryptotis*. Taxa are listed from left to right in order of increasing body size.

PC 1 scores within each of the larger groupings (Fig. 8). These regressions may be roughly interpreted as general interspecific trends of increasing lengths of metacarpal, proximal phalanx, and middle phalanx and corresponding decrease in length of distal phalanx and width of metacarpal (PC 2) with increasing overall size of digit III (PC 1).

Patterns of Variation Among Taxa

***Cryptotis mexicana* group.** The three representatives of the *Cryptotis mexicana* group in our study have body sizes that are medium to large in relation to other species in the genus *Cryptotis*. This size range is generally representative of the group as a whole. In general, these species have short, broad metacarpals and phalanges, except for the distal phalanx, which is elongate (Tables 2–6). The kera-

TABLE 5. Widths (mm) of bones comprising digit III

Taxon of <i>Cryptotis</i>	n	Metacarpal (MW)	Proximal phalanx (PPW)	Middle phalanx (MPW)	Distal phalanx (DPW)
<i>floridana</i>	11	0.24 ± 0.03 0.20–0.29	0.24 ± 0.03 0.18–0.29	0.20 ± 0.02 0.17–0.24	0.22 ± 0.04 0.14–0.28
<i>parva</i>	10	0.23 ± 0.02 0.19–0.29	0.21 ± 0.02 0.19–0.24	0.20 ± 0.02 0.17–0.22	0.18 ± 0.03 0.14–0.23
<i>mexicana</i>	20	0.37 ± 0.03 0.33–0.42	0.35 ± 0.03 0.32–0.47	0.35 ± 0.03 0.29–0.41	0.25 ± 0.02 0.22–0.28
<i>mera</i>	2	0.27 ± 0.04 0.25–0.30	0.26 ± 0.01 0.25–0.27	0.24 ± 0.002 0.23–0.24	0.16 ± 0.03 0.13–0.18
<i>nigrescens</i>	16	0.30 ± 0.04 0.25–0.41	0.27 ± 0.03 0.21–0.35	0.26 ± 0.03 0.21–0.31	0.22 ± 0.06 0.15–0.36
<i>goldmani</i>	10	0.45 ± 0.04 0.40–0.55	0.49 ± 0.04 0.43–0.59	0.46 ± 0.05 0.39–0.57	0.38 ± 0.10 0.29–0.61
<i>goodwini</i>	12	0.55 ± 0.05 0.44–0.64	0.56 ± 0.05 0.44–0.63	0.56 ± 0.05 0.44–0.62	0.37 ± 0.06 0.31–0.54
<i>meridensis</i>	20	0.37 ± 0.02 0.32–0.40	0.35 ± 0.02 0.31–0.39	0.32 ± 0.04 0.21–0.36	0.25 ± 0.04 0.20–0.35

Statistics are mean ± SD and range.

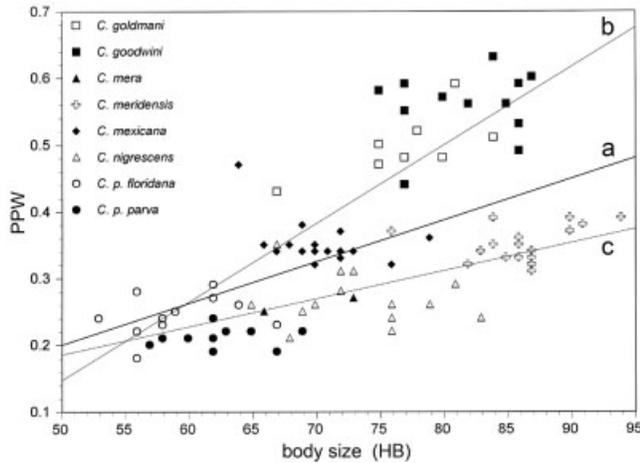


Fig. 7. Regressions of width of proximal phalanx (PPW) on body size (HB). Line a: Regression for all taxa ($PPW = 0.00623 HB + 0.113$; $F = 41.22$, $P = 0.000$, $R^2 = 29.8\%$; $n = 99$). Line b: Regression for the three members of the *Cryptotis mexicana* group (*C. goldmani*, *C. goodwini*, *C. mexicana*; $PPW = 0.018 HB + 0.441$; $F = 52.93$, $P = 0.000$, $R^2 = 57.6\%$; $n = 41$). Line c: Regression for the remaining taxa (*C. mera*, *C. meridensis*, *C. nigrescens*, *C. p. floridana*, *C. p. parva*; $PPW = 0.0214 HB + 0.00414$; $F = 96.60$, $P = 0.000$, $R^2 = 63.3\%$; $n = 58$).

tinous claw is likewise elongate, and, although it is not obvious from the distal phalanx, the claw is also much broadened (Woodman and Timm, 1999).

Among these species the relative length of distal phalanx, length of claw, and breadth of metacarpals and phalanges tend to increase rapidly with body size among species. The magnitude of differences in these variables makes the three taxa easy to distinguish from one another. These forefoot modifications seemingly form a graded series (*C. mexicana* → *C. goldmani* → *C. goodwini*), with *C. goodwini* possessing what would seem to be the most derived state of

TABLE 7. Factor loadings for the first two axes from PCA of five variables from the forefoot skeleton of eight taxa of *Cryptotis* (Fig. 8)

Variable	Correlations	
	PC 1	PC 2
DPL	-0.451	0.552
MPL	-0.421	-0.278
PPL	-0.492	-0.332
ML	-0.377	-0.530
MW	-0.486	0.475
Eigenvalue	2.8347	1.2239
Proportion of variation	56.7%	24.5%

the forefeet (i.e., short, broad metacarpals, proximal phalanges, and middle phalanges; long, broad distal phalanges). This sequence of taxa is slightly at odds, however, with morphological studies of the humerus, in which it has been suggested that *C. goldmani* is the most derived species in the *C. mexicana* group (Woodman and Timm, 1999).

***Cryptotis nigrescens* group.** *Cryptotis mera* and *C. nigrescens* are both medium-sized species. Although this size is representative of mean body size in the *C. nigrescens* group as a whole, the group also includes small-bodied species (Woodman and Timm, 1993). The metatarsal and phalanges of species in the *C. nigrescens* group are long and slender, with the exception of the distal phalanx and claw sheath, which are short and slender (Tables 2–6). This morphology of the manus appears to represent the generalized plesiomorphic condition for the genus (Woodman and Timm, 1999). The available sample for *C. mera* is limited, but the two individuals of this species fall within the range of variation for *C. nigrescens* for most digit III variables and characters.

***Cryptotis parva* group.** *Cryptotis parva floridana* and *C. p. parva* are small-bodied forms. In

TABLE 6. Proportional widths (%) of individual bones comprising digit III

Taxon of <i>Cryptotis</i>	n	Metacarpal (MW)	Proximal phalanx (PPW)	Middle phalanx (MPW)	Distal phalanx (DPW)
<i>floridana</i>	11	9 ± 1 7–11	16 ± 2 11–20	20 ± 3 17–26	32 ± 8 18–39
<i>parva</i>	10	10 ± 1 8–12	16 ± 1 15–19	24 ± 3 19–29	29 ± 6 21–40
<i>mexicana</i>	20	15 ± 1 12–17	24 ± 3 21–34	43 ± 6 32–52	19 ± 2 16–26
<i>mera</i>	2	10 ± 1 9–11	16 16–16	24 ± 2 23–25	21 ± 4 19–24
<i>nigrescens</i>	16	11 ± 1 9–13	16 ± 1 14–18	27 ± 2 22–30	27 ± 6 16–44
<i>goldmani</i>	10	17 ± 1 15–19	32 ± 2 28–35	44 ± 9 32–58	21 ± 4 17–28
<i>goodwini</i>	12	21 ± 2 16–24	34 ± 3 26–38	50 ± 7 41–64	19 ± 3 16–26
<i>meridensis</i>	20	11 ± 1 10–13	21 ± 2 18–24	31 ± 5 19–42	22 ± 4 17–32

Percentages were calculated by dividing the width of each bone by its length. Statistics are mean ± SD and range.

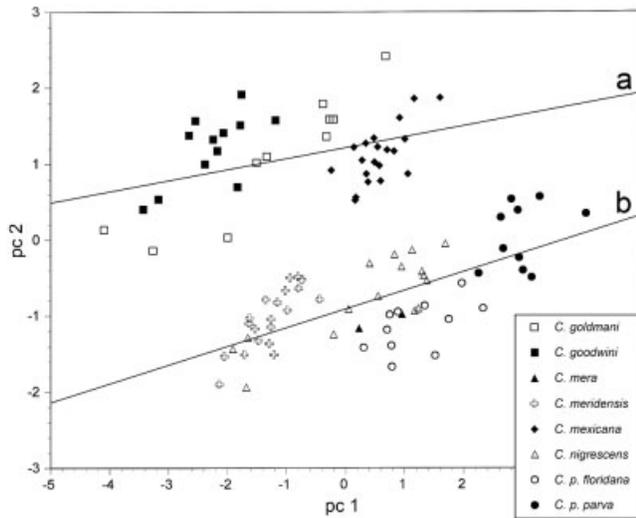


Fig. 8. PCA of five variables from the forefoot skeleton of eight taxa of *Cryptotis* (Table 7). Line a: Regression for the *C. mexicana* group ($PC2 = 0.140 PC1 + 1.22$; $F = 7.79$, $P = 0.008$; $R^2 = 16.3\%$; $n = 42$). Line b: Regression for the other five taxa ($PC2 = 0.243 PC1 - 0.914$; $F = 53.02$, $P = 0.000$; $R^2 = 48.2\%$; $n = 59$).

general, taxa in the *C. parva* group tend to be small, although this group includes both small- and medium-sized taxa. Like in the *C. nigrescens* group, the forefoot skeleton of taxa in the *C. parva* group exhibits the probable plesiomorphic condition for the genus. The metatarsal and phalanges of taxa are long and slender, with the exception of the distal phalanx and claw sheath, which are short and slender (Tables 2–6). *Cryptotis p. parva* can be separated from *C. p. floridana* and other members of the genus by having claw sheaths that are long relative to the length of the distal phalanx (Table 2). This characteristic may have functional significance, because the relatively short distal phalanx provides less underlying support for the claws. Alternatively, the difference in claw length may be a result of less wear on the claw in *C. p. parva*. Other than this difference, the distal phalanges are proportionally similar in length to those of *C. p. floridana* and members of the *C. nigrescens* group. The smallest taxon in our study, *C. p. floridana*, appears to be distinguished both from *C. p. parva* and from other

members of the genus by its exceptionally long digit in comparison with its body size (Table 2). In other respects, the digit and its component bones are proportional to those of *C. p. parva*. However, body size in our study was calculated from external measurements recorded on skin tags, and *C. p. floridana* originally was described as being larger than *C. p. parva* (Merriam, 1895; Bangs, 1898). The anomalously large digits that we recorded for *C. p. floridana* could be an artifact of how the original external measurements were taken for the particular specimens that we used.

***Cryptotis thomasi* group.** *Cryptotis meridensis* is one of the largest species in the genus (Woodman, 2002). Although named species in the *C. thomasi* group are predominantly large, the group also includes some medium-sized taxa. The distal phalanx and the claw sheath tend to be elongate, although not to the degree seen in the *C. mexicana* group. In addition, the claw is slender rather than broadened, as in the *C. mexicana* group (Woodman and Timm, 1999; Woodman, 2002). The metatarsals of *C. meridensis* are elongate, and the middle phalanx is somewhat shortened. The metatarsal and proximal and middle phalanges are moderately broadened. The relative breadth of the metacarpal appears proportional to those in the *C. nigrescens* and *C. parva* groups, but this is a consequence of its greater length in *C. meridensis* (Tables 2–6).

Parsimony Analysis of Forefoot Characters

We used the numerical data resulting from our analyses of the X-ray images to assist in defining morphological characters. In particular, these analyses helped us sort out interspecific variation in form from changes resulting from scaling among individuals and taxa of different body sizes. We partitioned the variation among eight transition series (TS) by plotting ratio means ± 1 SD for each taxon. Taxa with overlapping intervals were scored the same, whereas taxa with gaps between intervals were scored differently. Hence, the ratio values provide guidance about mean differences among samples rather than absolute measures of differences among all individuals. In addition, we included one

TABLE 8. Character matrix based on analysis of digit III for taxa of *Cryptotis*

Taxon of <i>Cryptotis</i>	Transition series								
	1	2	3	4	5	6	7	8	9
<i>parva</i>	0	0	1	0	0	0	0	1	0
<i>floridana</i>	1	0	0	0	0	0	0	0	0
<i>nigrescens</i>	0	0	0	0	0	0	0	0	0
<i>mera</i>	0	0	0	0	0	0	0	0	0
<i>meridensis</i>	0	1	0	0	1	0	1	1	0
<i>mexicana</i>	0	0	0	1	1	1	2	2	1
<i>goldmani</i>	0	0	0	1	2	1	3	3	2
<i>goodwini</i>	0	0	0	2	2	1	3	3	2

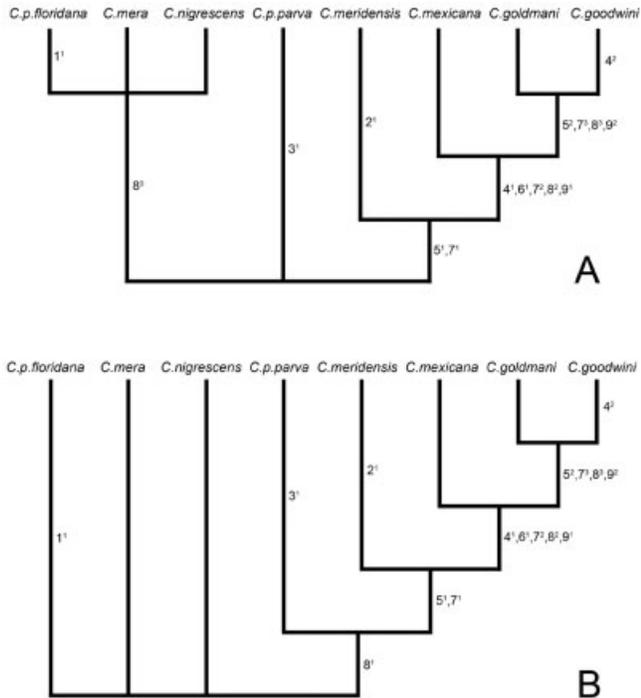


Fig. 9. Two most parsimonious trees derived from exhaustive phylogenetic analysis of nine transition series (16 steps; consistency index = 1.00; homoplasy index = 0.00; retention index = 1.00). Numbers along branches are transition series. Superscripts represent characters (Table 8).

other transition series (TS #9) involving the fore claw that is based on data in the literature. These transition series are described in the following list. The taxon scores for each transition series are summarized in Table 8.

1. Length of Digit III: 0 = short (mean P3L/HB < 8.0%); 1 = long (> 8.5%).
2. Length of metacarpal: 0 = short (mean ML/P3L < 54%); 1 = long (> 54%).
3. Length of claw supported by distal phalanx: 0 = long (mean DPL/CL > 45%); 1 = shorter (<45%).
4. Shape of metacarpal: 0 = long and narrow (mean MW/ML < 13%); 1 = moderately long and broad (15–19%); 2 = short and broad (> 19%).
5. Shape of proximal phalanx: 0 = long and narrow (mean PPW/PPL < 19%); 1 = moderately long and broad (19–28%); 2 = short and broad (> 28%).
6. Shape of middle phalanx: 0 = long and narrow (mean MPW/MPL < 36%); 1 = short and broad (> 36%).
7. Length of distal phalanx: 0 = short (mean DPL/P3L < 18%; shorter than either middle or proximal phalanx); 1 = moderately long (18–20%; subequal to, or slightly longer than, middle phalanx, but shorter than proximal phalanx); 2 = long (20–30%; much longer than middle phalanx, but slightly shorter than proximal phalanx); 3 = very

long (> 30%; longer than either middle or proximal phalanx).

8. Length of keratinous claw: 0 = short (mean CL/P3L < 34%); 1 = moderately long (34–41%); 2 = long (42–54%); 3 = very long (>54%).
9. Breadth of keratinous claw (modified from Woodman and Timm, 2000): 0 = narrow; 1 = moderately broad; 2 = very broad.

Exhaustive analysis of these transition series in PAUP yielded two shortest trees of 16 steps each (Fig. 9). Although these trees were constructed using only characters of the forefoot, their topologies correspond well with those of phylogenies presented by Woodman (2005) and Woodman and Timm (1999, 2000) that were based on a suites of external, craniomandibular, and postcranial skeletal characters. Those studies focused on the *Cryptotis mexicana* group, but also included selected members of the *C. nigrescens* group and *C. parva* group, and our analysis provides additional support for those trees. In addition, our analysis suggests that the *C. thomasi* group, represented by *C. meridensis*, shares a basal sister relationship with the *C. mexicana* group (Fig. 9). The relationships of the *C. thomasi* group within the genus had not previously been tested, and the inclusion of *C. meridensis* provides an interesting first approximation of the topology of a more inclusive phylogeny.

DISCUSSION

Previous studies of *Cryptotis* have indicated that certain members of the genus exhibit derived modifications of the forelimb that are distinct from the stereotypical morphology of shrews as modeled by long-tailed shrews of the genus *Sorex*. Whether the long, slender humerus, metacarpals, and proximal and middle phalanges, and the relatively short distal phalanges of terrestrial *Sorex* (Reed, 1951) are plesiomorphic for the family Soricidae remains to be tested. Regardless, the patterns of variation of these bones within *Cryptotis* suggest that they are modified with respect to the long-tailed shrews. The humeri are relatively shorter and more robust, with greater development of processes; the metacarpals, proximal phalanges, and distal phalanges are likewise more robust; and the distal phalanges are longer, even in the least derived small-eared shrew (Woodman and Timm, 1999).

Within the genus *Cryptotis*, members of the *C. nigrescens* group and the *C. parva* group appear to have the least modification of the forelimbs. In fact, members of these two groups are nearly indistinguishable using forelimb characters alone, except for the larger sizes of many members of the *C. nigrescens* group. Based on the morphology of *C. meridensis*, the most distinguishing characteristic of the *C. thomasi* group is the elongate metacarpal. In addition, the metacarpals, proximal phalanges, and mid-

dle phalanges are moderately broadened and the distal phalanges are elongate. The most derived characters appear among members of the *C. mexicana* group. These shrews exhibit progressive shortening and broadening of the metacarpals, proximal phalanges, and middle phalanges, and elongation of the distal phalanges.

The strong modifications of the humerus and manus of members of the *Cryptotis mexicana* group have been hypothesized to be adaptations that enhance digging. The greatly enlarged processes on the humerus; the broadened forefeet with shorter, more robust metacarpals and phalanges; and the elongate and broadened fore claws in some species have been characterized as appearing superficially convergent on a "mole-like" morphology (Woodman and Timm, 1999). Talpidae (moles) also tend to have larger numbers of carpals (*Scalopus*—Edwards, 1937; *Neurotrichus*, *Scapanus*—Reed, 1951). Scaphoid, lunate, and centrale are distinct, separate bones in moles. Like talpids, scaphoid and lunate are unfused in *Cryptotis*, but these shrews do not have a separate centrale. In at least some other shrews, like the more generalized, mostly terrestrial shrew, *Sorex*, scaphoid and lunate are fused into a single scapholunate (Reed, 1951). It would be edifying to survey the Soricidae regarding the pattern of fusion of carpals among genera and determine whether this character corresponds to phylogeny or represents a functional morphological adaptation more related to the animals' ecology.

Digital X-ray technology provides a technique for revealing bone that is preserved within dried skins and that otherwise would be unobservable without sacrificing the integrity of the original specimen. Because it is noninvasive, the technology can be used on specimens such as holotypes and rare or extinct species, whose inherent value should preclude destructive sampling. Even for species of small mammals that are represented by large numbers of dried skins, study of the manus and pes often is hindered because of the lack of value formerly attached to skeletal material, and the resulting paucity of specimens of this type. As we have shown in this study using skins of small-eared shrews, digital X-ray technology provides a means of obtaining appropriate samples sizes for carrying out statistical analyses and characterizing species.

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APPENDIX

Specimens Examined

All specimens and catalog numbers are from the Division of Mammals, National Museum of Natural History, Washington, DC (USNM).

Cryptotis goldmani (10). Mexico: Guerrero (70245, 70247, 126896, 126897, 126947); Oaxaca (68542, 68547, 71458–71460).

Cryptotis goodwini (12). Guatemala: Huehuetenango (77069); Jalapa (275681); Quezaltenango (77070, 77073, 77076–77078, 77080, 77082, 77084, 77086, 77087).

Cryptotis mera (2). Panama: Darien (178974, 178975).

Cryptotis meridensis (20). Venezuela: Mérida (579273, 579274, 579276–579283, 579285–579289, 579292–579294, 579299, 579300).

Cryptotis mexicana (20). Mexico: Oaxaca (68298, 68299, 68303, 68304, 68308, 68312, 68314, 68520, 68521, 68524, 68528, 68533, 68538, 68540, 68544, 68551, 68553, 68554, 68558, 68559).

Cryptotis nigrescens (16). Panama: Bocas del Toro (516623, 541022, 541032, 541035, 541042); Bocas del Toro/Chiriqui Border (541021, 541023–541025, 541039, 541043); Chiriqui (296743, 396514, 516628, 541030, 541037).

Cryptotis parva parva (10). USA: Nebraska: *Washington Co.* (36447–36449, 36452–36458).

Cryptotis parva floridana (11). USA: Florida: *Marion Co.* (210387–210389, 210391, 262203, 262205, 262344–262347); *Sarasota Co.* (262343).

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