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Coming of age: morphometric variation in the hand skeletons of juvenile and adult Lesser Treeshrews (Scandentia: Tupaiidae: *Tupaia minor* Günther, 1876)

Neal Woodman,* Ananth Miller-Murthy, Link E. Olson, and Eric J. Sargis

U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA (NW)
Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC-108, Washington, DC 20013, USA (NW, LEO, EJS)
Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT 06520, USA (AM-M, EJS)
University of Alaska Museum, University of Alaska Fairbanks, Fairbanks, AK 99775, USA (LEO)
Department of Anthropology, Yale University, P.O. Box 208277, New Haven, CT 06520, USA (EJS)

** Correspondent: woodmann@si.edu*

Morphometric analyses of the manus skeleton have proven useful in understanding species limits and morphological divergence among tupaiid treeshrews (Scandentia: Tupaiidae). Specimens in these studies are typically limited to mature individuals with fully erupted permanent dentition, which eliminates potentially confounding variation attributable to age, but also can exclude rare taxa and small island populations that are poorly represented in systematic collections. To determine the real limits associated with including immature animals in such studies, we used multivariate analyses to study sexual and age variation of the manus skeleton in two allopatric populations of the Lesser Treeshrew (*Tupaia minor* Günther, 1876) from the Malay Peninsula and from Borneo that we treated as separate samples. Individuals were aged using dental eruption of the permanent dentition. We also recorded the degree of epiphyseal fusion of the bones of the manus based on x-rays of study skins. We then tested our ability to distinguish the two populations using a series of discriminant function analyses of hand measurements from samples that included varying proportions of immature individuals and adults. We found no evidence of sexual dimorphism in hand proportions, permitting us to combine females and males in our samples. Epiphyseal fusion of the metacarpals and phalanges typically occurs by the time the third molars have completely erupted, and fusion of the distal epiphyses of the radius and ulna typically occurs by the time the permanent fourth premolars are in place. There is occasional asynchrony between dental age and epiphyseal fusion. In both populations, the hands of most infants and subadults provide morphometric values within the range of variation of adults, although they are typically distributed in the lower part of the adult range and have the potential to bias the sample toward lower mean size. The inclusion of infants and subadults when attempting to discriminate between two taxa generally results in lower rates of correct classifications, although the rates increase as the sample of immature individuals is limited to older subadults. As a general rule, we recommend that specimens of infants and subadults continue to be excluded from analyses when exploring taxonomic boundaries among treeshrews. In cases of extremely small sample sizes of adults, however, older subadults—in which the permanent third premolars are erupting or in place—can be used with appropriate caution.

Key words: digit, morphology, postcranium, ray, Southeast Asia, *Tupaia malaccana*

Systematic studies of small mammals have shown that interspecific differences in the proportions of the metacarpals and phalanges of the manus can often be as great as those from traditional skull proportions, providing a powerful tool for distinguishing taxa and delimiting species (Woodman and Morgan 2005; Woodman and Stephens 2010; Sargis et al. 2013a, 2013b, 2014, 2016). Traditional dried study skins of mammals typically preserve the complete manus skeleton, which is easily, inexpensively, and nondestructively revealed using digital x-ray imaging. Proportions of individual hand bones can then be reliably and repeatably measured from the resulting images (Woodman and Morgan 2005). Besides providing an additional morphological data set not directly correlated developmentally or functionally with more traditional data from skins and skulls, measurement of hand bones has the advantage of providing relatively large data sets for statistical analysis. These data are also useful for identifying specimens for which full suites of skull measurements are unavailable (Sargis et al. 2013a).

In our previous morphometric studies of the manus of tupaiid treeshrews (Scandentia: Tupaiidae), we used data only from adults, which we defined as individuals having completely erupted adult dentition (Sargis et al. 2013a, 2013b, 2014, 2016). By the time the permanent dentition is completely erupted in the Common Treeshrew, *Tupaia glis* (Diard, 1820), epiphyseal fusion of nearly all forelimb bones associated with major limb joints is completed (Shigehara 1980), so we assume the bones of the manus have also terminated growth by the time the adult dentition is in place and probably well before. We have encountered no unfused hand bones in any specimens dentally classified as adults in our samples (Sargis et al. 2013a, 2013b, 2014, 2016).

One problem commonly encountered when working with treeshrews is the low numbers of specimens available for study from a population of interest. A recent example for us is *T. minor sincepis* Lyon, 1911, a subspecies restricted to Singkep Island, Indonesia (Hawkins 2018). Among the six specimens available in museum collections (USNM 113145, 113146, 123104–123107), there is a single adult, the holotype (USNM 123105). The remaining five specimens are classified either as subadults or infants based on dental eruption. If measurements from the manus of one or more of the juvenile specimens could be included, it would increase our sample size, possibly providing a better sense of both intrapopulation variability and the potential for morphological overlap with more widespread populations of *T. minor* Günther, 1876, on Borneo, the Malay Peninsula, or Sumatra. This raises the questions of 1) when during development do the epiphyses of the metacarpals and phalanges of the hands of treeshrews a) unite and b) fully fuse; 2) at what relative age do the bones of these structures reach their adult proportions; and, most important, 3) can measurements from the manus of any preadult individuals be included as part of a sample meant to represent the adult population?

Studies of epiphyseal fusion in treeshrews and other mammals have dealt primarily with bones associated with the major limb joints (Brimacombe 2017). In *T. glis* (*sensu lato*), for example, epiphyseal fusion in the limbs proceeds sequentially from the bones of the elbow, to those of the hip, ankle, wrist, knee, and finally, the shoulder (Shigehara 1980). Little attention has focused on fusion of the metapodials and phalanges of the manus and pes. *Tupaia glis* exhibits negative allometry in postnatal lengthening of the hand (measured as metacarpal + proximal phalanx of ray III) relative both to body weight and more relevantly, to total forelimb length (Schilling and Petrovitch 2006). The decrease in relative length of the metacarpal and proximal phalanx during development suggests that bone growth of the manus rays occurs early in development and ceases in a preadult stage. Hence, bones of the rays in some preadult stages should not have different proportions from those of adult treeshrews.

We investigated epiphyseal fusion and changes in the proportions of the bones of the manus by inspecting x-rays of the manus of 85 adults and 24 subadults (based on dental eruption) from two allopatric populations of the Lesser Treeshrew, a mostly arboreal species that is relatively small in size (~54 g; Emmons 2000; Sargis 2001, 2002). Because fusion of the bones of the manus does not necessarily signify end of growth or attainment of adult proportions, we measured the metacarpals and phalanges of the manus and used multivariate techniques to investigate variation in measurements among different dental age groups within each population. Finally, we tested how including various subsets of subadults in our data set affects our ability to distinguish the two populations from one another.

Materials and Methods

We aged, imaged, and measured 109 specimens of Lesser Treeshrews from the Malay Peninsula (n = 59) and from Borneo (n = 50). These two populations have been recognized as *Tupaia minor malaccana* Anderson, 1879 and *T. minor minor*, respectively (Hawkins 2018). Although the validity of the two subspecies is a question of interest that we will address in the future, for the purposes of this paper, they represent two well-sampled populations of *T. minor*. To avoid potentially confounding geographic variation within our sample, we treated the two populations as distinct entities throughout the study. This also permitted us to test how the inclusion of subadults affects both intrapopulation and interpopulation variation. All specimens are catalogued in the collection of the Division of Mammals, National Museum of Natural History (USNM), Washington, DC (Appendix I).

As used herein, the term "digit" refers to that part of the manus associated with the proximal, middle, and distal phalanges (i.e., thumb and fingers). "Ray" refers to that part of the manus associated with the phalanges plus the metacarpal (i.e., thumb and fingers plus palm).

To measure individual hand bones, we followed procedures employed in previous studies of treeshrews (Sargis et al. 2013a, 2013b, 2014, 2016) and soricids (Woodman and Morgan 2005; Woodman and Stephens 2010). The right and left manus of study skins were x-rayed with a scale using a Thermo Scientific Kevex x-ray source interfaced with a desktop computer running Kevex X-ray Source Control Interface (version 4.1.3; Palo Alto, California) in the Division of Fishes, USNM. Digital images were captured using Varian Medical Systems Image Viewing and Acquisition software (VIVA version 2.0; Waltham, Massachusetts) and transferred to ImageJ (Schneider et al. 2012) for measuring. Measurements were taken from the most complete image of either the right or left side and supplemented where necessary with measurements from the other side. Original measurements for the samples are provided in Supplementary Data SD1.

We recorded the following measurements from all five rays, with the exception that depths (dorsopalmar distances) of bones were substituted for widths (mediolateral distances) in ray I because of its typical orientation in the images (Fig. 1): MD, metacarpal depth; ML, metacarpal length; MW, metacarpal width; PPD, proximal phalanx depth; PPL, proximal phalanx length; PPW, proximal phalanx width; MPL, middle phalanx length; MPW, middle phalanx width; DPD, distal phalanx depth; DPL, distal phalanx length; DPW, distal phalanx width (see Sargis et al. 2013a). The numeral prior to the standard measurement abbreviation designates the respective ray. Summary statistics of all variables from the manus are presented in Table 1. All multivariate analyses were run in Systat 11.00.01 (Systat Software, Inc., Chicago, Illinois) using 19 $\log_{10}$-transformed hand variables (1ML, 1PPL, 1MD, 1PPD, 1DPD, 2ML, 2DPL, 2MW, 2PPW, 3ML, 3DPL, 3MW, 4ML, 4DPL, 4MW, 4PPW, 5ML, 5DPL, 5MW). Because of missing data resulting from postmortem reorientation of the bones of the hand, this suite of variables represents a compromise between number of variables and number of specimens.

Age classification.—Shigehara (1980) determined that the beginning of eruption of the permanent upper dentition in *T. glis* follows the order: $M^1 > M^2 > M^3 > (P^4, P^3) > P^2 > (I^2, I^1, C^1)$, and the completion of eruption follows the order $M^1 > M^2 > M^3 > P^4 > P^3 > P^2 > I^2 > (I^1, C^1)$. The sequence for beginning of eruption of the permanent lower dentition is: $M_1 > M_2 > M_3 > P_2 > I_3 > P_4 > (I_1, C_1) > P_3 > I_2$, while that for completion of eruption is $M_1 > M_2 > M_3 > (P_2, I_3) > P_4 > I_1 > P_3 > C_1 > I_2$. Lower teeth generally erupt before the corresponding upper teeth (Shigehara 1980). These sequences differ from those reported for *T. glis* by both Lyon (1913) and Slaughter et al. (1974) (which differ from each other), most notably in the relative eruption sequence of P^2, P^3, and P^4. These differences may be attributable to taxonomic differences, as the concept of *T. glis* has changed over the past century, but reconciling these differences is hindered by the failure of some (e.g., Slaughter et al. 1974; Shigehara 1980) to include lists of specimens examined. We also acknowledge a degree of arbitrariness in classifying a relative dental stage during the period of rapid tooth eruption and replacement in small-bodied mammals.

We determined the relative age of each individual by inspecting the upper and lower dentition. In our limited sample, upper molars and premolars in Malayan specimens tended to erupt before their lower counterparts, whereas in Bornean specimens, lower teeth tended to erupt first. Neither pattern was universal within either population. Regardless, the eruption patterns are sufficiently general to establish a usable age classification. Herein, we use three general age categories (infant, subadult, adult) based on dentition. We further classified infants and subadults using a numerical scale from 1 to 7 to represent the relative stage of tooth eruption. These numbers reflect only those stages that we observed within our sample rather than a complete sequence of tooth eruption.

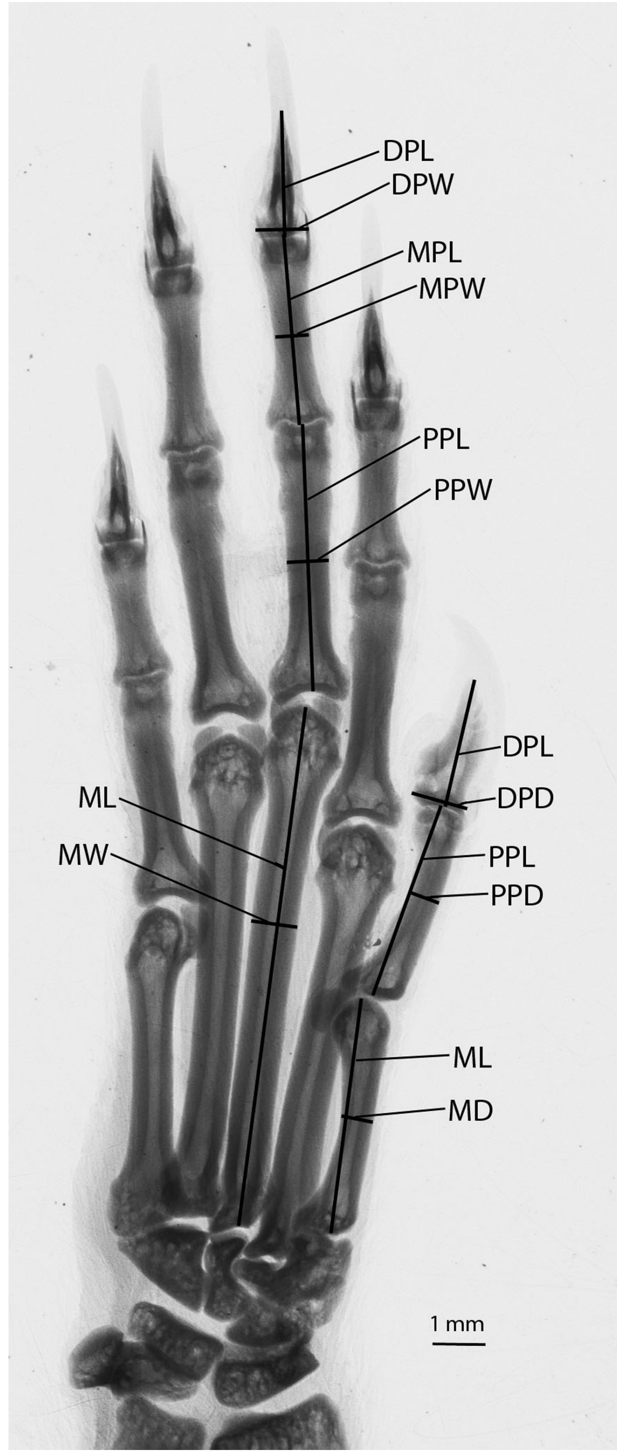

Fig. 1.—Digital x-ray of the right manus (palmar view) of *Tupaia belangeri* (USNM 201431), from Sargis et al. (2013a), illustrating the measurements used in this study. DPD, distal phalanx depth; DPL, distal phalanx length; DPW, distal phalanx width; MD, metacarpal depth; ML, metacarpal length; MW, metacarpal width; MPL, middle phalanx length; MPW, middle phalanx width; PPD, proximal phalanx depth; PPL, proximal phalanx length; PPW, proximal phalanx width. The original negative image was converted to a positive image.

Table 1.—Measurements of individual bones of the manus from the Malayan and Bornean populations of *Tupaia minor*. Statistics are mean ± *SD* and range. Sample sizes are in parentheses. Abbreviations are explained in the text.

Malayan population			Bornean population		
Adult (n = 45)	Subadult (n = 12)	Infant (n = 2)	Adult (n = 40)	Subadult (n = 5)	Infant (n = 5)
1ML					
3.14 ± 0.12	3.14 ± 0.14	3.11	3.12 ± 0.17	3.09 ± 0.08	2.82 ± 0.24
2.92–3.40	2.90–3.43	3.06–3.17	2.83–3.47	3.02–3.22	2.52–3.09
					(n = 4)
1PPL					
2.84 ± 0.11	2.79 ± 0.09	2.88	2.78 ± 0.16	2.73 ± 0.11	2.64 ± 0.33
2.63–3.04	2.61–2.93	2.84–2.93	2.50–3.15	2.62–2.90	2.16–2.95
1DPL					
1.93 ± 0.17	1.86 ± 0.07	1.88	1.89 ± 0.21	1.85 ± 0.12	1.69 ± 0.19
1.52–2.40	1.73–2.00	1.82–1.95	1.26–2.47	1.72–2.00	1.43–1.90
	(n = 11)		(n = 38)		
1MD					
0.47 ± 0.03	0.45 ± 0.03	0.50	0.49 ± 0.04	0.46 ± 0.05	0.49 ± 0.03
0.41–0.54	0.41–0.49	0.48–0.53	0.42–0.57	0.43–0.56	0.44–0.53
1PPD					
0.42 ± 0.04	0.40 ± 0.04	0.44	0.42 ± 0.04	0.40 ± 0.04	0.38 ± 0.04
0.34–0.50	0.32–0.44	0.40–0.48	0.33–0.51	0.37–0.47	0.36–0.44
1DPD					
0.88 ± 0.07	0.84 ± 0.06	0.76	0.85 ± 0.07	0.86 ± 0.06	0.77 ± 0.06
0.71–1.07	0.72–0.91	0.75–0.77	0.68–1.04	0.76–0.90	0.70–0.86
	(n = 11)				
2ML					
5.66 ± 0.25	5.63 ± 0.23	5.41	5.54 ± 0.32	5.46 ± 0.11	5.30 ± 0.29
5.20–6.22	5.26–5.88	5.24–5.58	4.93–6.30	5.29–5.59	4.98–5.61
2PPL					
3.96 ± 0.16	3.87 ± 0.18	4.00	3.87 ± 0.25	3.82 ± 0.09	3.68 ± 0.30
3.65–4.33	3.57–4.15	3.94–4.05	2.92–4.46	3.74–3.96	3.37–4.03
(n = 42)	(n = 10)		(n = 39)		
2MPL					
2.43 ± 0.24	2.46 ± 0.13	2.14	2.36 ± 0.21	2.29 ± 0.22	2.23 ± 0.20
1.88–2.88	2.28–2.63		1.88–2.83	2.09–2.49	2.03–2.54
(n = 18)		(n = 1)	(n = 24)	(n = 4)	
2DPL					
2.04 ± 0.14	1.83 ± 0.23	1.87	1.96 ± 0.21	1.82 ± 0.22	1.76 ± 0.15
1.75–2.32	1.31–2.11	1.87–1.87	1.14–2.27	1.61–2.18	1.54–1.93
(n = 44)	(n = 11)		(n = 36)		
2MW					
0.55 ± 0.03	0.54 ± 0.03	0.56	0.54 ± 0.04	0.53 ± 0.04	0.51 ± 0.03
0.43–0.62	0.47–0.58	0.54–0.59	0.48–0.62	0.47–0.59	0.47–0.55
2PPW					
0.49 ± 0.03	0.47 ± 0.05	0.51	0.50 ± 0.05	0.48 ± 0.03	0.46 ± 0.05
0.43–0.57	0.36–0.52	0.48–0.55	0.35–0.58	0.45–0.52	0.40–0.54
(n = 44)			(n = 39)		
2MPW					
0.39 ± 0.05	0.36 ± 0.04	0.37	0.34 ± 0.03	0.37 ± 0.04	0.33 ± 0.07
0.32–0.52	0.31–0.41		0.28–0.41	0.34–0.41	0.26–0.43
(n = 26)	(n = 6)	(n = 1)	(n = 19)	(n = 3)	
2DPW					
0.75 ± 0.05	0.70 ± 0.04	0.74	0.73 ± 0.04	0.73	0.72
0.67–0.88	0.62–0.73	0.73–0.74	0.66–0.79	0.71–0.74	0.66–0.78
(n = 19)	(n = 6)		(n = 16)	(n = 2)	(n = 2)
3ML					
6.74 ± 0.25	6.72 ± 0.29	6.61	6.63 ± 0.33	6.48 ± 0.20	6.26 ± 0.39
6.35–7.34	6.15–7.20	6.40–6.81	6.01–7.32	6.18–6.72	5.83–6.76
(n = 43)			(n = 39)		
3PPL					
4.23 ± 0.19	4.15 ± 0.17	4.35	4.17 ± 0.18	4.09 ± 0.10	4.05 ± 0.30
3.67–4.49	3.95–4.46	4.33–4.37	3.63–4.50	4.01–4.23	3.79–4.37
(n = 34)	(n = 7)		(n = 36)		
3MPL					
2.66 ± 0.33	2.73 ± 0.15	—	2.74 ± 0.28	2.55	2.38 ± 0.23
2.13–3.20	2.58–2.93		2.20–3.29		2.14–2.62
(n = 12)	(n = 4)		(n = 16)	(n = 1)	(n = 4)
3DPL					
2.18 ± 0.18	2.07 ± 0.21	2.08	2.12 ± 0.21	1.92 ± 0.17	2.05 ± 0.21
1.66–2.54	1.67–2.34	2.07–2.08	1.35–2.62	1.74–2.19	1.79–2.27

Table 1.—Continued

Malayan population			Bornean population		
Adult (*n* = 45)	Subadult (*n* = 12)	Infant (*n* = 2)	Adult (*n* = 40)	Subadult (*n* = 5)	Infant (*n* = 5)
3MW					
0.56 ± 0.03 0.50–0.61 (*n* = 44)	0.54 ± 0.03 0.50–0.60	0.54 0.50–0.58	0.55 ± 0.03 0.47–0.63 (*n* = 39)	0.54 ± 0.02 0.51–0.57	0.52 ± 0.04 0.49–0.59
3PPW					
0.52 ± 0.04 0.47–0.62 (*n* = 43)	0.50 ± 0.02 0.47–0.54 (*n* = 10)	0.54 0.50–0.58	0.53 ± 0.03 0.47–0.60 (*n* = 34)	0.50 ± 0.03 0.47–0.54 (*n* = 4)	0.49 ± 0.08 0.39–0.58
3MPW					
0.42 ± 0.05 0.34–0.54 (*n* = 16)	0.38 ± 0.04 0.32–0.42 (*n* = 5)	—	0.35 ± 0.03 0.30–0.41 (*n* = 14)	0.38 ± 0.03 0.36–0.40 (*n* = 2)	0.37 ± 0.09 0.24–0.47
3DPW					
0.74 ± 0.05 0.67–0.85 (*n* = 28)	0.72 ± 0.03 0.67–0.76 (*n* = 8)	0.74 0.73–0.74	0.75 ± 0.05 0.66–0.86 (*n* = 28)	0.74 ± 0.01 0.73–0.75 (*n* = 3)	0.75 ± 0.06 0.70–0.82 (*n* = 3)
4ML					
6.01 ± 0.24 5.50–6.62 (*n* = 43)	6.02 ± 0.23 5.53–6.41	6.08 6.00–6.16	5.91 ± 0.35 4.70–6.42 (*n* = 38)	5.80 ± 0.18 5.52–5.98	5.58 ± 0.16 5.44–5.81 (*n* = 4)
4PPL					
4.11 ± 0.21 3.53–4.50 (*n* = 41)	4.13 ± 0.19 3.90–4.53 (*n* = 10)	4.13 4.09–4.18	4.01 ± 0.24 3.20–4.32 (*n* = 34)	3.98 ± 0.10 3.88–4.14	3.92 ± 0.33 3.53–4.30
4MPL					
2.68 ± 0.24 2.30–3.04 (*n* = 13)	2.69 ± 0.20 2.46–3.06 (*n* = 7)	—	2.55 ± 0.29 2.13–3.12 (*n* = 21)	2.36 ± 0.18 2.18–2.53 (*n* = 3)	2.52 ± 0.18 2.32–2.76
4DPL					
2.08 ± 0.19 1.45–2.39	2.06 ± 0.17 1.72–2.29	1.95 1.83–2.07	2.05 ± 0.18 1.59–2.39 (*n* = 39)	1.91 ± 0.16 1.76–2.16	1.92 ± 0.21 1.65–2.12
4MW					
0.55 ± 0.03 0.49–0.61 (*n* = 44)	0.52 ± 0.02 0.50–0.56	0.54 0.52–0.55	0.54 ± 0.05 0.44–0.69 (*n* = 36)	0.53 ± 0.03 0.49–0.57	0.49 ± 0.02 0.48–0.52 (*n* = 4)
4PPW					
0.49 ± 0.03 0.43–0.55 (*n* = 42)	0.46 ± 0.03 0.40–0.50 (*n* = 10)	0.49 0.47–0.51	0.50 ± 0.04 0.40–0.57 (*n* = 39)	0.47 ± 0.02 0.44–0.51	0.45 ± 0.02 0.42–0.48
4MPW					
0.39 ± 0.04 0.30–0.48 (*n* = 25)	0.38 ± 0.03 0.34–0.41 (*n* = 8)	0.41 (*n* = 1)	0.36 ± 0.05 0.29–0.48 (*n* = 17)	0.35 ± 0.06 0.28–0.40 (*n* = 4)	0.34 ± 0.04 0.30–0.39
4DPW					
0.72 ± 0.03 0.66–0.80 (*n* = 25)	0.69 ± 0.04 0.66–0.72 (*n* = 2)	0.71 (*n* = 1)	0.76 ± 0.06 0.68–0.96 (*n* = 21)	0.74 ± 0.02 0.73–0.76 (*n* = 2)	0.78 (*n* = 1)
5ML					
4.07 ± 0.16 3.80–4.44	4.07 ± 0.17 3.72–4.31 (*n* = 11)	4.16 4.15–4.16	4.05 ± 0.26 3.47–4.67	3.95 ± 0.13 3.72–4.07	3.73 ± 0.18 3.55–4.01
5PPL					
3.40 ± 0.15 3.02–3.66 (*n* = 34)	3.43 ± 0.17 3.18–3.63 (*n* = 9)	3.36 3.28–3.44	3.25 ± 0.33 2.12–3.86 (*n* = 37)	3.29 ± 0.13 3.14–3.43	3.10 ± 0.39 2.67–3.41
5MPL					
1.99 ± 0.09 1.91–2.08 (*n* = 3)	2.00 1.72–2.28 (*n* = 2)	—	2.10 ± 0.21 1.75–2.49 (*n* = 13)	2.11 (*n* = 1)	2.05 ± 0.04 2.02–2.09 (*n* = 3)
5DPL					
1.78 ± 0.13 1.44–2.05	1.69 ± 0.15 1.37–1.90	1.60 1.47–1.73	1.74 ± 0.21 0.96–2.16 (*n* = 39)	1.56 ± 0.13 1.37–1.70	1.53 ± 0.19 1.28–1.79
5MW					
0.59 ± 0.05 0.47–0.68	0.56 ± 0.05 0.51–0.66 (*n* = 11)	0.61 0.60–0.61	0.53 ± 0.05 0.41–0.69 (*n* = 39)	0.51 ± 0.04 0.46–0.57	0.48 ± 0.04 0.44–0.55

Table 1.—Continued

	Malayan population			Bornean population		
	Adult ($n = 45$)	Subadult ($n = 12$)	Infant ($n = 2$)	Adult ($n = 40$)	Subadult ($n = 5$)	Infant ($n = 5$)
5PPW	0.48 ± 0.04 0.41–0.58 ($n = 41$)	0.46 ± 0.04 0.40–0.53	0.49 0.48–0.51	0.47 ± 0.04 0.39–0.54 ($n = 36$)	0.44 ± 0.03 0.41–0.48	0.43 ± 0.03 0.41–0.47 ($n = 4$)
5MPW	0.38 ± 0.07 0.30–0.51 ($n = 7$)	0.37 ± 0.03 0.35–0.39 ($n = 2$)	0.39 ($n = 1$)	0.33 ± 0.04 0.30–0.42 ($n = 11$)	0.31 ($n = 1$)	0.34 ± 0.04 0.29–0.38 ($n = 3$)
5DPW	0.71 ± 0.06 0.61–0.85 ($n = 32$)	0.67 ± 0.04 0.58–0.70 ($n = 7$)	0.66 0.65–0.66	0.67 ± 0.09 0.30–0.76 ($n = 29$)	0.69 ± 0.05 0.64–0.76	0.63 0.62–0.64 ($n = 2$)

INFANT: an individual in which M^3 and M_3 have not yet completed eruption. We defined a tooth as "erupting" from the time the clearly visible crown is at or projecting beyond the alveolar margin, until it is firmly rooted in solid bone with no surrounding bony lip.

- Stage 1—M^1/M_1 erupting.
- Stage 2—M^1/M_1 erupted, M^2/M_2 erupting.
- Stage 3—M^2/M_2 erupted, M^3/M_3 erupting.
- Stage 4—M^3 or M_3 erupted but corresponding M_3 or M^3 still erupting.

SUBADULT: an individual in which M^3 and M_3 are completely erupted, but a complete complement of permanent dentition is not yet present, or deciduous teeth remain in place.

- Stage 5—M^3/M_3 erupted, P^4 or P_4 or both either deciduous or erupting.
- Stage 6—P^4/P_4 erupted, P^3/P_3 erupting.
- Stage 7—P^3/P_3 erupted, canines or incisors erupting.

ADULT: an individual in which all permanent teeth are completely erupted and no deciduous teeth remain.

Sexual dimorphism.—Treeshrews generally exhibit little sexual dimorphism in size (Emmons 2000), although published data are scarce and reports are sometimes contradictory (Ralls 1976; Collins and Tsang 1987; Endo et al. 1999; Lu et al. 2014; Sargis et al. 2018). We investigated general sexual size dimorphism among our samples of adult *T. minor* in order to gauge the potential extent of sexual dimorphism in hand variables. We lacked weights and other common body-size measures for most specimens, so we used external head-and-body length (HB) as a proxy for overall body size, realizing that external measurements can vary as a result of intraobservational error, interobservational error, and postmortem changes in the body (Sumner 1927; Blackwell et al. 2006; Stephens et al. 2015). We tested HB of the Malayan ($n = 19$ females, 19 males) and Bornean ($n = 12$ females, 16 males) populations individually using two-sample *t*-tests.

We next examined sexual dimorphism in hand proportions by carrying out separate principal components analyses (PCAs) using correlation matrices of the 19 hand variables from adult Malayan ($n = 21$ females, 21 males) and Bornean individuals ($n = 14$ females, 23 males). Plots of principal component scores for the first two eigenvectors from these analyses were inspected visually for any indication of separation of the sexes by size or shape.

Intrapopulation age variation.—We expected infants and subadults would yield smaller measurements, thereby potentially biasing sample means toward lower values. To test for such a difference within each population, we carried out separate PCAs on the Malayan and Bornean populations using correlation matrices of the 19 hand variables and including adults, subadults, and infants in the samples. We compared the distributions and mean principal component scores of subadults and infants relative to those of adults.

Effect of age variation on interpopulation analyses.—Our primary concern was whether the inclusion of infants or subadults would either increase or decrease our ability to distinguish two closely related populations of treeshrews morphometrically. To examine this question directly, we carried out a series of complete canonical discriminant function analyses (DFAs) using the Malayan and Bornean populations as our *a priori* samples to be contrasted. Females and males were combined within each population. As a gauge of expected differences between the two populations, we first carried out a DFA using only adult individuals. We subsequently carried out DFA using 1) adults, subadults, and infants; 2) adults and subadults; 3) adults plus stage 6–7 subadults only; and 4) adults plus stage 7 subadults only. We used the correlations of variables with scores on the canonical variates to determine which variables were most influential in each model, and we used classification matrices to determine how the presence of subadults and infants affected the ability of the models to correctly identify adult members of each group. Sample sizes of age groups included in analyses varied in some cases as a result of missing data for some individuals.

Results

Age structure.—Based on our dental criteria, we identified 45 adults, 12 subadults, and 2 infants in our Malayan sample of *T. minor* and 40 adults, 5 subadults, and 5 infants in our Bornean sample. The subsamples of infants and subadults from the two populations yielded the following numbers of individuals at seven stages of tooth eruption:

Infants

Stage 1—1 Bornean.
Stage 2—1 Bornean.
Stage 3—1 Malayan, 2 Bornean.
Stage 4—1 Malayan, 1 Bornean.

Subadults

Stage 5—9 Malayan, 2 Bornean.
Stage 6—1 Malayan, 2 Bornean.
Stage 7—2 Malayan, 1 Bornean.

Sexual dimorphism.—There was no obvious sexual dimorphism in HB either among adult Malayan (females, mean HB = 128.7, males, mean HB = 128.4, $t_{0.05[38]} = 0.214$, $P = 0.831$) or adult Bornean *T. minor* (females, mean HB = 126.21, males, mean HB = 126.17, $t_{0.05[34]} = 0.029$, $P = 0.977$). Recognizing the error inherent in external body measurements, which certainly cannot be recorded accurately to 0.1 mm under the best of circumstances, we assume these results indicate there is little to no difference in body length between males and females.

The first two eigenvectors from the PCA of Malayan females and males account for > 53% of the variance in the model. The first eigenvector mostly represents the overall proportions of the metacarpals, whereas the second eigenvector is a contrast between a variety of length variables and a variety of width variables (Table 2). The first eigenvector from the PCA of Bornean females and males is a contrast between the lengths of the metacarpals of the five rays and several width/depth variables (Table 2). The second eigenvector is most strongly influenced by widths of certain metacarpals and proximal phalanges. Together, the two eigenvectors comprise > 49% of the variance for Bornean specimens. Despite the somewhat different variable loadings in the two analyses, plots of principal component scores for the first two eigenvectors from the PCAs of Malayan (Fig. 2A) and Bornean specimens (Fig. 2B) show no discernible pattern of variation between females and males in either population. We therefore combined males and females in subsequent investigations of age variation.

Observed patterns of epiphyseal fusion.—Bones preserved in the forelimbs of traditional study skins of mammals typically include the distal ends of the radius and ulna, as well as the carpals, metacarpals, and phalanges. Our inspection of manus x-rays permitted us to judge timing of epiphyseal fusion of these bones relative to the sequence of dental eruption present in our two samples (Fig. 3).

Our single Bornean individual in the youngest dental age group (dental eruption state 1; USNM 487980) exhibits unfused distal epiphyses of the metacarpals and phalanges. The distal epiphyses of the radius and ulna are unfused, and they

Table 2.—Component loadings for the first two eigenvectors from principal components analyses (PCAs) assessing sexual dimorphism in the hands of adult Malayan (see Fig. 2A) and adult Bornean (see Fig. 2B) *Tupaia minor*. Abbreviations of variables are explained in the "Materials and Methods."

Malayan population			Bornean population		
Component loadings			Component loadings		
Variable	1	2	Variable	1	2
4ML	0.835	0.296	3ML	0.894	0.302
3ML	0.803	0.421	2ML	0.889	0.161
2ML	0.779	0.330	4ML	0.873	0.241
4PPW	0.768	–0.370	5ML	0.862	0.313
3MW	0.763	–0.368	1ML	0.836	–0.013
1ML	0.758	0.371	1PPL	0.539	0.098
2MW	0.741	–0.440	1DPD	0.233	0.395
5ML	0.741	0.506	3DPL	0.094	–0.006
4MW	0.709	–0.375	4PPW	0.069	0.745
5MW	0.673	–0.231	4DPL	0.024	0.049
2PPW	0.642	–0.445	5MW	–0.007	0.836
1MD	0.542	–0.446	2DPL	–0.086	0.162
3DPL	0.537	0.397	5DPL	–0.090	0.080
1PPD	0.503	–0.539	4MW	–0.107	0.896
1PPL	0.461	0.426	3MW	–0.277	0.859
1DPD	0.357	0.185	1PPD	–0.423	0.265
2DPL	0.329	0.292	2MW	–0.425	0.780
4DPL	0.266	0.060	2PPW	–0.452	0.512
5DPL	0.177	0.138	1MD	–0.520	0.082
Eigenvalue	7.546	2.593		5.092	4.218
Total variance explained (%)	39.717	13.647		26.799	22.199

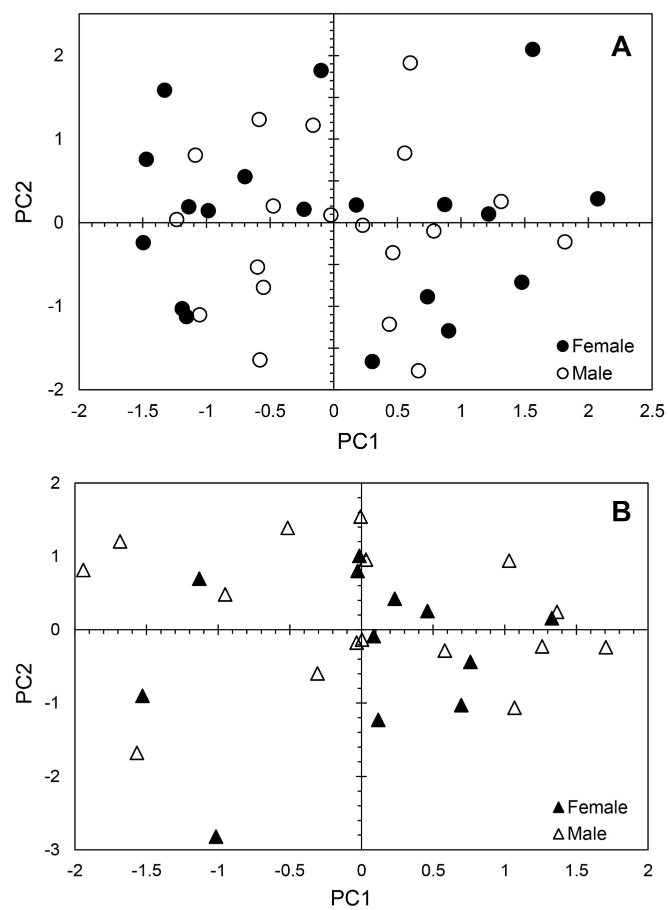

Fig. 2.—Plots of principal component scores for the first two eigenvectors from principal components analyses (PCAs) of the hands of adult females and males of (A) Malayan and (B) Bornean populations of *Tupaia minor* (Table 2). The overlap between the sexes suggests a lack of sexual dimorphism in the size and proportions of the hands.

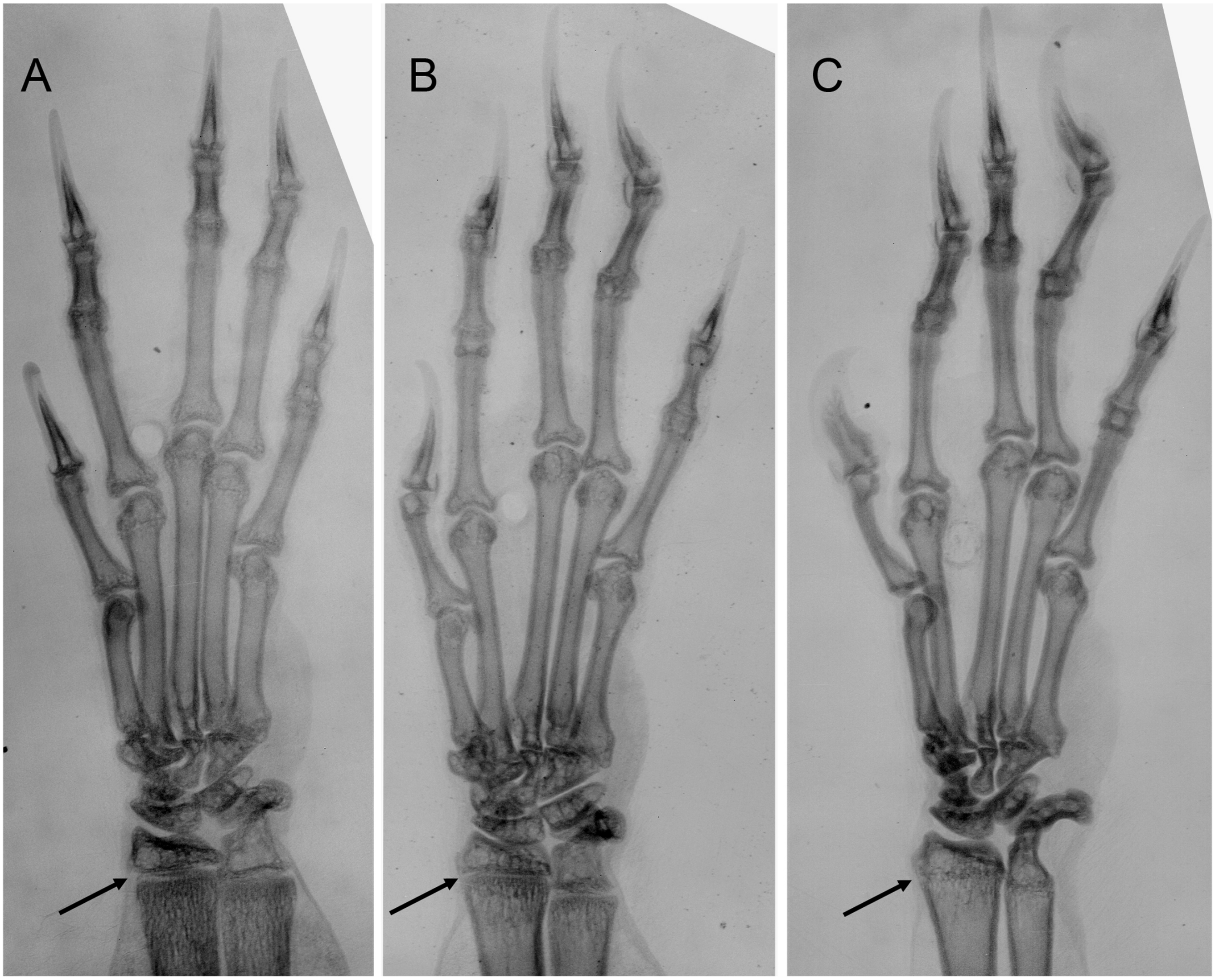

Fig. 3.—Inverted digital x-ray images of left hands of *Tupaia minor* illustrating relative fusion of epiphyses of bones of the wrist and hand: (A) Malayan infant (stage 3: USNM 487987); (B) Bornean subadult (stage 5: USNM 487983); (C) Malayan subadult (stage 5: USNM 488003). Arrows point to area of fusion between the distal epiphysis and the diaphysis of the left radius. Note that the epiphyses of the metacarpals and phalanges appear to be fused in all three specimens.

are separated from their respective diaphyses by broad gaps marking the metaphyses. Much of the bone, particularly in the epiphyses, appears porous.

In our single Bornean representative of stage 2 (USNM 487986), the epiphyses of the metacarpals and phalanges appear to have united with their respective diaphyses. The epiphyseal lines are irregular, and the bone of the epiphyses still appears somewhat porous. The gaps between the epiphyses and diaphyses of the radius and ulna are much narrower, but the epiphyses of those bones remain unfused.

The epiphyses of the metacarpals and phalanges appear fused in all three individuals representing stage 3 (1 Malayan, 2 Bornean specimens: USNM 487987, 292468, 300904, respectively), and the articular surfaces of these bones are distinct and similar in appearance to those of adults. Gaps between the epiphyses and shafts of the radius and ulna remain, and the distal ends of these bones are still unfused (Fig. 3).

In all specimens from stage 4 through adult, the metacarpals and phalanges appear complete and fully formed. In contrast, the epiphyses of the radius and ulna are unfused in both individuals representative of stage 4 (1 Malayan, 1 Bornean: USNM 487994, 300907) and in 10 of the 11 individuals in subadult stage 5 (Malaysia: USNM 291267–291270, 488003, 488005, 488007, 488008, 488017; Borneo: USNM 317180, 487983). The epiphyseal lines of the radius and ulna are reduced to distinct, narrow lines in one Malayan individual (USNM 291267) in the stage 5 group, and in another Malayan specimen (USNM 488003), the epiphyses and diaphyses of the radius and ulna are united (Fig. 3C). This latter specimen is one of the older individuals in stage 5, with both P^4 and P_4 in the process of erupting. However, in two other stage 5 individuals of slightly more advanced dental age (1 Malayan, 1 Bornean specimen with P^4 erupted/P_4 erupting: USNM 488003, 317180), the epiphyses of both bones are unfused. All six individuals that represent dental stages 6 and 7 have fused radial and ulnar epiphyses (Malayan: USNM 487962, 488019, 488022; Borneo: USNM 292470, 317183, 198681). Among the 85 adults, only one Bornean specimen (USNM 145575) has unfused distal epiphyses of the radius and ulna.

Based on these observations, it appears that the typical pattern in *T. minor* is for the epiphyses of the metacarpals and phalanges to be fused and fully formed parts of their respective bones by the time M^3 or M_3 or both are completely erupted (stages 4–5). The epiphyses of the radius and ulna fuse later, between the times the P^4/P_4 begin to erupt (stage 5) and both teeth are in place (stage 6). Like the relative eruption sequences of the upper and lower dentition, however, there is some variation in this timing and some asynchrony between the dental eruption sequence and the sequence of epiphyseal fusion.

Intrapopulation age variation.—We used PCA to assess variation among the three primary age groups within each population. A plot of principal component scores for the first two eigenvectors from the PCA of the Malayan population is shown in Fig. 4A. Together, the first two axes comprise > 55% of the variance in the model (Table 3). The relative positions of adults in this plot are similar to their locations in the plot that resulted

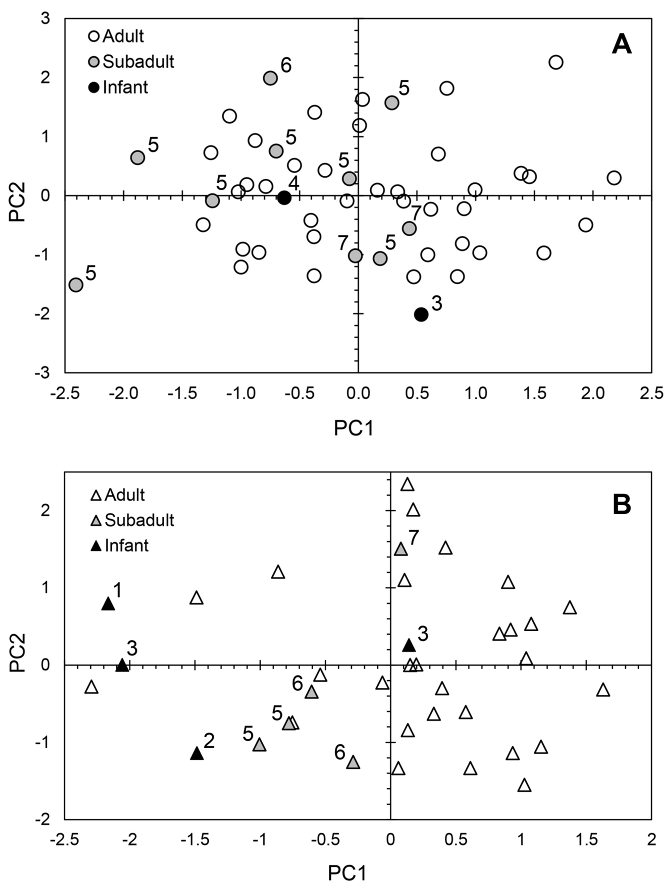

Fig. 4.—Plots of principal component scores for the first two eigenvectors from principal components analyses (PCAs) of the hands of infants, subadults, and adults of (A) Malayan and (B) Bornean populations of *Tupaia minor* (Table 3). The numerals associated with infants and subadults are the individual's tooth eruption stages (see "Materials and Methods").

from the PCA of possible sexual dimorphism in this population (Fig. 2A), and the component loadings on the first two axes from this analysis (Table 3) resemble those from the sexual dimorphism analysis as well (Table 2). The first eigenvector here mostly represents overall proportions of the five metacarpals. Although most infants and subadults plot within the distributional limits of the adults along this axis, they cluster toward the lower end (smaller hand bones) of the distribution, and two subadults (dental stage 5) plot well below even the smallest adults. The mean score for eigenvector 1 calculated for the 12 infants and subadults (–0.524) is significantly lower than that for the 38 adults (0.165; $t_{19.1} = 2.201$, $P = 0.040$). Despite the typical tendency to be smaller in size, one infant (stage 3) and three subadults (stages 5, 7) have component scores that are greater than the mean value for Malayan adults. Although the inclusion of infants and subadults with adults in the sample lowers the mean component score from 0.165 to 0.000, that decrease is not significant ($t_{80.9} = 0.780$, $P = 0.438$).

The second eigenvector from the PCA of the Malayan population is a contrast between lengths and negatively weighted widths/depths of bones. Along this axis, the infants and subadults again plot mostly within the distribution of the adults. Two exceptions are one infant (stage 3) and one subadult (stage 5), both of which plot low on this axis, indicating that these individuals have relatively shorter, broader hand bones than any of the adults. The mean score calculated from infants and subadults (–0.085) on this axis is only slightly lower than that for adults (0.027; $t_{15.4} = 2.92$, $P = 0.774$). The inclusion of infants and subadults with adults in the sample lowers the mean

Table 3.—Component loadings for the first two eigenvectors from principal components analyses (PCAs) assessing age differentiation in the hands of Malayan (see Fig. 4A) and Bornean (see Fig. 4B) *Tupaia minor*. Abbreviations of variables are explained in the "Materials and Methods."

Malayan population			Bornean population		
	Component loadings			Component loadings	
Variable	1	2	Variable	1	2
3ML	0.821	0.314	4PPW	0.759	0.299
4ML	0.805	0.255	4ML	0.729	–0.548
4PPW	0.791	–0.296	5ML	0.720	–0.552
3MW	0.790	–0.305	3ML	0.702	–0.623
5ML	0.741	0.437	4MW	0.672	0.450
5MW	0.716	–0.269	1ML	0.607	–0.585
2MW	0.712	–0.470	5MW	0.598	0.295
2ML	0.711	0.333	2ML	0.594	–0.639
4MW	0.709	–0.376	3MW	0.584	0.610
1ML	0.683	0.337	2DPL	0.513	0.340
2PPW	0.641	–0.443	1DPD	0.490	–0.098
1MD	0.616	–0.483	2MW	0.454	0.745
3DPL	0.572	0.499	4DPL	0.413	0.258
1PPD	0.527	–0.568	1PPL	0.401	–0.337
1PPL	0.473	0.300	5DPL	0.389	0.225
1DPD	0.445	0.287	3DPL	0.331	0.204
2DPL	0.386	0.425	2PPW	0.317	0.641
4DPL	0.315	0.279	1PPD	0.279	0.549
5DPL	0.255	0.350	1MD	–0.066	0.617
Eigenvalue	7.745	2.750		5.474	4.541
Total variance explained (%)	40.765	14.475		28.810	23.902

component score from 0.027 to 0.000, which is not a significant decrease ($t_{82.2}$ = 0.129, P = 0.898).

A plot of scores for the first two eigenvectors from the PCA of the three age groups of the Bornean population is shown in Fig. 4B. The two components together account for > 52% of the variation in the data. The first component represents overall size of the bones of the hand (Table 3). The four infants and five subadults all have scores on this axis that are within the range of the 28 adults. As was the case for the Malayan population, the scores of infants and subadults of the Bornean population are distributed mostly along the lower end of the first eigenvector and, as a group, the hands of infants and subadults average significantly smaller overall size (mean component score = −0.908) than those of adults (mean component score = 0.292; $t_{13.8}$ = 3.655, P = 0.003). This is not the case for every individual, however, as scores for one infant (stage 3) and a subadult (stage 7) are slightly larger than the adult mean score. Despite the differences in size, the decrease in the mean component score from 0.292 to 0.000 that results from the inclusion of infants and subadults with adults in the sample is not significant ($t_{61.7}$ = 1.256, P = 0.214).

The second component in the PCA of the Bornean population is a contrast between widths and negatively weighted lengths of metacarpals and phalanges (Table 3). Most infants and subadults plot along the lower end of the second eigenvector, and their mean principal component score (−0.215) is lower than that for adults (0.069), indicating they have relatively longer, narrower hand bones. However, the difference between the means of these two groups is not significant ($t_{14.5}$ = 0.769, P = 0.454). The inclusion of infants and subadults with adults in the sample lowers the mean component score from 0.069 to 0.000, which is not a significant change ($t_{57.6}$ = 0.273, P = 0.786).

In general, the relative proportions of the hands of infants and subadults of both populations are well within the ranges of respective adults, but, as a group, infants and subadults tend to cluster among the smaller hand sizes and, in the Bornean population, infants and subadults also group with adults having proportionally longer, narrower hand bones. The inclusion of infants and most subadults does not significantly change the mean component score on either axis relative to the mean calculated only from adults.

Effect of age variation on interpopulation analyses.—We used a series of complete DFAs to describe how inclusion of various age groups might affect the correct identification of individuals from the Malayan and Bornean populations. Our first DFA of variables from only adult individuals of the two populations yielded an overall correct classification rate of 94% and established a standard for comparison with subsequent analyses that included infants and subadults in the samples. Only two individuals of each populations were incorrectly classified as members of the other population (Table 4). Because it has a smaller sample size in this analysis, however, this number represents a slightly greater proportion of the Bornean population, resulting in a higher rate of misclassification (7%) than for the Malayan population (5%). Five variables are significantly correlated with scores for the first canonical variate (CV1), indicating they most heavily influenced the model (Table 5). The negative correlation of the width variable 5MW with the canonical variate is highly significant (P < 0.001), indicating that it has the most influence. The positive correlation of another width variable, 1MD, is very significant (P < 0.01), and the negative correlations of three length variables (−1PPL, −2ML, −3ML) are significant (P < 0.05).

DFA using variables from all adults, subadults, and infants in the two populations yielded an overall correct classification

Table 4.—Classification matrices from discriminant function analyses (DFA) investigating the effect of age variation on the ability to differentiate populations of Malayan and Bornean *Tupaia minor*.

	Infants		Subadults		Adults		Total	
		Correct		Correct		Correct		Correct
	n	*n* (%)	*n*	*n* (%)	*n*	*n* (%)	*n*	*n* (%)
Adults, subadults, and infants								
Malayan	2	2 (100%)	10	10 (100%)	38	33 (87%)	50	45 (90%)
Bornean	4	4 (100%)	5	4 (80%)	28	25 (89%)	37	33 (89%)
Total	6	6 (100%)	15	14 (93%)	66	58 (88%)	87	78 (90%)
Adults and all subadults								
Malayan			10	10 (100%)	38	36 (95%)	48	46 (96%)
Bornean			5	4 (80%)	28	24 (86%)	33	28 (85%)
Total			15	14 (93%)	66	60 (91%)	81	74 (91%)
Adults and stage 6–7 subadults								
Malayan			3	3 (100%)	38	36 (95%)	41	39 (95%)
Bornean			3	2 (67%)	28	25 (89%)	31	27 (87%)
Total			6	5 (83%)	66	61 (92%)	72	66 (92%)
Adults and stage 7 subadults								
Malayan			2	2 (100%)	38	35 (92%)	40	37 (93%)
Bornean			1	1 (100%)	28	26 (93%)	29	27 (93%)
Total			3	3 (100%)	66	61 (92%)	69	64 (93%)
Adults only								
Malayan					38	36 (95%)	38	36 (95%)
Bornean					28	26 (93%)	28	26 (93%)
Total					66	62 (94%)	66	62 (94%)

Table 5.—Correlations (loadings) of input variables with the canonical variates from five discriminant function analyses (DFAs) investigating the effect of age variation on the ability to differentiate Malayan and Bornean populations of *Tupaia minor*. Significant correlations: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Abbreviations of variables are explained in the "Materials and Methods."

	Adults, subadults, infants	Adults, subadults	Adults, subadults (stage 6 and 7)	Adults, subadults (stage 7)	Adults only
Variable	CV1	CV1	CV1	CV1	CV1
1ML	0.542*	1.997	2.258	2.183	2.988
1PPL	2.637*	−4.195*	−4.075*	−5.189*	−4.947*
1MD	−17.777***	12.483***	9.904**	14.098***	14.237**
1PPD	11.007	−5.624	−4.875	−5.385	−6.160
1DPD	−2.947	5.223	5.271*	7.455	7.765
2ML	0.716**	−1.582**	−1.784**	−1.345**	−1.623*
2DPL	−0.948	2.574	2.978	3.572	4.031
2MW	15.945	−19.172	−19.443	−25.404	−26.066
2PPW	−11.864	18.410	20.056	22.206	22.103
3ML	−0.043**	−0.400*	−0.830*	−0.707*	−0.704*
3DPL	0.845*	−1.651*	−1.603	−1.323	−1.350
3MW	−6.273	5.158	5.808	8.871	9.499
4ML	1.872*	−1.664	−1.441	−1.750	−2.147
4DPL	−0.081*	0.555	0.571	0.911	0.953
4MW	−11.046	14.735	10.839	8.460	9.028
4PPW	−21.494	19.296	19.405	22.372	23.783
5ML	−3.801*	4.648	5.153	5.369	5.417
5DPL	1.826	−2.099	−2.506	−1.937	−2.169
5MW	27.578***	−29.177***	−28.170***	−30.222***	−30.827***
Eigenvalues	1.855	1.946	1.813	2.354	2.292
Canonical correlations	0.806	0.813	0.803	0.838	0.834

rate of 90% (Table 4). All infants were correctly classified, as were 14 of 15 subadults (93%). Only 58 of 66 adults (88%) were classified correctly, a drop of 6% (four fewer individuals) compared to the adult-only model. Misclassifications included five Malayan and three Bornean individuals. This model was influenced by the most variables. Six variables are significantly and positively correlated with scores on the canonical variate (Table 5: 5MW, 2ML,1ML, 1PPL, 3DPL, 4ML), and four are significantly negatively correlated (1MD, 3ML, 4DPL, 5ML). The large number of variables and their contrasting weights makes the interpretation of the canonical variate more challenging. In general, the results of this analysis suggest that inclusion of subadults and infants of all stages makes the two populations appear more similar in hand morphology, and it makes it more difficult to distinguish them accurately.

Analysis of all adults and subadults (infants excluded) of the Malayan and Bornean populations yielded an overall correct classification rate of 91% (Table 4). As in the previous DFA, 14 of 15 subadults (93%) were correctly classified. Among the adults, 60 of 66 individuals (91%) were classified correctly, two fewer than in the adult-only model, but two more than in the model that included infants. Both of the additional misclassified individuals were Bornean specimens, reducing the correct classification rate for adults from this population by 3% compared to the previous model and 7% compared to the adult-only model. Six variables exerted significant influence on this model (Table 5: 1MD, 5MW, 2ML, 1PPL, 3ML, 3DPL).

Analysis of adults and stage 6–7 subadults (stages 1–5 excluded) of the two populations yielded an overall correct classification rate of 92% (Table 4). Among subadults, five of six individuals (83%) were correctly classified. The one misclassified subadult was a Bornean specimen. Among adults, 61 of 66 individuals (92%) were classified correctly, one fewer than in the adult-only model and one more than in the previous model. Two misclassified adults were from the Malayan population and three were Bornean specimens. As in the preceding analysis, six variables are significantly correlated with scores on the canonical variate (Table 5: 5MW, 1MD, 2ML, 1PPL, 1DPD, 3ML).

Analysis of adults and stage 7 subadults (stages 1–6 excluded) yielded an overall correct classification rate of 93% (Table 4). All three subadults in the analysis were correctly classified, as were 61 of 66 adults (92%). This is the same rate as in the previous model, but in this case, the misclassified individuals are three Malayan and two Bornean specimens. The same five variables are significantly correlated with scores on the canonical variate as in the adult-only model (1MD, 5MW, 2ML, 1PPL, 3ML).

In summary, none of the four models that included infants or subadults performed better than or equal to the adults-only model as measured by the rate of total correct classifications of either adults or all specimens of the two populations (Table 4). The percentages of correct classifications were lowest in the model that included both infants and subadults, and the rates of correct classifications tended to increase as infants and increasing numbers of subadults were excluded from the analyses.

For the Malayan populations, the total correct classification rates both of adults and of all specimens in the adults + all subadults model and the adults + stage 6–7 subadults model were either equal to, or slightly superior than, those rates in the adult-only model (Table 4). In contrast, rates of correct classifications of Bornean specimens were lower in most models that included infants or subadults, except for the adults + stage 7 subadults model. One factor that may account for the trends in the classification rates of the two populations among the models is the decreased influence exerted by a smaller number of infants and subadults as they were removed from the analyses. In the model that included both infants and all subadults, these individuals comprised 24% of the entire sample, whereas subadults comprised 19% of the sample in the analysis in which infants were excluded, 8% of the analysis in which infants and stage 5 subadults were excluded, and 4% of the sample in which infants and stage 5–6 subadults were excluded (Table 4). Also relevant is the effect of the unequal distribution of individuals among infants and the three subadult stages. Stage 5 subadults represented 43% of the sample of infants and subadults (Table 4), exerting an equal numerical influence as any other two stages combined. In general, the results of these analyses suggest that inclusion of subadults and infants of all ages makes the two populations appear more similar in hand morphology, making it more difficult to distinguish them accurately.

Five variables contributed consistently and significantly to each of the five models (Table 5). These included two width and depth variables, 5MW and 1MD, which together exerted the most influence in each model. In each case, one of these variables was positively correlated, and the other negatively correlated, with scores on the canonical variate. Also contributing to each model were three length variables, one of which (3ML) was always negatively correlated with scores on the canonical variate, and two of which (1PPL, 2ML) were always correlated with the same sign as 5MW.

Discussion

The Lesser Treeshrew, *T. minor*, is a mostly arboreal species that forages diurnally in the forest canopy over a territory of 1–2 ha. Emmons (2000:193) noted that the daylong activity, long distances traveled, and large home ranges of Bornean species of treeshrews, including *T. minor*, are required to meet their daily caloric intake. It would seem advantageous for a species that depends upon its hands and feet for rapid climbing, clinging, balancing, and grasping (Sargis 2001), to complete bone development in these regions relatively quickly once it is able to leave the natal nest. However, early fusion of the manus and pes may be a more general pattern among mammals, as a correlation between epiphyseal fusion and locomotor behavior has not been demonstrated (Brimacombe 2017).

Our examination of the hands of *T. minor* indicates that epiphyseal fusion of the metacarpals and phalanges typically occurs by the time M^3 or M_3 or both are completely erupted. This occurs well in advance of the fusion of the epiphyses of the radius and ulna, which typically happens between the time the permanent P^4/P_4 begin to erupt and the time both teeth are fully erupted. Occasionally, the epiphyses of the radius and ulna may remain unfused until after all the permanent dentition is in place and all deciduous teeth are lost. Despite early fusion of bones of the manus, the metacarpals and phalanges do not typically reach adult proportions in *T. minor* until the permanent P^4/P_4 have nearly completed eruption or are completely erupted. This is about the same time as when the epiphyses of the radius and ulna are finally fused. The additional growth of the metacarpals and phalanges may result from additional bone remodeling after the epiphyses have fused.

The relative proportions of the hand skeletons of infant and subadult *T. minor* are typically within the overall size range exhibited by adults. Within the adult distribution, however, most infants and subadults tend to have smaller proportions and cluster with smaller adults. The inclusion of infants and subadults in the sample tends to lower the mean values for the population. Although in our study the decrease in mean values was not statistically significant, the inclusion of nonadults affected the nature of the samples and potentially biased them in unexpected ways. In the cases of the Malayan and Bornean populations, the inclusion of infants and subadults decreased our ability to accurately identify some individuals of the two populations based on morphometric analysis.

Given the influences exerted by infants and subadults on the identification of adults of the Malayan and Bornean samples of *T. minor* in our study, the best practice is to exclude all infants and subadults from morphometric analyses of the manus in treeshrews, as we did in our previous studies of other species of *Tupaia* (Sargis et al. 2013a, 2013b, 2014, 2016). In cases of low sample size, or where adult specimens are not available, including stage 7 subadults and even stage 6 subadults in the study should not overly influence outcomes. Most individuals younger than stage 6, however, are unlikely to have reached adult hand proportions and should certainly be excluded from morphometric analyses.

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Supplementary Data

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

Supplementary Data SD1.—Original measurements of the manus from Bornean and Malayan samples of *Tupaia minor* used in this study.

Literature Cited

Anderson, J. 1879. Anatomical and zoological researches: comprising an account of the zoological results of the two expeditions to western

Yunnan in 1868 and 1875; and a monograph of the two cetacean genera, *Platanista and Orcella*. Volume 1—Text. Bernard Quaritch. London, United Kingdom. [Although the title page is printed with the date 1878, this work was not published until early 1879.]
Blackwell, G. L., S. M. Bassett, and C. R. Dickman. 2006. Measurement error associated with external measurements commonly used in small-mammal studies. Journal of Mammalogy 87:216–223.
Brimacombe, C. S. 2017. The enigmatic relationship between epiphyseal fusion and bone development in primates. Evolutionary Anthropology 26:325–335.
Collins, P. M., and W. N. Tsang. 1987. Growth and reproductive development in the male tree shrew (*Tupaia belangeri*) from birth to sexual maturity. Biology of Reproduction 37:261–267.
Diard, P.-M. 1820. Asiatic society. The Asiatic Journal and Monthly Register for British India and Its Dependencies 10:477–478.
Emmons, L. H. 2000. Tupai: a field study of Bornean treeshrews. University of California Press. Berkeley, California.
Endo, H., et al. 1999. Geographic variation in the skull morphology of the common tree shrew (*Tupaia glis*). Journal of Veterinary Medical Science 61:1027–1031.
Günther, A. 1876. Remarks on some Indian and, more especially, Bornean mammals. Proceedings of the Zoological Society of London 1876:424–428.
Hawkins, M. T. R. 2018. Family Tupaiidae (treeshrews). Pp. 242–269 in Handbook of the mammals of the world. 8. Insectivores, sloths and colugos (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions. Barcelona, Spain.
Lu, D., C. Q. Zhou, and W. B. Liao. 2014. Sexual size dimorphism lacking in small mammals. North-Western Journal of Zoology 10:53–59.
Lyon, M. W. 1911. Descriptions of four new treeshrews. Proceedings of the Biological Society of Washington 24:167–170.
Lyon, M. W. 1913. Treeshrews: an account of the mammalian family Tupaiidae. Proceedings of the United States National Museum 45:1–188.
Ralls, K. 1976. Mammals in which females are larger than males. The Quarterly Review of Biology 51:245–276.
Sargis, E. J. 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). Journal of Zoology (London) 253:485–490.
Sargis, E. J. 2002. A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. Mammalia 66:579–598.
Sargis, E. J., V. Millien, N. Woodman, and L. E. Olson. 2018. Rule reversal: ecogeographical patterns of body size variation in the common treeshrew (Mammalia, Scandentia). Ecology and Evolution 8:1634–1645.
Sargis, E. J., N. Woodman, N. C. Morningstar, T. N. Bell, and L. E. Olson. 2016 [2017]. Skeletal variation and taxonomic boundaries among mainland and island populations of the common treeshrew, *Tupaia glis* (Mammalia: Scandentia: Tupaiidae). Biological Journal of the Linnean Society. doi:10.1111/bij.12876 [120:286–312] (published online 26 September 2016; in print 1 February 2017).
Sargis, E. J., N. Woodman, N. C. Morningstar, A. T. Reese, and L. E. Olson. 2013b. Morphological distinctiveness of Javan *Tupaia hypochrysa* (Scandentia, Tupaiidae). Journal of Mammalogy 94:938–947.
Sargis, E. J., N. Woodman, N. C. Morningstar, A. T. Reese, and L. E. Olson. 2014. Island history affects faunal composition: the treeshrews (Mammalia: Scandentia: Tupaiidae) from the Mentawai and Batu Islands. Biological Journal of the Linnean Society 111:290–304.
Sargis, E. J., N. Woodman, A. T. Reese, and L. E. Olson. 2013a. Using hand proportions to test taxonomic boundaries within the *Tupaia glis* species complex (Scandentia, Tupaiidae). Journal of Mammalogy 94:183–201.
Schilling, N., and A. Petrovitch. 2006. Postnatal allometry of the skeleton in *Tupaia glis* (Scandentia: Tupaiidae) and *Galea musteloides* (Rodentia: Caviidae) – a test of the three-segment limb hypothesis. Zoology 109:148–163.
Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.
Shigehara, N. 1980. Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew, with reference to its systematic problem. Primates 21:1–19.
Slaughter, B. H., R. H. Pine, and N. E. Pine. 1974. Eruption of cheek teeth in Insectivora and Carnivora. Journal of Mammalogy 55:115–125.
Stephens, R. B., K. H. Karau, C. J. Yahnke, S. R. Wendt, and R. J. Rowe. 2015. Dead mice can grow—variation of standard external mammal measurements from live and three postmortem body states. Journal of Mammalogy 96:185–193.
Sumner, F. B. 1927. Linear and colorimetric measurements of small mammals. Journal of Mammalogy 8:177–206, pl. 16–19.
Woodman, N., and J. 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 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.

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Appendix I

Specimens Examined

Malayan sample (*Tupaia minor malaccana*, $n = 59$)

Females.—Malaysia: Johor: Sungei Malayu (USNM 143271). Selangor: Kuala Lumpur, Batu Caves (USNM 152186); Bekok, Labis Forest Reserve (USNM 487960, 487961, 487962, 487965, 487967, 487969); Subang Forest Reserve (USNM 487988, 487992, 487993, 487998, 488000, 488002, 488003, 488005, 488006, 488007); Tanjong Duablas, Kuala Langat Forest Reserve (USNM 487990, 488015, 488022, 488023). Wilayah Persekutuan: near Kuala Lumpur, Kepong (USNM 290150, 291267, 291268); Batu (Kepong), Bukit Legong Forest Reserve (USNM 488016, 488018); Sungei Buloh, Sungei Buloh Forest Reserve, Bukit Lanjan (USNM 487996, 488019).

Males.—Malaysia: Johor: Sembrong River (USNM 112618). Pahang: Rompin, Bukit Payong, Kampong Bukit (USNM 487970). Selangor: 6 mi N of Kuala Lumpur (USNM 290151); Bekok, Labis Forest Reserve (USNM 487963, 487964, 487966, 487968); Subang Forest Reserve (USNM 487989, 487999, 488001, 488004, 488008); Tanjong Duablas, Kuala Langat Forest Reserve (USNM 487994, 488011, 488012, 488013, 488017, 488021); Bukit Kemandul, Sungai

Rasu, Batu (USNM 487997); no locality (USNM 291270). Wilayah Persekutuan: Batu (Kepong), Bukit Legong Forest Reserve (USNM 487987, 487991, 487995, 488009, 488014); Sungei Buloh, Sungei Buloh Forest Reserve, Bukit Lanjan (USNM 488020); Batang Berjuntai, Batang Berjuntai Forest (USNM 488010).

Sex unknown.—Malaysia: Pahang: Rompin, Bukit Payong, Kampong Bukit (USNM 487971). Selangor: near Kuala Lumpur (USNM 291269); no locality (USNM 355346).

Bornean sample (*T. m. minor*, *n* = 50)

Females.—Indonesia: Borneo: mouth of Simpang River (USNM 145575); Birang River (USNM 176422, 176426, 176427, 176428); Segah River, S Bank (USNM 176429); Mahakkam River (USNM 198680). Malaysia: Borneo: Sabah: Mount Kinabalu, Bundu Tuhan (USNM 292470); Mount Kinabalu National Park, Ranau District, Poring (USNM 487972, 487976, 487978, 487985); Petergas (USNM 317179); Ranau (USNM 300905, 317181); ½ mile N of Ranau (USNM 300904); Kampong Morok, Ranau District, Morok Forest (USNM 487980, 487986); no locality (USNM 396669, 396672).

Males.—Indonesia: Borneo: Mankol, Kendawangan River (USNM 153857); Batoe Panggal, Mahakam River, N. Bank (USNM 176419, 176420); Birang River (USNM 176421, 176423, 176424, 176425); Sungai Menganne (USNM 197197); Sungai Karangan (USNM 198038); Laham, Mahakkam River (USNM 198681). Malaysia: Borneo: Sabah: Mount Kinabalu, Bundu Tuhan (USNM 292468); Mount Kinabalu National Park, Ranau District, Poring (USNM 487974, 487975, 487977, 487979, 487982, 487983); Petergas (USNM 317178); Ranau (USNM 300901, 300902, 300906, 300907, 317180, 317182, 317183); ½ mile N of Ranau (USNM 300903); Kampong Nalapak, Ranau District, Hutan Malacau (USNM 487981); Kampong Morok, Ranau District, Morok Forest (USNM 487984); no locality (USNM 396668). Sarawak: Kadit, Nanga Pelagus (USNM 311453).