



Taxonomic boundaries in Lesser Treeshrews (Scandentia, Tupaiidae: *Tupaia minor* Günther, 1876)

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The Lesser Treeshrew, *Tupaia minor* Günther, 1876, is a small mammal from Southeast Asia with four currently recognized subspecies: *T. m. minor* from Borneo; *T. m. malaccana* from the Malay Peninsula; *T. m. humeralis* from Sumatra; and *T. m. sincepis* from Singkep Island and Lingga Island. A fifth subspecies, *T. m. caedis*, was previously synonymized with *T. m. minor*; it was thought to occur in northern Borneo and on the nearby islands of Banggi and Balambangan. These subspecies were originally differentiated based on pelage color, a plastic feature that has proven to be an unreliable indicator of taxonomic boundaries in treeshrews and other mammals. To explore infraspecific variation among *T. minor* populations across the Malay Peninsula, Borneo, Sumatra, and smaller islands, we conducted multivariate analyses of morphometric data collected from the hands and skulls of museum specimens. Principal component and discriminant function analyses reveal limited differentiation in manus and skull proportions among populations of *T. minor* from different islands. We find no morphometric support for the recognition of the four allopatric subspecies and no support for the recognition of *T. m. caedis* as a separate subspecies on Borneo.

Key words: cranium, digit, hand, mandible, manus, morphology, ray, skull, Southeast Asia, subspecies

Treeshrews (order Scandentia) are small-bodied mammals endemic to South and Southeast Asia (Emmons 2000; Hawkins 2018). *Tupaia minor* Günther, 1876, the Lesser Treeshrew, is one of the smallest (~54 g; Sargis 2002) of the 23 extant species. It is mostly arboreal and has been observed grasping branches with both its hands and feet, as well as using its relatively long tail to balance in trees (Emmons 2000; Sargis 2001). *Tupaia minor* is found in the tropical rainforests of Borneo, Sumatra, the Malay Peninsula, and smaller islands from near sea level up to elevations of 1,700 m (Corbet and Hill 1992; Cassola 2016; Hawkins 2018). The geographic range and infraspecific taxonomy of *T. minor* have not been thoroughly reevaluated since Lyon's (1913) revision of Tupaiidae, after which two additional subspecies of *T. minor* were described.

Tupaia minor contains four currently recognized subspecies (Table 1): *T. m. minor* from Borneo and the nearby islands of Balambangan, Banggi, and Laut; *T. m. malaccana* Anderson, 1879 from the Malay Peninsula; *T. m. sincepis* Lyon, 1911 (also misspelled *sincepsis* or *sincipis*; e.g., Lyon 1911, 1913) from Singkep Island; and *T. m. humeralis* Robinson and Kloss, 1919 from Sumatra (Fig. 1). These subspecies were differentiated based primarily on subtle, qualitative differences in pelage, a plastic feature that varies seasonally, with individual age, and over time in collections (Davis et al. 2013). *Tupaia m. malaccana*, originally described as a different species (Table 1), was noted by Lyon (1913:114) to have a “less blackish” tail than other subspecies of *T. minor*. Similarly, *T. m. humeralis* was originally described as “more olivaceous” than *T. m. minor* with “longer whiter neck stripes” than *T. m. malaccana* (Robinson

Table 1.—Synonyms associated with *Tupaia minor* and sample size of each subspecies in our two data sets. Symbols: * indicates that the holotype is included in the sample; ^ indicates taxon not recognized as a subspecies by Helgen (2005) or Hawkins (2018).

Subspecies names of <i>Tupaia minor</i>	Original name	Island	Manus	Skull
<i>T. m. minor</i> Günther, 1876	<i>Tupaia minor</i>	Borneo, Laut	73	44*
<i>T. m. malaccana</i> Anderson, 1879	<i>Tupaia malaccana</i>	Malay Peninsula	48	20
<i>T. m. sincepis</i> Lyon, 1911	<i>Tupaia sincepis</i>	Singkep, Lingga	5*	—
<i>T. m. humeralis</i> Robinson and Kloss, 1919	<i>Tupaia minor humeralis</i>	Sumatra	10	9
<i>T. m. caedis</i> Chasen and Kloss, 1932^	<i>Tupaia minor caedis</i>	Borneo, Banggi, Balambangan	18	28*
Total			154	101

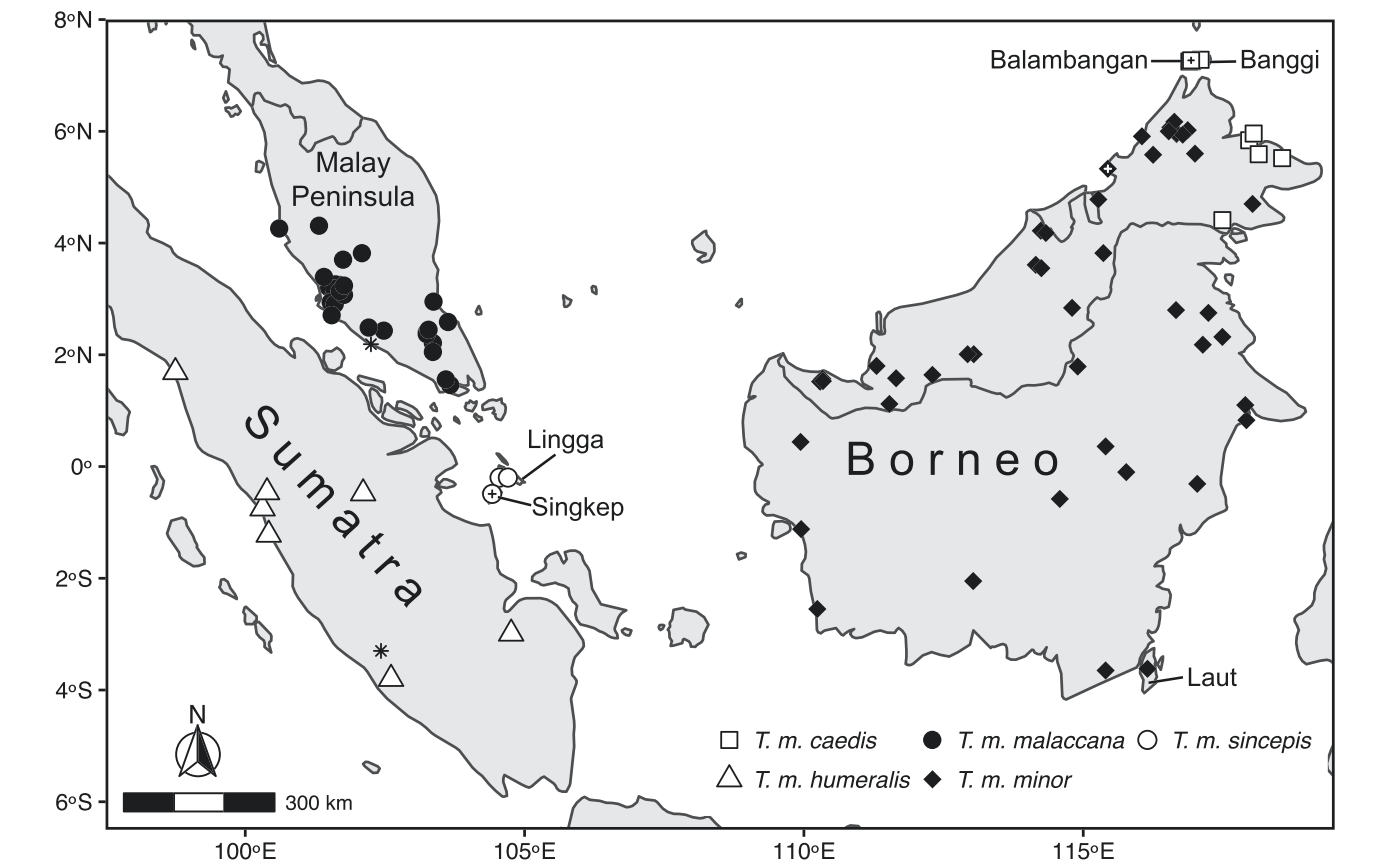


Fig. 1.—Locality map for specimens in our study. Symbols inscribed with crosses indicate type localities of subspecies (see Appendix I); black asterisks represent type localities of taxa for which the holotypes were not inspected.

and Kloss 1919:266). In addition to pelage, size differences were referenced for certain subspecies: Lyon (1913:114–116) observed that *T. m. sincepis* is a “fairly distinct form” due to its “slightly larger size” as well as its darker tail, and *T. m. malaccana* was noted to have a “slightly larger” skull than other subspecies. *Tupaia minor* is also found on Lingga Island, but the subspecies there was never determined (Hawkins 2018). Lyon (1913:114) claimed that the Lingga individuals were “rather intermediate” between *T. m. sincepis* and *T. m. malaccana*, more closely resembling the latter. For the purposes of this study, we considered *T. minor* from Lingga as *T. m. sincepis* due to its close proximity to Singkep (Fig. 1; Table 1).

A fifth subspecies, *T. m. caedis* Chasen and Kloss, 1932, was originally described for the populations that occur on the islands of Balambangan and Banggi as well as parts of northeastern Borneo, but this taxon was not recognized by Corbet and Hill (1992), Helgen (2005), or Hawkins (2018). *Tupaia m.*

caedis was described based on minor pelage differences that graded into what was considered to be typical pelage for the nominate subspecies. Chasen and Kloss (1932:41) noted that “[t]o define the geographic limits of the two races is not easy” due to the gradation and the fact that the type locality of *T. m. minor* is within the “intermediate area” in northern Borneo where *T. m. caedis* was also supposedly present. The distinctiveness of these two populations, as well as the other three currently recognized subspecies, has never been tested with quantitative osteological data or reexamined in a biogeographic context.

About 13 Ma, *T. minor* diverged from a clade of treeshrews that includes species that are either endemic to Borneo (*T. picta* and *T. montana*) or have part of their range on Borneo (*T. splendidula* and *T. tana*; Roberts et al. 2011), suggesting a possible Bornean origin followed by dispersal to other landmasses (with *T. m. minor* remaining a Bornean endemic). Borneo was

connected to the Malay Peninsula and Sumatra through most of the Pleistocene, only splitting into different islands with the flooding of the Sunda Shelf around 400 ka (Husson et al. 2020) and separating even more recently from nearby smaller islands like Banggi and Balambangan (Voris 2000). Populations of *T. minor* were presumably panmictic while these land bridges were still intact, as was the case for other Sundaland mammals with similar geographic ranges (Wilting et al. 2011). Though all four currently recognized *T. minor* subspecies are allopatric, their fairly recent connectivity may have implications for their distinctiveness.

The criteria used to designate subspecies are often subjective and arbitrary (Simpson 1961; Mayr and Ashlock 1991), particularly in mammals (Gippoliti and Amori 2007). Most treeshrew species and subspecies were described in the early 20th century (see Sargis et al. 2013b:fig. 1), and many were differentiated based on coloration, an unreliable proxy for taxonomic distinction (Schiaffini 2020; Juman et al. 2021b). Some have argued that when justified with inconsistent criteria, subspecies amount to little more than “arbitrary partitions of continuous variation” (Padial and De la Riva 2021:731) that may in fact obscure the true evolutionary history of a taxon (Burbrink et al. 2000). For example, the boundary between *T. m. caedis* and *T. m. minor* on Borneo was admitted to be difficult to determine, even in the original description (Chasen and Kloss 1932). But the concept of subspecies continues to be used to designate unique populations for conservation (Braby et al. 2012), and it is therefore worth examining—with nonarbitrary criteria—infraspecific variation in the context of taxonomic circumscription (Patton and Conroy 2017; Reydon and Kunz 2021). We have shown osteological morphometric data to be less arbitrary, more reliable, and more repeatable than qualitative observations of pelage, and measurements from the skull and hands have been used to delineate treeshrew species and subspecies in previous studies (Sargis et al. 2013a, 2013b, 2014a, 2014b, 2017; Juman et al. 2021b).

For the purposes of this study, we define a subspecies under the general lineage species concept (de Queiroz 1998) as a “partially isolated lineage” moving toward “evolutionary independence” (Braby et al. 2012:711). To meet this definition, subspecies must be both allopatric (Mayr and Ashlock 1991) and have diagnosable morphological differences (Braby et al. 2012; Schiaffini 2020). To assess the proposed *T. minor* subspecies, we conducted separate multivariate analyses of the manus and skull to explore the possible differences (i) between populations of *T. m. minor* and the previously recognized *T. m. caedis* on Borneo and nearby smaller islands, and (ii) among all *T. minor* populations from Borneo, Sumatra, the Malay Peninsula, Lingga, Singkep, Banggi, Balambangan, and Laut. We also mapped the distribution of each hypothesized subspecies based on our voucher localities (Fig. 1).

MATERIALS AND METHODS

Our study includes all four of the currently recognized *T. minor* subspecies, as well as the previously recognized *T. m. caedis* (Appendix I). To assess skeletal variation across populations of *T. minor*, we recorded 38 manus and 20 craniomandibular

measurements (in mm) from museum specimens. Previous studies have shown that hand proportions are useful for assessing taxonomic boundaries in treeshrews, providing results that are congruent with those from skull morphometrics and molecular data (Sargis et al. 2013a, 2013b, 2014b, 2017; Juman et al. 2021b). We also georeferenced 98 specimen localities—including three type localities—and generated a locality map using the ggplot2, rnaturalearth, and ggspatial packages in R (Wickham 2016; South 2017; R Core Team 2018; Dunnington 2020; Fig. 1).

Manus.—We x-rayed the left and right manus of 154 adult (those with fully erupted permanent dentition; see Woodman et al. 2020) *T. minor* specimens from the following museums: American Museum of Natural History (AMNH), New York City, New York; Field Museum of Natural History (FMNH), Chicago, Illinois; and United States National Museum of Natural History (USNM), Washington, District of Columbia. This sample included *T. m. caedis* as well as all four subspecies of *T. minor*, including the holotype of *T. m. sincepis* (Table 1; Appendix I).

Specimens were x-rayed and measured following the protocol outlined in Sargis et al. (2013a, 2013b, 2014b, 2017), Woodman et al. (2020), and Juman et al. (2021b). AM-M measured the metacarpals and phalanges in ImageJ (Schneider et al. 2012). Measurements were generally obtained from the left manus but supplemented with measurements from the right when necessary. The following measurements were recorded from each of the five rays (38 total), except that (mediolateral) widths were replaced with (dorsopalmar) depths for ray I due to its lateral orientation (see Sargis et al. 2013a, 2013b, 2014b, 2017; Woodman et al. 2020; Juman et al. 2021b): 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, and DPW = distal phalanx width. Original measurements and summary statistics are provided in Supplementary Data SD1.

Skull.—We recorded 20 craniomandibular measurements (Supplementary Data SD1; Sargis et al. 2013a, 2014a, 2014b, 2017, 2018; Juman et al. 2021a, 2021b) from 101 adult specimens using Mitutoyo digital calipers that read to 0.01 mm, with a foot pedal for inputting data. Examined specimens are housed in the following museums: FMNH; Museum of Comparative Zoology at Harvard University (MCZ), Cambridge, Massachusetts; and the Natural History Museum (NHMUK), London, United Kingdom (Appendix I). This sample consisted of three subspecies of *T. minor* as well as *T. m. caedis*, including the holotypes of *T. m. minor* and *T. m. caedis* (Table 1; Appendix I). We were unable to include the fourth subspecies *T. m. sincepis* in this sample.

Multivariate analyses.—We used R with function princomp() and package ggplot2 to conduct and plot separate principal component analyses (PCAs) for the manus and skull data sets. Correlation matrices computed from ln-transformed measurements were used in the PCA. Linear discriminant function analyses (DFAs) were performed on ln-transformed data with the MASS package in R (Venables and Ripley 2002). Linear regression models were fitted using ordinary least squares with the function lm(). Missing data prevented the inclusion of all

our measurements in the analyses, so the eight most complete variables were selected from each data set to optimize sample sizes (particularly from underrepresented small island populations). As a result, our analyses have slight differences in numbers and combinations of variables. We used these methods to investigate variation among the following samples. For each set of analyses, the sample sizes for the manus and the skull are listed for the included subspecies or island populations. Treeshrews generally exhibit little sexual size dimorphism (Emmons 2000; Juman et al. 2021a, 2021b), and Woodman et al. (2020) found no significant differences in external or manus measurements between female and male *T. minor* in either the Malayan or Bornean populations. Therefore, we combined males and females in all our analyses.

1. *Geographic variation on Borneo*: We conducted PCAs for all mainland Bornean individuals using: (a) eight manus variables (1ML, 1PPL, 1MD, 1PPD, 1DPD, 2PPL, 2MW, 5ML; $n = 85$) and (b) eight skull variables (UTL, PPL, LIB, MH, MCH, MCW, MCIL, LTL; $n = 45$). The samples included: *T. m. minor* ($n = 67$ manus, 32 skull), *T. m. caedis* ($n = 18, 13$). We also tested for latitudinal and longitudinal patterns of morphometric variation on Borneo with linear regressions on Principal Component 1.
2. *Geographic variation across all islands*: To assess variation among populations of *T. minor* from Borneo, Sumatra, the Malay Peninsula, and smaller islands, we performed PCAs on: (a) eight manus variables (1ML, 1PPL, 1MD, 1PPD, 2MW, 2PPW, 3DPL, 4PPW; $n = 140$) and (b) eight skull variables (UTL, PPL, LTPL, MH, MCH, MCW, MCIL, LTL; $n = 68$). The samples included: Borneo ($n = 83$ manus, 45 skull), the Malay Peninsula ($n = 44, 11$), Sumatra ($n = 9, 5$), Laut ($n = 1, 0$), Lingga ($n = 2, 0$), Singkep ($n = 1, 0$), Balambangan ($n = 0, 5$), and Banggi ($n = 0, 2$). We also conducted DFAs (cross-validated with a jackknife technique) on the same combinations of variables, defining the populations from Borneo, Sumatra, and the Malay Peninsula as *a priori* groups and including the populations from the smaller islands as unknowns.

RESULTS

Geographic variation on Borneo.—In our PCA of eight manus variables from mainland Bornean individuals, PC1 is a size vector most influenced by length variables, representing over 46% of the variation (Table 2A). PC2 explains more than 22% of the variation and represents a contrast between length variables and negatively weighted width and depth variables, particularly 1MD (Table 2A). All *T. m. caedis* individuals have scores within the range of variation of *T. m. minor* on each eigenvector, and a bivariate plot of PC1 vs. PC2 shows *T. m. caedis* as a subset of *T. m. minor* (Fig. 2A).

In our PCA of eight skull variables from mainland Bornean individuals, PC1 accounts for over 54% of the variation and represents overall skull size, though it is more heavily influenced by length variables than widths or heights (Table 2B). With the exception of one individual, the range of variation of

T. m. caedis on PC1 is completely within the range of *T. m. minor* (Fig. 2B). PC2, which explains more than 20% of the variation, represents a contrast of upper tooththrow length (UTL) with negatively weighted mandibular condyle dimensions (MCH and MCW) (Table 2B). Along this eigenvector, all *T. m. caedis* specimens have scores within the range of variation of *T. m. minor*. In the bivariate plot of PC1 vs. PC2, individuals of *T. m. caedis* appear as a subset of *T. m. minor* (Fig. 2B).

Additional testing for latitudinal and longitudinal patterns of morphometric variation among populations of *T. m. minor* (*sensu lato*) revealed no identifiably consistent trends. The following regression analyses yielded nonsignificant *P*-values and low *R*-squared values for the manus and skull, respectively: PC1 vs. latitude ($R^2 = 0.0004, 0.0181$; $P = 0.860, 0.378$) and PC1 vs. longitude ($R^2 = 0.0161, 0.0190$; $P = 0.248, 0.367$). Populations previously separated as *T. m. caedis* and *T. m. minor* from the mainland of Borneo are indistinguishable morphometrically. We therefore combined them into a single Bornean sample in subsequent analyses.

Geographic variation across all islands.—In our PCA of eight manus variables from all available individuals, PC1 is a size vector most influenced by depth and width variables, representing over 45% of the variation (Table 3A). PC2 accounts for over 18% of the variation and represents a contrast of length variables (1ML and 1PPL) with a negatively weighted depth variable (1MD) (Table 3A). With the exception of one large specimen from Sumatra, individuals from populations on the Malay Peninsula, Sumatra, and all three smaller islands fall within the range of variation exhibited by the Bornean population on

Table 2.—Component loadings from principal component analyses (PCAs) of manus and skull variables among mainland Bornean individuals. Abbreviations for manus and skull variables are defined in the “Materials and Methods” and Supplementary Data SD1. Loadings in boldface type are discussed in the text.

	Principal component	
	1	2
A) PCA of eight manus variables (Fig. 2A)		
1PPL	0.81	0.08
2PPL	0.80	0.31
5ML	0.78	0.41
1ML	0.77	0.39
1PPD	0.62	−0.57
2MW	0.58	−0.59
1DPD	0.53	0.14
1MD	0.40	−0.80
Eigenvalue	3.68	1.76
Percentage of total variance explained	46.05	22.06
B) PCA of eight skull variables (Fig. 2B)		
MCIL	0.89	0.23
PPL	0.84	0.32
LTL	0.84	0.43
UTL	0.80	0.47
MH	0.75	−0.40
MCH	0.60	−0.62
LIB	0.55	−0.40
MCW	0.51	−0.60
Eigenvalue	4.34	1.62
Percentage of total variance explained	54.25	20.31

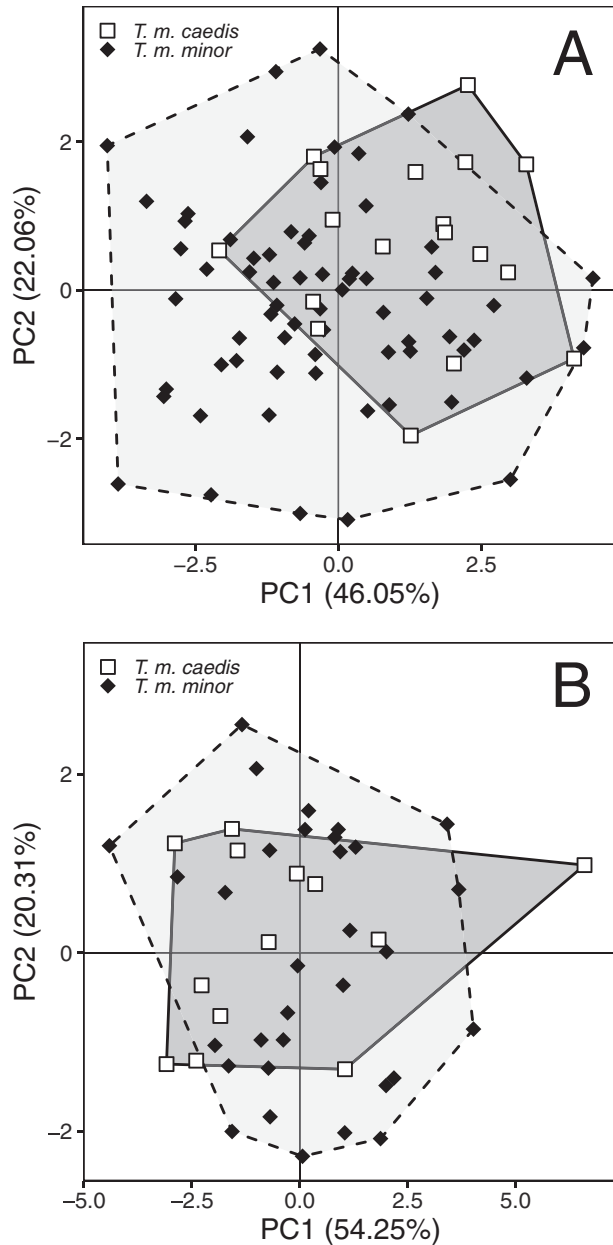


Fig. 2.—Plots of principal component (PC) scores from principal component analyses of all mainland Bornean individuals (*T. m. minor* and *T. m. caedis*). (A) Plot based on eight manus variables (Table 2A). (B) Plot based on eight skull variables (Table 2B).

each of the first two eigenvectors (Fig. 3A). The distributions for the Sumatran and the Peninsular Malaysian populations are offset along PC1, with the Sumatran population plotting to the right, mostly in positive morphospace, indicating larger average hand size (Fig. 3A). Specimens from the three smaller islands (Lingga, Laut, and Singkep) plot within the distribution of the Bornean population (Fig. 3A). The Singkep specimen and one of the Lingga specimens also overlapped with the Peninsular Malaysian population in the PCA, whereas the other Lingga specimen plotted within the Sumatran morphospace (Fig. 3A).

Our DFA of the same eight manus variables produced a correct classification rate of 72% (jackknifed correct classification of

Table 3.—Component loadings from principal component analyses (PCAs) of manus and skull variables among individuals from all islands. Abbreviations for manus and skull variables are defined in the “Materials and Methods” and [Supplementary Data SD1](#). Loadings in boldface type are discussed in the text.

	Principal component	
	1	2
A) PCA of eight manus variables (Fig. 3A)		
2MW	0.84	−0.22
2PPW	0.81	−0.19
4PPW	0.78	0.09
1PPD	0.77	−0.25
1MD	0.67	−0.50
1PPL	0.54	0.59
1ML	0.46	0.73
3DPL	0.34	0.40
Eigenvalue	3.64	1.45
Percentage of total variance explained	45.54	18.12
B) PCA of eight skull variables (Fig. 3B)		
PPL	0.90	0.25
MCIL	0.90	0.13
UTL	0.87	0.28
LTPL	0.87	0.26
LTL	0.85	0.32
MH	0.67	−0.60
MCH	0.54	−0.77
MCW	0.50	−0.53
Eigenvalue	4.83	1.56
Percentage of total variance explained	60.38	19.53

60%; Table 4A). Ten Bornean specimens (12%) were misclassified as belonging to the Peninsular Malaysian population, and one (1%) was misclassified as Sumatran. Almost half of the specimens from the Malay Peninsula (48%) were misclassified as belonging to the Bornean population, but none as Sumatran. Only three (33%) of the Sumatran individuals were correctly classified; four (44%) were misclassified as Bornean and two (22%) as Peninsular Malaysian. The specimens from Laut, Lingga, and Singkep were all classified as members of the Bornean population.

In our PCA of eight skull variables from all available individuals, PC1 accounts for over 60% of the variation and represents overall skull size, most influenced by length variables (Table 3B). PC2, which explains more than 19% of the variation, represents negatively weighted mandibular dimensions (MH, MCH, and MCW) (Table 3B). The range of variation of *T. minor* from the Malay Peninsula, Sumatra, and the two smaller islands is within the range of variation of the Bornean population along PC1. Similarly, along PC2, all but one Sumatran individual fall within the range of variation of the Bornean population. A plot of PC1 vs. PC2 (Fig. 3B) shows populations from the other four regions mostly as subsets of Bornean *T. minor*.

A DFA of the same eight skull variables produced a correct classification rate of 79% (jackknifed correct classification of 72%; Table 4B). One Bornean specimen (2%) was misclassified as Sumatran. Nine specimens from the Malay Peninsula (82%) and three specimens from Sumatra (60%) were misclassified as belonging to the Bornean population. All specimens

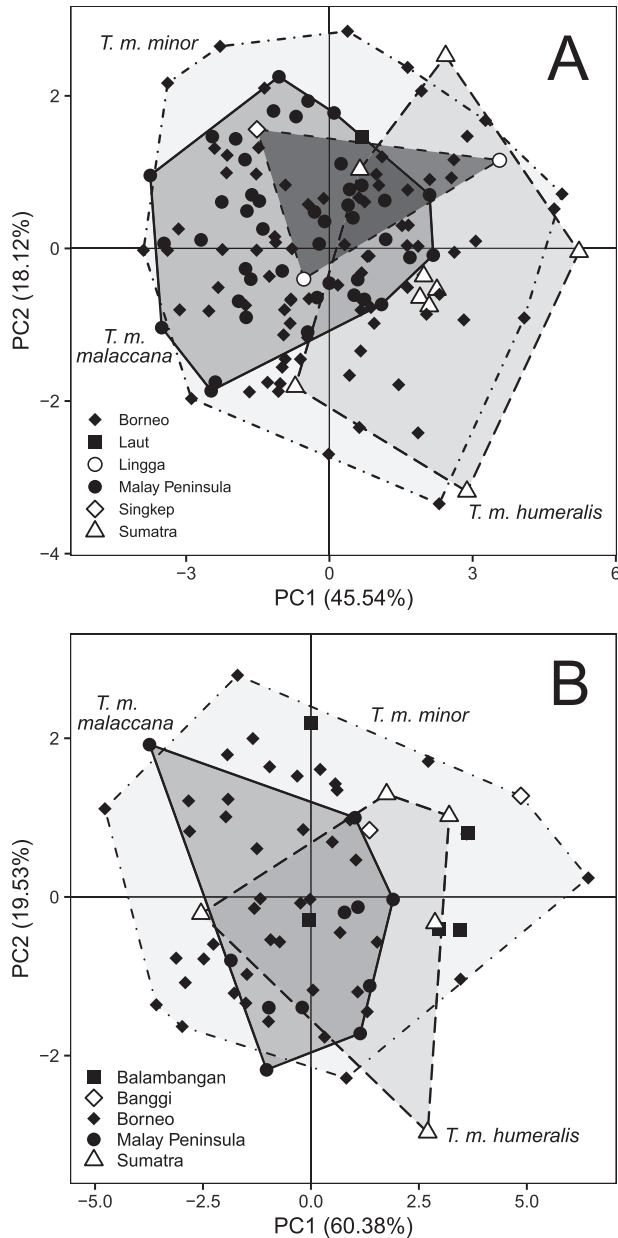


Fig. 3.—Plots of principal component (PC) scores from principal component analyses of all available individuals. Polygons represent subspecies designations while symbols indicate islands. (A) Plot of four subspecies based on eight manus variables (Table 3A). *Tupaia m. caedis* and *T. m. minor* are combined in the Bornean sample as *T. m. minor*; Lingga and Singkep are plotted together as *T. m. sincepis*. (B) Plot of three subspecies based on eight skull variables (Table 3B). *Tupaia m. minor* and *T. m. caedis*, including individuals from Banggi and Balambangan, are combined in the Bornean sample as *T. m. minor*.

from Balambangan and Banggi were classified as belonging to the Bornean population.

DISCUSSION

Four subspecies of *T. minor* are currently recognized, most of them differentiated based on subjective variation in pelage (Anderson 1879; Lyon 1911; Lyon 1913; Robinson and Kloss 1919). The taxon *T. m. caedis* was also originally distinguished

from *T. m. minor* based on subtle gradation in pelage color across northern Borneo (Chasen and Kloss 1932). This division appears to be in line with emerging evidence that some Bornean taxa, including many bird and small mammal species, contain divergent northeastern and southwestern lineages (Gorog et al. 2004; Lim et al. 2010; Hinckley et al. 2022). However, we found no evidence of latitudinally or longitudinally structured morphometric variation across *T. minor* individuals on Borneo. Our study supports the synonymization of *T. m. caedis* with *T. m. minor* (Corbet and Hill 1992; Helgen 2005; Hawkins 2018), as it is neither allopatric (Fig. 1) nor diagnosably distinct from the latter taxon in its manus or skull proportions (Fig. 2).

The four recognized subspecies are allopatric (Fig. 1), but our analyses of their hands and skulls provided no morphometric support for their continued recognition (Fig. 3; Table 4). There is some separation in manus proportions between populations from the Malay Peninsula and Sumatra (Fig. 3A), with the latter averaging slightly larger than the former, contrary to Lyon's (1913) observation that *T. m. malaccana* was larger than other subspecies. However, this pattern is not as clear for the skull (Fig. 3B), and analyses of both data sets show the Peninsular Malaysian and Sumatran populations as subsets of the Bornean sample with which they almost completely overlap (Fig. 3). Similarly, DFA of both data sets generated high rates of misclassification of Peninsular Malaysian and Sumatran individuals as members of the Bornean population, potentially due to the larger Bornean sample (Table 4). *Tupaia m. sincepis* also overlaps with the three other taxa in morphospace (Fig. 3A). Thus, these four populations (*T. m. minor*, *T. m. malaccana*, *T. m. humeralis*, and *T. m. sincepis*) fail to meet our criterion of diagnosable morphometric differences and do not warrant recognition at the subspecies level. This conclusion is congruent with a previous study of subspecies within the Large Treeshrew, *Tupaia tana* (Juman et al. 2021b). We therefore consider the names *Tupaia malaccana* Anderson, 1879; *Tupaia sincepis* Lyon, 1911; *Tupaia minor humeralis* Robinson and Kloss, 1919; and *Tupaia minor caedis* Chasen and Kloss, 1932 to be junior synonyms of *Tupaia minor* Günther, 1876.

In contrast to our results for *T. tana* (Juman et al. 2021b), we observed no island effect on manus or skull proportions in *T. minor*. Individuals from Banggi and Balambangan fall within the Bornean range of cranial variation (Fig. 3B) and were classified as belonging to the Bornean population in our DFA (Table 4B). The same is true for the single specimen from Laut in the manus analyses (Fig. 3A; Table 4A). The one individual from Singkep and the two from Lingga both fall within the range of Bornean cranial variation (Fig. 3A) and were classified as belonging to the Bornean population in our DFA (Table 4A). Lyon's (1913) note that *T. m. sincepis* is larger than other subspecies is not supported by our analysis, nor is his observation that individuals from Lingga are intermediate in size between those from Singkep and the Malay Peninsula (Fig. 3A). These island populations were represented by small samples in our study, and future morphometric analyses with more robust sample sizes may better elucidate infraspecific variation in this species. Additionally, a molecular analysis would provide further insight into the degree of genetic differentiation among

Table 4.—Classification table from discriminant function analyses (DFAs) among individuals from all islands, with small island populations included as unknowns. Abbreviations for manus and skull variables are defined in the “Materials and Methods” and [Supplementary Data SD1](#).

Actual group	Predicted group			
A) DFA of eight manus variables: 1ML, 1PPL, 1MD, 1PPD, 2MW, 2PPW, 3DPL, and 4PPW				
Island	Borneo	Sumatra	Malay Peninsula	Correct classification rate
Borneo	72	1	10	86.7%
Sumatra	4	3	2	33.3%
Malay Peninsula	21	0	23	52.3%
Singkep	1	0	0	—
Lingga	2	0	0	—
Laut	1	0	0	—
Overall classification rate				72.1%
B) DFA of eight skull variables: UTL, PPL, LTPL, MH, MCH, MCW, MCIL, and LTL				
Island	Borneo	Sumatra	Malay Peninsula	Correct classification rate
Borneo	44	1	0	97.8%
Sumatra	3	2	0	40.0%
Malay Peninsula	9	0	2	18.2%
Banggi	2	0	0	—
Balambangan	5	0	0	—
Overall classification rate				78.7%

these populations, as a lack of morphological distinction may not correspond to a similar genetic pattern. A phylogeographic study might also determine whether *T. minor* originated on Borneo (Roberts et al. 2011) or colonized Borneo repeatedly, as has been demonstrated for other Sundaland small mammals (Camacho-Sanchez and Leonard 2020).

Our findings suggest that the previously recognized subspecies of *T. minor* do not represent morphologically distinct populations, a conclusion that may help inform both international and local conservation decisions. The Lesser Treeshrew is listed as a species of “Least Concern” on the *IUCN Red List of Threatened Species*, but the population is noted to be “decreasing” (Cassola 2016). Oil palm production is driving heavy deforestation on Borneo, Sumatra, and the Malay Peninsula (Miettinen et al. 2016), and *T. minor* has been observed to experience localized population crashes in logged areas (Hawkins 2018). Although this species has been found in plantations and gardens in addition to forest (Corbet and Hill 1992), it is still unknown how it will respond to widespread habitat loss and conversion to oil palm plantations (Hawkins 2018). Additionally, Bornean wildlife may be further threatened by urbanization associated with the upcoming relocation of the Indonesian capital to Kalimantan. Our revision of the infraspecific taxonomy of *T. minor* clarifies that the smaller island populations (such as those on small islands like Lingga and Singkep) are not taxonomically distinct pockets of diversity, thereby enabling a broader focus on conservation issues that affect the entire distribution of the Lesser Treeshrew and not just those of particular subspecies.

The entire geographic range of the Lesser Treeshrew falls within the Sundaland biodiversity hotspot, which is increasingly endangered by land conversion, habitat fragmentation, and logging (Myers et al. 2000; Hawkins 2018; Tee et al. 2018). However, this region remains poorly studied compared to other areas with lower biodiversity and fewer anthropogenic threats (Sodhi et al. 2004). For example, mammal species richness in Southeast Asia is thought to be underestimated by over 50% (Francis et al. 2010).

Our study highlights the importance of reevaluating infraspecific taxonomic boundaries with nonarbitrary data to better understand mammalian diversity in this critical region, as well as to inform conservation efforts that rely on subspecies designations. It also emphasizes the need for more biological surveys, particularly on smaller islands, to provide larger samples for future studies.

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Descriptions of manus and skull measurements, original measurements of the *Tupaia minor* specimens used in this study, and corresponding summary statistics.

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- Tupaia m. humeralis* Robinson and Kloss, 1919 ($n = 19$).—INDONESIA: SUMATRA (NHMUK 64.4.12.4), South Sumatra (NHMUK 81.3.15.5); Padang Pandjang (NHMUK 40.368, 40.369, 40.372); Anci Kloof (NHMUK 40.363, 40.365, 40.366); Pasei Gauling (NHMUK 19.11.5.25); Benkoelen, Boekit Sanggoel (AMNH M-106509, M-106510, M-106511, M-106514); Palembang (AMNH M-102526, M-102527, M-102528); Tarussan Bay (USNM 141076); Tapanula Bay (USNM 114550); Indragiri River (USNM 113166).
- Tupaia m. malaccana* Anderson, 1879 ($n = 83$).—MALAYSIA: PENINSULAR MALAYSIA (USNM 291265, 291266, 291271, 487973); Selangor (USNM 291270, 355346); Kuala Lumpur (USNM 291269; NHMUK 55.1410, 55.1411); Kuala Lumpur, 6 mi N (USNM 290151); Kepong (USNM 290150, 291267, 291268; FMNH 65880); Batu (NHMUK 55.1408); Batu Caves (USNM 152186); Bukit Legong Forest Reserve (USNM 487987, 487991, 487995, 488009, 488014, 488016, 488018; NHMUK 66.1152, 66.1153); Cheras (NHMUK 8.7.20.13, 55.1409, 55.1418); Klang Gates (NHMUK 55.1415); Semangko Pass (NHMUK 8.7.20.11); Sembrong River (USNM 112618); Sungai Malayu (USNM 143271); Kampong Bukit (USNM 487970, 487971); Subang Forest Reserve (USNM 487988, 487989, 487992, 487993, 487998, 487999, 488000, 488001, 488002, 488003, 488004, 488005, 488006, 488007, 488008); Kuala Langat Forest Reserve (USNM 488017); Bukit Mandol (USNM 487990, 487994, 488011, 488012, 488013, 488015, 488021, 488022, 488023); Sungai Buloh Forest Reserve, Bukit Lanjan (USNM 487996, 488019, 488020); Batang Berjuntai (USNM 488010); Labis Forest Reserve, Tamok (USNM 487960, 487961, 487962, 487963, 487964, 487965, 487968); Kudong (USNM 487966); Kersiak (USNM 487967, 487969); Bukit Kemandul, Sungai Rasu (USNM 487997); Talum, Perak (NHMUK 3.2.5.1); Johore (NHMUK 85.8.19.5); Kangka Aming (NHMUK 5.12.7.8); Nyalas, Malacca (NHMUK 55.1412); Tonjong Antu, Dindings (NHMUK 55.1227); Bukit Tampin, Negeri Sembilan (NHMUK 55.1417); Pahang, Benom Foothills (NHMUK 55.1416); Gunong Benom (NHMUK 67.1478); Labang Endau (NHMUK 55.1414).
- Tupaia m. minor* Günther, 1876 ($n = 119$).—MALAYSIA: BORNEO: North Borneo (NHMUK 71.2555, 71.2556), Sabah (USNM 396668, 396669, 396672), Mount Kinabalu (USNM 292468, 292470; MCZ 36402, 57003; NHMUK 93.4.1.4); Mount Kinabalu National Park (USNM 487972, 487974, 487975, 487976, 487977, 487978, 487979, 487982, 487983, 487985); Ranau (USNM 300901, 300905, 300906, 300907, 317180, 317181, 317182, 317183); Ranau, 0.5 mi N (USNM 300903, 300904); Kampong Lasing (USNM 300902); Kampong Morok (USNM 487980, 487984, 487986); Kampong Nalapak (USNM 487981); Petergas (USNM 317178, 317179); mainland opposite Labuan (type locality; NHMUK 76.5221, 76.5222, 76.5223, 76.5224, 76.5225—cotypes); Quoin Hill, Tawau (NHMUK 71.2543, 71.2546, 71.2547, 71.2548, 71.2549); Beaufort

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APPENDIX I

SPECIMENS EXAMINED

Specimens from the following institutions were included in this study: American Museum of Natural History, New York (AMNH); The Natural History Museum, London (NHMUK); Field Museum of

Forest Reserve (NHMUK 71.2552, 71.2553); Tinampah (NHMUK 71.2554). Sarawak: Kuching (MCZ 36809, 36810); Kapit, 5 Mi E, Nanga Balleh (USNM 311452); Kadit, Nanga Pelagus (USNM 311453); Stapok (FMNH 80094, 80095, 80096, 80097, 80098); Pa Main (FMNH 88379, 88380, 88381); Ulu Selio (FMNH 88590); Rock Road 6 mi (NHMUK 71.2551); Lingit (NHMUK 55.683); Paku (NHMUK 55.676, 55.682); Udan (NHMUK 55.677); Sungei Lenin (NHMUK 55.678); Entawa (NHMUK 55.679); Sungei Pelandok (NHMUK 55.680, 55.681); Baram River (NHMUK 88.8.13.5); Trusan (NHMUK 88.8.13.6); Mount Dulit (NHMUK 92.2.7.8, 92.2.7.9, 99.12.9.11); Tutan River (NHMUK 94.6.2.5). INDONESIA: Laut Island (USNM 151881). BORNEO: Simpang River (USNM 145575); Kendawangan River (USNM 153857); Batoe Panggal, Mahakam River (USNM 176419, 176420); Birang

River (USNM 176421, 176422, 176423, 176424, 176425, 176426, 176427, 176428); Segah River (USNM 176429); Sungai Menganne (USNM 197197); Sungai Karangan (USNM 198038); Mahakkam River (USNM 198680); Laham (USNM 198681); Long Navang (MCZ 22254); Mara (AMNH M-103414, M-103438, M-103439); Parit (AMNH M-103616, M-103617, M-103618); Peleben (AMNH M-103896, M-103897, M-103899, M-103900, M-103901, M-103902, M-103903, M-103904, M-103905, M-103906); Landak (AMNH M-106750, M-106911, M-106998); Karanginton, Martapoeia River (NHMUK 10.4.5.76, 10.4.5.77); Poeroektjahoe (NHMUK 10.4.5.79).

Tupaia m. sincepis Lyon, 1911 ($n = 5$).—INDONESIA: LINGGA ARCHIPELAGO: Singkep Island (type locality; USNM 123105—holotype); Lingga Island (USNM 101599, 101600, 113068); Lingga Peak (USNM 101598).