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Ecogeographic variation and taxonomic boundaries in Large Treeshrews (Scandentia, Tupaiidae: *Tupaia tana* Raffles, 1821) from Southeast Asia

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The Large Treeshrew, *Tupaia tana* Raffles, 1821, is a small mammal (~205 g) from Southeast Asia with a complicated taxonomic history. Currently, 15 subspecies are recognized from Borneo, Sumatra, and smaller islands, and many were originally differentiated based on minor pelage differences and small sample sizes. We explored intraspecific variation in *T. tana* using quantitative osteological data obtained from the hands and skulls of museum specimens. Multivariate analyses reveal extensive overlap among *T. tana* populations in morphospace, indicating that the majority of currently recognized subspecies are not morphometrically distinct. In contrast, the separation between Bornean and Sumatran populations of *T. tana* is sufficient to recognize them as different subspecies. Comparisons of Bornean specimens to those on small, offshore islands reveal that the latter average smaller body size. This pattern is inconsistent with Foster's island rule, which predicts that island populations of small mammals (< 5 kg) will average larger body size relative to mainland forms. A similar lack of support for ecogeographic rules has been noted in *T. glis* (Diard, 1820), suggesting that these "rules" are poor predictors of geographic variation in treeshrews.

Key words: cranium, hand, island rule, mandible, manus, morphology, skull

Treeshrews (order Scandentia) are small mammals endemic to the tropical rainforests of South and Southeast Asia (Emmons 2000; Hawkins 2018). The geographic ranges and taxonomic boundaries of most treeshrews have not been comprehensively evaluated since Lyon's (1913) monographic revision of this group. One species with a particularly complicated taxonomic history is *Tupaia tana* Raffles, 1821, the Large Treeshrew, which inhabits Borneo, Sumatra, and smaller offshore islands (Fig. 1). *Tupaia tana* has 17 synonyms (Helgen 2005) and 15 currently recognized subspecies (Helgen 2005; Hawkins 2018). Some of these taxa were first described as species and later synonymized with *T. tana* (Table 1), but they were considered distinctive enough to retain as subspecies. Many were originally differentiated solely based on very subtle differences in pelage (Lyon 1913), a soft tissue feature known to vary seasonally, with individual age, and over time in collections (Davis et al. 2013). Several *T. tana* subspecies are sympatric, particularly in northeastern Borneo (Fig. 1), where these populations were originally described as distinct species (Table 1).

Some offshore island subspecies were described based on perceived differences in size. For example, Lyon (1913:142, 144) noted that *T. t. sirhassenensis* Miller, 1901 and *T. t. bunoae* Miller, 1900, both endemic to the Riau Islands (Fig. 1), were "slightly smaller" than *T. t. tana* and *T. t. utara* (Lyon, 1913), and Chasen and Kloss (1932) described *T. t. banguei* Chasen and Kloss, 1932, from Banggi Island north of Borneo, as smaller than *T. t. paitana* (Lyon, 1913), a north Bornean subspecies. These size relationships hint at the inverse of a commonly observed ecogeographic pattern. The island rule (or Foster's rule) refers to the phenomenon of island populations

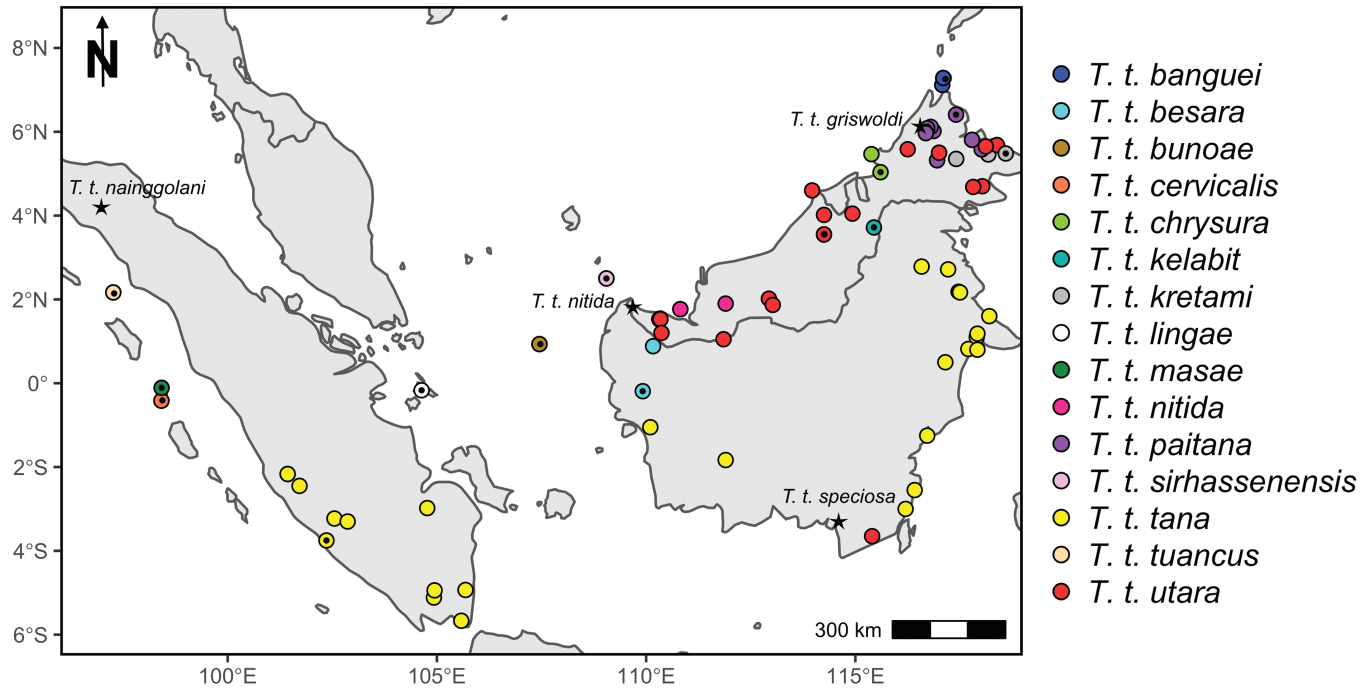

Fig. 1.—Locality map for specimens in our study. Black dots inside symbols represent type localities of subspecies (see Appendix I); labeled stars represent type localities of taxa for which the holotypes were not inspected.

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

Subspecies names of *Tupaia tana*	Original name	Island	Manus	Skull
T. t. banguei Chasen and Kloss, 1932	*Tupaia tana banguei*	Banggi	2	4*
T. t. besara (Lyon, 1913)	*Tana tana besara*	Borneo	3*	3*
T. t. bunoae Miller, 1900	*Tupaia bunoae*	Tambelan Islands	4*	4*
T. t. cervicalis Miller, 1903	*Tupaia cervicalis*	Tanahbala	2*	2*
T. t. chrysura Günther, 1876	*Tupaia tana chrysura*	Borneo	—	2*
T. t. griswoldi (Coolidge, 1938)^	*Tana tana griswoldi*	Borneo	—	—
T. t. kelabit Davis, 1958	*Tupaia tana kelabit*	Borneo	1	1
T. t. kretami Davis, 1962	*Tupaia tana kretami*	Borneo	8	13*
T. t. lingae (Lyon, 1913)	*Tana lingae*	Lingga	1*	1*
T. t. masae (Lyon, 1913)	*Tana cervicalis masae*	Tanahmasa	1*	2*
T. t. nainggolani (Sody, 1936)^	*Tana tana nainggolani*	Sumatra	—	—
T. t. nitida Chasen, 1933	*Tupaia tana nitida*	Borneo	6	10
T. t. paitana (Lyon, 1913)	*Tana paitana*	Borneo	31	47*
T. t. sirhassenensis Miller, 1901	*Tupaia sirhassenensis*	Riau Islands	3*	4*
T. t. speciosa (Wagner, 1841)	*Cladobates speciosus*	Borneo, Sumatra	—	—
T. t. tana Raffles, 1821	*Tupaia tana*	Borneo, Sumatra	63	76*
T. t. tuancus (Lyon, 1913)^	*Tana tana tuancus*	Tuangku	2*	2*
T. t. utara (Lyon, 1913)	*Tana tana utara*	Borneo	6	30*
Total			133	201

of large-bodied mammals exhibiting smaller body size than their mainland counterparts (dwarfism) and, conversely, small-bodied mammals averaging larger body size on islands than on the mainland (gigantism—Foster 1964). *Tupaia tana* averages approximately 205 g (Sargis 2002), falling within the < 5 kg range of "small" mammals (Merritt 2010). According to the island rule, *T. tana* should therefore exhibit larger body size on offshore islands relative to mainland populations. Although this pattern is well established in certain taxonomic groups (Lomolino 1985, 2005; Lomolino et al. 2013), it is not consistently supported across all mammal taxa (Meiri et al. 2006, 2008). A previous study found that neither the island rule nor Bergmann's rule—another ecogeographic pattern in which body size increases with latitude—apply to the Common Treeshrew, *Tupaia glis* (Diard, 1820) (Sargis et al. 2018), but additional species of treeshrews, such as *T. tana*, need to be examined to determine whether a common pattern exists in Scandentia.

In addition to ecogeographic rules, there has never been a thorough taxonomic and geographic revision encompassing all currently recognized subspecies of *T. tana*. Current range maps for *T. tana* include northern, western, and southwestern Sumatra,

many nearby islands (with the exception of the northern Riau islands and some islands west of Sumatra), and most of Borneo (Cassola 2016; Hawkins 2018). As a result of lower sea level during much of the Pleistocene, Borneo, Sumatra, and the offshore islands inhabited by *T. tana* were connected to one another until approximately 400 ka (Husson et al. 2020), possibly permitting fairly recent gene flow among what are now isolated populations, as is the case in other Sundaland mammals (Roberts et al. 2011; Wilting et al. 2011). This connectivity may have impacted the distinctiveness of *T. tana* populations at the subspecies level.

Defensibly circumscribed subspecies remain useful for mapping and protecting infraspecific variation (Braby et al. 2012). However, the concept of subspecies has been widely debated for decades, with many arguing that the criteria used to define subspecies are arbitrary and inconsistently applied (e.g., Simpson 1961; Mayr and Ashlock 1991), particularly in mammal studies (Gippoliti and Amori 2007). Local populations differ among one another in subtle ways, including in their pelage, and as Mayr and Ashlock (1991:44) pointed out, "[i]t would be absurd and would lead to nomenclatural chaos if each population of this type were given the formal trinomial name that is customary for subspecies." Yet this is precisely what has happened with *T. tana* and countless other mammal species, including other treeshrews (e.g., see accumulation curve of treeshrew species and subspecies in Sargis et al. 2013b: figure 1). Simpson (1961:173) noted, "when there are semiarbitrary subgroups in a species, their designation as subspecies should hardly raise any question if the data are adequate." This is not the case for *T. tana* because the pelage "data" (e.g., Lyon 1913) are arbitrary and problematic. For example, Lyon (1913:145) described *T. t. lingae* as "almost identical in color" to *T. t. sirhassenensis* but with a narrower dorsal stripe, a difference he stated was likely "more apparent than real" due to a "small albinistic spot" on the stripe of the single available specimen of *T. t. lingae*. Even in early descriptions, pelage differences are characterized as unreliable; *T. t. sirhassenensis* was noted as "intermediate in color" between *T. t. tana* and *T. t. utara*, with "some specimens" resembling the former and others the latter (Lyon 1913:142). Unlike subtle pelage features, morphometric data are nonarbitrary, and we consider them to be "adequate" because measurements from the skull and hands have proven reliable for distinguishing treeshrew species and subspecies (Sargis et al. 2013a, 2013b, 2014a, 2014b). These different types of characters (e.g., arbitrary, qualitative, soft tissue, pelage versus nonarbitrary, quantitative, hard tissue, osteology) may be in conflict (Patton and Conroy 2017), and a different subspecies classification will be recognized "depending on whether coloration or the results of the multivariate analysis are given primacy" (Mayr and Ashlock 1991:98). We recognize this potential conflict, and we give primacy to the results of multivariate morphometric analyses because they are less arbitrary, more reliable, and more repeatable (e.g., Sargis et al. 2014a) than qualitative and inconsistent descriptions of subtle coloration differences. We consider previous pelage-based subspecies delineations to be testable hypotheses (Patton and Conroy 2017) that we will test with quantitative morphometric analyses of skull and hand characters (Sargis et al. 2013a, 2013b, 2014a, 2014b, 2017).

Given the considerations outlined above, we follow Braby et al. (2012:711) in defining a subspecies under the general lineage species concept (de Queiroz 1998) as a "partially isolated lineage" moving toward "evolutionary independence." In practice, we recognize subspecies as allopatric (Mayr and Ashlock 1991), phenotypically distinct populations with at least one diagnosable character (Braby et al. 2012). Specifically, we carried out separate multivariate analyses of manus and skull characters to assess the phenotypic distinctiveness of 1) 14 of the 15 currently recognized subspecies as well as one potentially distinctive island population previously recognized as *T. t. tuancus* (Lyon, 1913); 2) the eight Bornean *T. tana* subspecies; 3) the populations of *T. tana* from Borneo and Sumatra; and 4) the offshore island populations relative to the mainland Bornean and Sumatran populations. We also investigated sexual size dimorphism in this species. Finally, we mapped the distribution of each subspecies based on our voucher localities and used this to reevaluate recent range maps for *T. tana* (Fig. 1).

Materials and Methods

Our study includes 14 of the 15 currently recognized subspecies (Appendix I), with the exception of *T. t. speciosa* (Wagner, 1841). We also included *T. t. tuancus* (Lyon, 1913) from Tuangku Island, which was not recognized by Helgen (2005) or Hawkins (2018). To assess skeletal variation across populations of *T. tana*, we recorded 38 manus and 20 craniomandibular measurements (in mm) from museum specimens. Previous treeshrew studies have shown that hand proportions are useful for assessing taxonomic boundaries, and they provide results that are congruent with those from skull morphometrics and molecular data (Sargis et al. 2013a, 2013b, 2014b, 2017). We also georeferenced 74 specimen localities—including 18 type localities—and generated a locality map using the ggplot2, rnaturalearth, and ggspatial packages in R (R Core Team 2013; Wickham 2016; South 2017; Dunnington 2020) (Fig. 1).

Manus.—We x-rayed the left and right manus of 133 adult *T. tana* specimens (those with fully erupted permanent dentition; see Woodman et al. 2020) from the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), and United States National Museum of Natural History (USNM). This sample included 14 different subspecies of *T. tana*, including the holotypes of seven subspecies (Table 1; Appendix I).

Specimens were x-rayed using a Kevex–Varian digital X-ray system (Division of Fishes, USNM) at 30 kV, 356 µA with a Thermo Scientific Kevex X-ray source interfaced with a desktop computer using Kevex X-ray Source Control Interface (version 4.1.3; Palo Alto, California). Images were acquired with Varian Medical Systems Image Viewing and Acquisition (VIVA version 2.0; Waltham, Massachusetts) and transferred to ImageJ (ImageJ 1.x—Schneider et al. 2012).

The first author (MMJ) measured the metacarpals and phalanges using the Straight Line tool in ImageJ, resetting the scale for

each individual image (Set Scale, under Analyze). 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): 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.—The first author (MMJ) recorded 20 craniomandibular measurements (Supplemental Data SD1; Sargis et al. 2013a, 2014a, 2014b, 2017) from 201 adult specimens using Mitutoyo digital calipers. These included nearly all of the specimens of *T. tana* from the manus analyses, with additional specimens from The Natural History Museum, London (NHMUK), and the Museum of Comparative Zoology, Harvard University (MCZ). This sample included 15 subspecies of *T. tana*, including the holotypes of 13 subspecies (Table 1; Appendix I; Supplementary Data SD1).

Multivariate analyses.—To examine skeletal variation among the subspecies of *T. tana*, we used R with function princomp() and package ggplot2 to carry out and plot separate principal component analyses (PCA) for the manus and skull data sets. Correlation matrices computed from ln-transformed measurements were used in the PCA. Discriminant function analyses (DFA) were undertaken on ln-transformed data with the MASS package in R (Venables and Ripley 2002). Missing data prevented the inclusion of some manus and skull measurements in analyses. Therefore, seven to eight variables were selected from each data set based on their completeness in the samples in order to optimize the number of individuals included (particularly from island populations with smaller sample sizes). 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 tests, the sample sizes for the manus and the skull are listed, respectively, for each included subspecies.

1. *Sexual Size Dimorphism*: We compared males and females from: (a) all available individuals (n = 72 male, 74 female); (b) our Bornean sample (n = 46 male, 51 female); and (c) our Sumatran sample (n = 19 male, 17 female), by carrying out two-sample analyses of variance (ANOVA) with skull (condylopremaxillary) length as a response variable and sex as a binary grouping variable. We also carried out linear complete DFA on each sample using eight skull variables (MTL, PPL, LB, LIB, PBPL, LTPL, MCH, MCW).
2. *Borneo, Sumatra, and Offshore Islands*: We then carried out a PCA for all available individuals using: (a) eight manus variables (1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5ML, 5MW, 5PPW; n = 103); and (b) eight skull variables (MTL, PPL, LB, LIB, PBPL, LTPL, MCH, MCW; n = 154).
3. *Borneo*: To assess variation among eight mainland Bornean subspecies, we undertook a PCA on: (a) eight manus variables (1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5ML, 5MW, 5PPW; n = 62); and (b) eight skull variables (MTL, PPL, LB, LIB, PBPL, LTPL, MCH, MCW; n = 101). The sample included: *T. t. besara* (Lyon, 1913) (n = 1 manus, 3 skull), *T. t. chrysura* Günther, 1876 (n = 0, 2), *T. t. kelabit* Davis, 1958 (n = 0, 1), *T. t. kretami* Davis, 1962 (n = 6, 10), *T. t. nitida* Chasen, 1933 (n = 4, 4), *T. t. paitana* (n = 24, 44), *T. t. tana* (n = 23, 18), and *T. t. utara* (n = 4, 19).
4. *Borneo versus Sumatra*: We further compared the populations on Borneo and Sumatra using DFAs including: (a) eight manus variables (1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5ML, 5MW, 5PPW; n = 95); and (b) eight skull variables (MTL, PPL, LB, LIB, PBPL, LTPL, MCH, MCW; n = 141). Included samples: Bornean *T. tana* (n = 62 manus, 101 skull) and Sumatran *T. tana* (n = 33, 40).
5. *Borneo versus Offshore Islands*: We examined variation among "mainland" Borneo and offshore island populations by undertaking a PCA on: (a) seven manus variables (1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5MW, 5PPW; n = 69); and (b) eight skull variables (MTL, PPL, LB, LIB, PBPL, LTPL, MCH, MCW; n = 113). The Bornean sample included: *T. t. besara* (n = 1 manus, 3 skull), *T. t. chrysura* (n = 0, 2), *T. t. kelabit* (n = 0, 1), *T. t. kretami* (n = 6, 10), *T. t. nitida* (n = 4, 4), *T. t. paitana* (n = 24, 44), *T. t. tana* (n = 23, 18), and *T. t. utara* (n = 4, 19). The offshore island sample included: *T. t. banguei* (n = 2, 4), *T. t. sirhassenensis* (n = 3, 4), and *T. t. bunoae* (n = 2, 4).
6. *Sumatra versus Offshore Islands*: We also compared the Sumatran *T. t. tana* population to subspecies found on neighboring islands with a PCA on (a) seven manus variables (1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5PPL, 5PPW; n = 32); and (b) eight skull variables (PPL, MB, LIB, ZB, BB, MCH, MCW, MCIL; n = 44). The samples included Sumatran *T. t. tana* (n = 27 manus, 37 skull) and the offshore island samples: *T. t. cervicalis* Miller, 1903 (n = 2, 2), *T. t. masae* (Lyon, 1913) (n = 1, 2), *T. t. tuancus* (n = 2, 2), and *T. t. lingae* (Lyon, 1913) (n = 0, 1).

Results

Sexual Size Dimorphism.—We detected no sexual dimorphism in our sample. ANOVA on condylopremaxillary length by sex was not significant for the overall sample (t = −0.001, P = 0.999), the Bornean sample (t = 1.076, P = 0.287), or the Sumatran sample (t = −0.091, P = 0.928). DFA of the eight skull variables revealed respective overall correct classification rates of around 66%, 70%, and 69% by sex (Table 2). Females and males were therefore combined in all subsequent analyses.

Borneo, Sumatra, and Offshore Islands.—In our PCA of eight manus variables from all available individuals, PC1 is a size vector with high positive loadings, accounting for more than

Table 2.—Discriminant function analysis (DFA) classification table by sex. The DFA was conducted with eight skull variables: MTL, PPL, LB, LIB, PBPL, LTPL, MCH, and MCW (abbreviations are defined in Supplementary Data SD1).

Actual group	Predicted group		
A) DFA of individuals from all islands			
Sex	Female	Male	Correct classification rate
Female	48	26	64.9%
Male	24	48	66.7%
Overall classification rate			65.8%
B) DFA of individuals from Borneo			
Sex	Female	Male	Correct classification rate
Female	39	12	76.5%
Male	17	29	63.0%
Overall classification rate			70.1%
C) DFA of individuals from Sumatra			
Sex	Female	Male	Correct classification rate
Female	11	6	64.7%
Male	5	14	73.7%
Overall classification rate			69.4%

Table 3.—Component loadings from principal component analyses (PCA) 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 (Figs. 2A and 2B)		
2PPW	0.86	–0.08
1PPD	0.81	–0.09
4PPW	0.81	–0.24
5PPW	0.74	–0.36
1MD	0.67	0.16
2PPL	0.63	**0.60**
5MW	0.57	**–0.43**
5ML	0.55	**0.67**
Eigenvalue	4.05	1.23
Percentage of total variance explained	50.66	15.35
B) PCA of eight skull variables (Figs. 2C and 2D)		
PPL	0.92	0.34
PBPL	0.92	0.34
LTPL	0.90	0.38
MTL	0.84	0.24
LB	0.75	–0.33
MCH	0.72	**–0.40**
MCW	0.70	**–0.46**
LIB	0.69	**–0.44**
Eigenvalue	5.25	1.11
Percentage of total variance explained	65.62	13.86

50% of the variation (Table 3A). PC2, which explains over 15% of the variation, represents a contrast of two length variables, 2PPL and 5ML, with a negatively weighted width variable, 5MW (Table 3A). The plot of these two components revealed considerable overlap among subspecies in morphospace (Fig. 2A). *Tupaia t. tuancus* is the only taxon that does not overlap with other subspecies, plotting low along PC2, but this island population is represented by only a single individual in this analysis (Fig. 2A). Grouping by island category shows the Sumatran population as a subset of the more variable Bornean one, and the offshore island individuals overlap with both (Fig. 2B).

In our PCA of eight skull variables from all available individuals, PC1 represents size and explains over 65% of the variation (Table 3B). PC2 accounts for almost 14% of the variation and represents three negatively weighted variables (least interorbital breadth, LIB; mandibular condyle height, MCH; mandibular condyle width, MCW; Table 3B). A bivariate plot of the component scores reveals considerable overlap among subspecies on both axes (Fig. 2C) but also shows some separation by island category, particularly along PC1 (Fig. 2D). Although they overlap along this component, the Bornean population plots mostly in positive morphospace while the Sumatran population plots largely in negative morphospace (Fig. 2D), demonstrating that the Bornean population averages larger skull size. Individuals from offshore islands plot only in negative morphospace (Fig. 2D), indicating smaller average body size in these populations relative to the mainland populations, particularly that from Borneo.

Borneo.—We first examined Bornean subspecies with a PCA of eight manus variables (Table 4A). PC1, representing size, accounts for nearly 55% of the variation. PC2 explains almost 13% of the variation and represents a contrast of two length variables, 2PPL and 5ML, with the negatively weighted width variable 5MW (Table 4A). In a plot of these two components, the included subspecies overlap considerably along both axes (Fig. 3A).

Our second PCA included eight skull variables from Bornean subspecies (Table 4B). PC1 once again represents size and explains over 58% of the variance. PC2 accounts for nearly 18% of the variance and is most influenced by two negatively weighted breadth variables (lacrimal breadth, LB; least interorbital breadth, LIB; Table 4B). Once again, the resulting bivariate plot reveals considerable overlap among the Bornean subspecies along both axes; *T. t. kretami* and *T. t. nitida* are distinct from each other in morphospace, but both overlap with *T. t. paitana* and *T. t. utara* (Fig. 3B).

Borneo versus Sumatra.—In the plot of scores from our skull PCA, there was some separation between the Bornean and Sumatran populations (Fig. 2D). We further investigated this differentiation with linear complete DFAs of just the Bornean and Sumatran individuals. These analyses yielded high correct classification rates, again suggesting separation between these two populations. In the DFA of the manus data set, > 75% of individuals were correctly classified (Table 5A), and in the DFA of the skull data set, more than 89% of individuals were correctly classified (Table 5B). Bornean individuals were accurately classified at higher rates than Sumatran individuals in both analyses (Table 5).

Borneo versus Offshore Islands.—Our first PCA examining individuals from Borneo and nearby offshore islands included

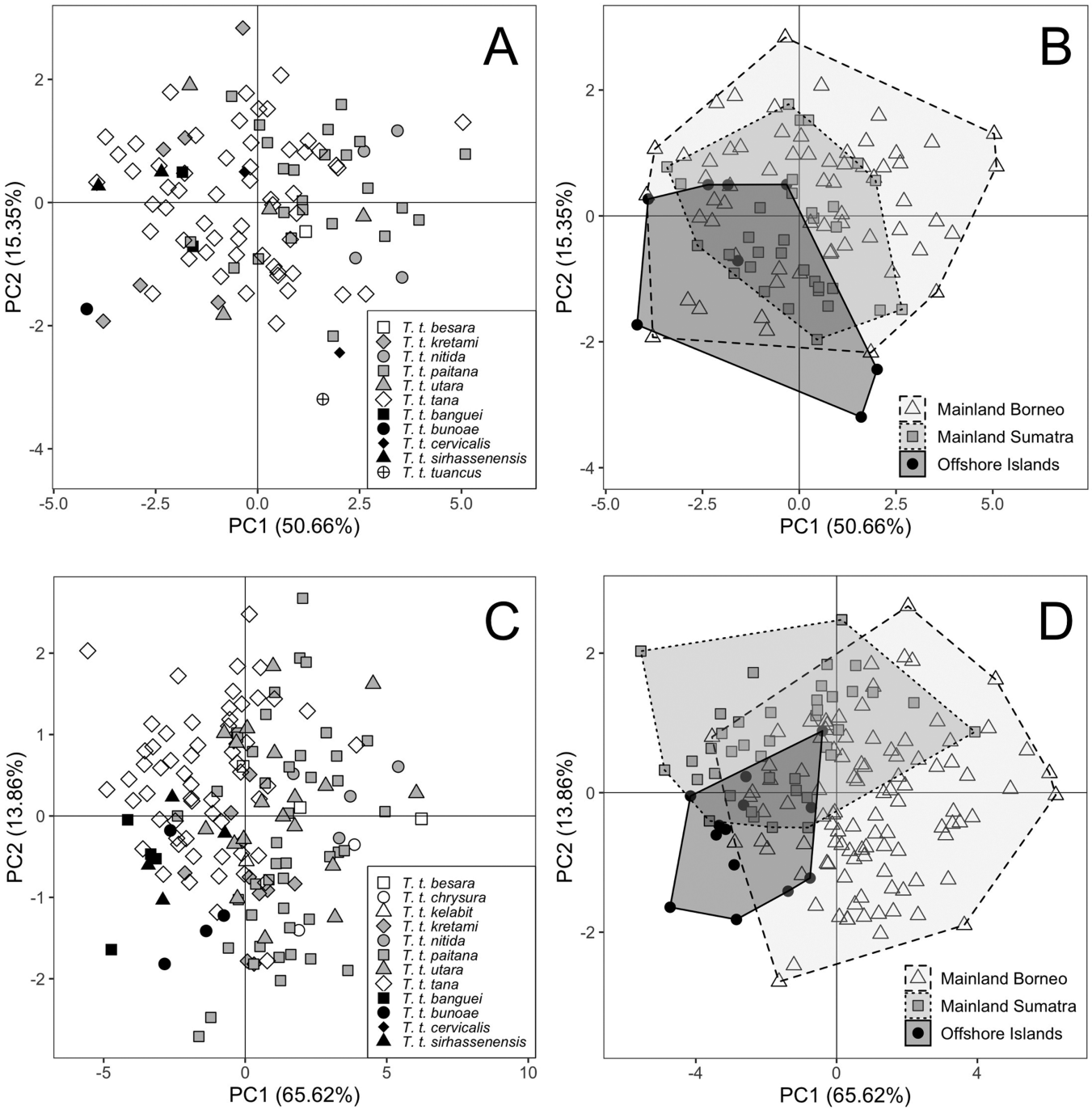

Fig. 2.—Plots of principal component (PC) scores from principal component analyses of all *Tupaia tana* subspecies: A) Plot of 11 subspecies based on eight manus variables (Table 3A). B) Polygons for general locality overlaid on 2A illustrate the overlap in morphospace among individuals from different islands. C) Plot of 12 subspecies based on eight skull variables (Table 3B). D) Polygons for general locality overlaid on 2C illustrate some separation among individuals from different islands.

seven manus variables (Table 6A). PC1 is a size vector accounting for over 58% of the variation. PC2 explains more than 12% of the variance and represents a contrast between 1MD and negatively weighted 5MW (Table 6A). In the plot of these two components, populations from mainland Borneo and offshore islands overlap considerably on PC2 (Fig. 4A). Along PC1, the mainland population occurs equally in negative and positive morphospace, whereas the offshore island sample plots only in negative morphospace, illustrating the smaller average size of island individuals relative to those from the mainland.

In the PCA of eight skull variables from Bornean and offshore island individuals, PC1 accounts for more than 62% of the variation and represents size (Table 6B). PC2 represents a contrast between maxillary toothrow length (MTL) and two negatively weighted breadth variables (lacrimal breadth, LB;

least interorbital breadth, LIB), and it explains more than 14% of the variation (Table 6B). A bivariate plot of scores on these two components (Fig. 4B) is congruent with the plot from the manus PCA (Fig. 4A), revealing overlap along PC2 but some separation along PC1. Offshore island individuals plot to the left in negative morphospace while mainland Bornean individuals are spread across PC1, demonstrating the smaller average size of the former relative to the latter (Fig. 4B). There is no clear pattern regarding which particular subspecies plot outside of the mainland polygon (Figs. 4A and 4B).

Table 4.—Component loadings from principal component analyses (PCA) of manus and skull variables among 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. 3A)		
2PPW	0.87	0.03
4PPW	0.83	–0.18
1PPD	0.79	–0.17
5PPW	0.80	–0.23
1MD	0.72	0.03
2PPL	0.65	**0.57**
5ML	0.63	**0.56**
5MW	0.57	**–0.51**
Eigenvalue	4.39	1.03
Percentage of total variance explained	54.82	12.85
B) PCA of eight skull variables (Fig. 3B)		
PBPL	0.92	0.29
PPL	0.91	0.35
LTPL	0.90	0.29
MTL	0.81	0.34
MCH	0.66	–0.32
MCW	0.65	–0.34
LB	0.57	**–0.61**
LIB	0.55	**–0.65**
Eigenvalue	4.65	1.42
Percentage of total variance explained	58.13	17.78

Sumatra versus Offshore Islands.—Our first PCA of individuals from Sumatra and nearby offshore islands included seven manus variables (Table 7A). PC1 accounts for more than 40% of the variance, representing depth and width of the bones of the manus. PC2 explains more than 24% of the variance and represents two length variables (2PPL and 5PPL; Table 7A). A bivariate plot of PC1 and PC2 reveals some separation between mainland Sumatran and offshore island populations along both axes (Fig. 4C). Island individuals plot entirely in positive morphospace along PC1 and further into negative morphospace along PC2, indicating they average shorter and wider/deeper bones of the manus in comparison to mainland individuals.

Our final PCA included eight skull variables from Sumatran and offshore island individuals (Table 7B). PC1 is a size vector accounting for nearly 49% of the variance. PC2 explains 17% of the variation and represents a contrast between mastoid breadth (MB) and negatively weighted mandibular condyle width and height (MCW and MCH; Table 7B). In a plot of these two components, the mainland and offshore island populations overlap along PC1 (Fig. 4D). They overlap along PC2 as well, but mainland individuals plot farther into positive morphospace, while island individuals plot farther into negative morphospace, indicating narrower mastoid breadth and wider, higher mandibular condyles. There is no discernible pattern among the different island subspecies, and they do not exhibit smaller size relative to the Sumatran population (Figs. 4C and 4D).

Discussion

We found no evidence that *T. tana* is sexually dimorphic with respect to body size (Table 2). This is congruent with earlier

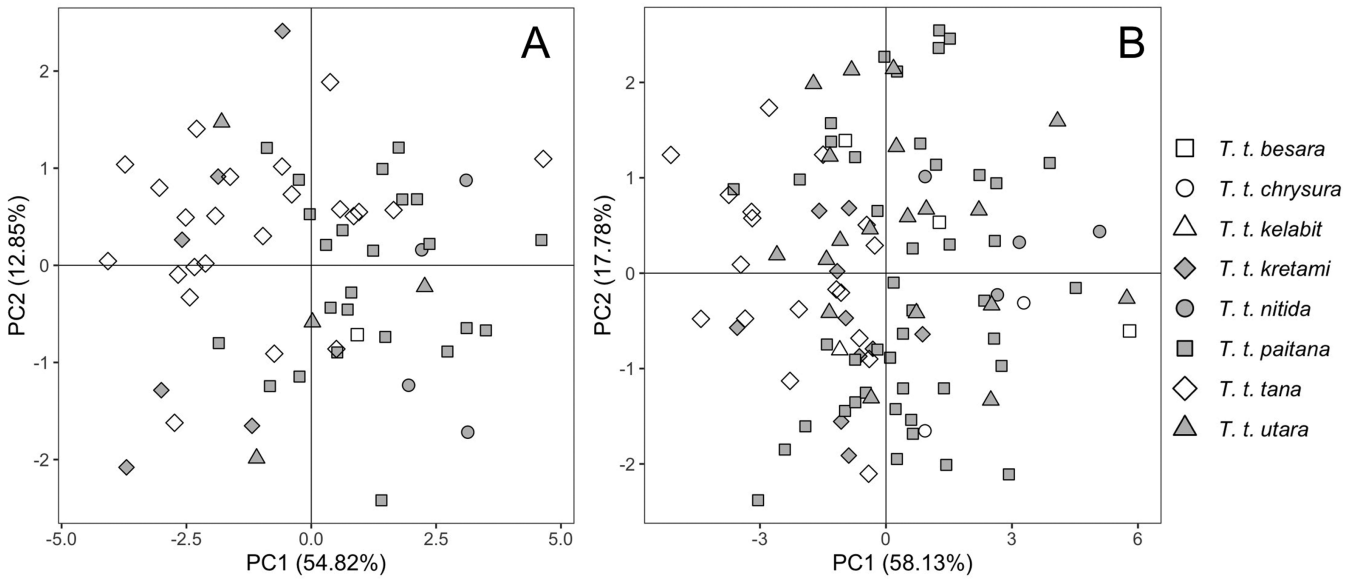

Fig. 3.—Plots of principal component (PC) scores from principal component analyses of Bornean *Tupaia tana* subspecies, illustrating considerable overlap in morphospace among different subspecies: A) Plot of seven Bornean subspecies based on eight manus variables (Table 4A). B) Plot of eight Bornean subspecies based on eight skull variables (Table 4B).

Table 5.—Classification table from discriminant function analysis (DFA) between individuals from Borneo and Sumatra. 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: 1MD, 1PPD, 2PPL, 2PPW, 4PPW, 5ML, 5MW, and 5PPW			
Island	Borneo	Sumatra	Correct classification rate
Borneo	55	7	88.7%
Sumatra	16	17	51.5%
Overall classification rate			75.3%
B) DFA of eight skull variables: MTL, PPL, LB, LIB, PBPL, LTPL, MCH, and MCW			
Island	Borneo	Sumatra	Correct classification rate
Borneo	92	9	91.1%
Sumatra	6	34	85.0%
Overall classification rate			89.4%

Table 6.—Component loadings from principal component analyses (PCA) of manus and skull variables among individuals from mainland Borneo and offshore 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 seven manus variables (Fig. 4A)		
2PPW	0.88	0.18
4PPW	0.85	0.16
1PPD	0.82	–0.08
5PPW	0.81	–0.28
1MD	0.68	**0.54**
2PPL	0.67	0.06
5MW	0.61	**–0.67**
Eigenvalue	4.11	0.89
Percentage of total variance explained	58.71	12.70
B) PCA of eight skull variables (Fig. 4B)		
PBPL	0.93	0.24
PPL	0.92	0.32
LTPL	0.92	0.25
MTL	0.81	**0.40**
MCH	0.68	–0.21
LB	0.67	**–0.55**
MCW	0.67	–0.26
LIB	0.63	**–0.62**
Eigenvalue	4.99	1.17
Percentage of total variance explained	62.36	14.68

conclusions about a lack of sexual size dimorphism in the Large Treeshrew (Emmons 2000) and the Lesser Treeshrew, *T. minor* (Woodman et al. 2020).

Fifteen subspecies of *T. tana* are currently recognized, most of them originally differentiated based on arbitrary aspects of pelage color and pattern, and to a lesser degree on size differences (e.g., Lyon 1913; Chasen and Kloss 1932; Chasen 1933; Davis 1962). Based on our locality map, seven of these subspecies have overlapping ranges: *T. t. tana* (which has nomenclatural priority), *T. t. utara*, *T. t. nitida*, *T. t. kelabit*, *T. t. chrysura*, *T. t. paitana*, and *T. t. kretami*. In addition, *T. t. speciosa*, recognized by Helgen (2005) but not included in our study, is sympatric with *T. t. tana* based on its restricted type locality in southern Borneo (Chasen 1940). Eight other taxa, mostly from isolated offshore islands, are allopatric: *T. t. lingae*, *T. t. cervicalis*, *T. t. tuancus*, *T. t. masae*, *T. t. sirhassenensis*, *T. t. bunoae*, *T. t. banguei*, and *T. t. besara*. Our analyses of the hands and skulls of 14 subspecies (and another previously recognized one) revealed insufficient separation in morphospace among these populations, thereby providing no morphometric support for the recognition of this many subspecies (Figs. 2 and 4).

We also found extensive morphometric overlap among the eight Bornean subspecies, again suggesting a lack of skeletal evidence to support their recognition as distinct taxa (Fig. 3). Our data reveal limited variation in size among these populations, though some subspecies were originally differentiated based on subtle body size variation. Lyon (1913:142) noted that *T. t. utara* is "a trifle larger" than *T. t. tana* in skull size; this is supported by our data, though both overlap considerably with *T. t. paitana* (Fig. 3). Although *T. t. nitida* and *T. t. kretami* are distinct from one another, they overlap in morphospace with *T. t. tana*, *T. t. utara*, and *T. t. paitana* (Fig. 3). *Tupaia t. nitida* and *T. t. kretami* also overlap with *T. t. utara* and *T. t. paitana* in their geographic ranges (Fig. 1). *Tupaia t. besara* was described by Lyon (1913:141) as "very large" but generally exhibits a size range similar to that of *T. t. nitida* (Supplementary Data SD1). Davis (1962:46) noted that *T. t. kretami* "is slightly smaller" than *T. t. paitana*, a difference supported by our manus data, but these two populations overlap considerably in skull size (Fig. 3). Our results suggest that none of the Bornean populations are osteologically distinct. In addition, seven of the eight subspecies on Borneo are sympatric with at least one other subspecies (Fig. 1), thereby failing to meet the criterion of allopatry (Mayr and Ashlock 1991; Braby et al. 2012).

In contrast, we noted a higher degree of morphometric separation between Bornean and Sumatran populations (Fig. 2D; Table 5B). Based on this evidence, we restrict the name *T. t. tana* Raffles, 1821 to the Sumatran population, as the type locality for the nominate subspecies is on Sumatra (Fig. 1). We recognize the entire Bornean population as *T. t. speciosa* (Wagner, 1841) (Table 1; Fig. 1), the name used by Lyon (1907, 1911) for this population. Future molecular studies could assess the lack of morphometric differentiation among populations on Borneo as well as the divergence of *T. t. speciosa* on Borneo from *T. t. tana* on Sumatra, which may have occurred 400 ka (Husson et al. 2020). Although *T. tana* and its closest relatives belong to a Bornean clade (Roberts et al. 2011), recent studies have suggested that Borneo was colonized fairly recently by some small mammals (Camacho-Sanchez and Leonard 2020); this might be further investigated in *T. tana* in an extensive molecular phylogeographic analysis.

Our morphometric comparisons of populations from mainland Borneo to those from nearby offshore islands revealed

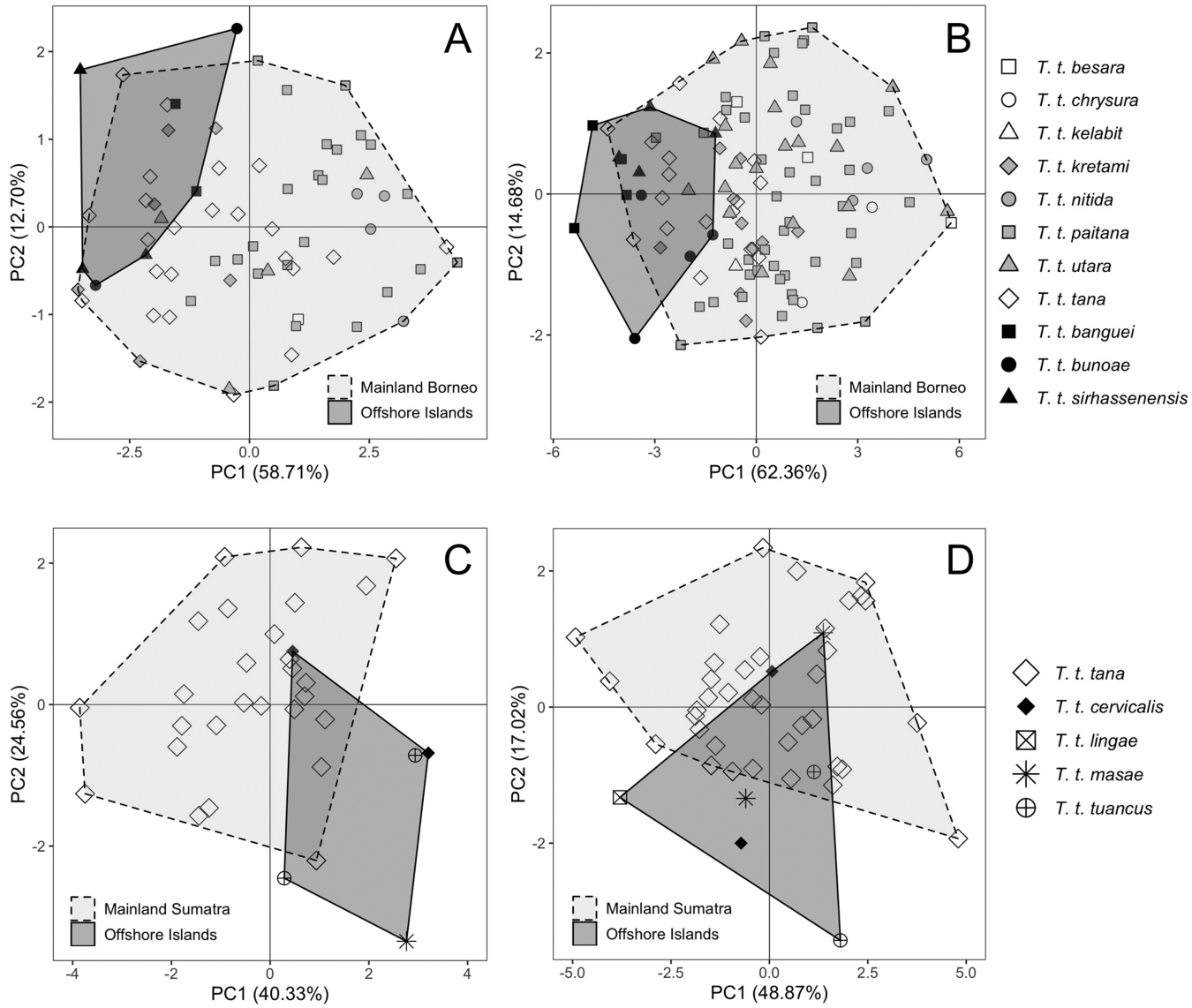

Fig. 4.—Plots of principal component (PC) scores from principal component analyses of *Tupaia tana* subspecies from mainland and nearby offshore islands: A) Plot of Bornean individuals based on seven manus variables (Table 6A). B) Plot of Bornean individuals based on eight skull variables (Table 6B). Separation along PC1 (tracking body size) in 4A and 4B illustrates that offshore island individuals average smaller size than those from Borneo. C) Plot of Sumatran individuals based on seven manus variables (Table 7A). D) Plot of Sumatran individuals based on eight skull variables (Table 7B).

that average body size is smaller in the island populations (Figs. 4A and 4B). This finding supports descriptions of subspecies occupying islands; *T. t. banguei*, *T. t. bunoae*, and *T. t. sirhassenensis* were noted as smaller than mainland Bornean taxa (Lyon 1913; Chasen and Kloss 1932). However, there is insufficient morphometric separation between the mainland and offshore island populations to recognize them as distinct subspecies (Figs. 4A and 4B), though the island populations are allopatric. We therefore consider *T. t. banguei*, *T. t. bunoae*, and *T. t. sirhassenensis* to be junior synonyms of *T. t. speciosa*.

This island effect on body size suggests the inverse of Foster's (1964) island rule, which predicts that island populations of small mammals will exhibit larger body size relative to mainland forms. Previous studies have challenged the applicability of this ecogeographic pattern across all mammals (Meiri et al. 2006, 2008), including in another species of treeshrew (Sargis et al. 2018). Our study casts further doubt on the universal validity of this "rule" among small mammals and demonstrates the importance of examining established ecogeographic patterns in particular taxa. Future biological surveys of offshore islands could reveal ecological factors that underlie this reversal in *T. tana*, but such data are currently lacking.

Similar comparisons of populations from mainland Sumatra to those from nearby offshore islands revealed incongruent results between the skull and manus data sets. Analysis of the manus data suggested that offshore island individuals average wider bones of the manus (Table 7A) than mainland Sumatran individuals (Fig. 4C), whereas analysis of skull variables revealed some distinction based on shape but not body size

Table 7.—Component loadings from principal component analyses (PCA) of manus and skull variables among individuals from mainland Sumatra and offshore 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 seven manus variables (Fig. 4C)		
4PPW	**0.85**	0.05
2PPW	**0.80**	0.29
1PPD	**0.77**	0.11
5PPW	**0.65**	–0.03
1MD	**0.57**	0.09
2PPL	–0.20	**0.91**
5PPL	–0.24	**0.88**
Eigenvalue	2.82	1.72
Percentage of total variance explained	40.33	24.56
B) PCA of eight skull variables (Fig. 4D)		
MCIL	0.86	0.16
PPL	0.83	0.12
ZB	0.82	–0.28
LIB	0.74	–0.08
BB	0.69	0.37
MB	0.61	**0.58**
MCW	0.47	**–0.73**
MCH	0.44	**–0.48**
Eigenvalue	3.91	1.36
Percentage of total variance explained	48.87	17.02

(Fig. 4D). Until expanded sample sizes are available for these allopatric offshore island populations, we recognize *T. t. cervicalis*, *T. t. lingae*, *T. t. masae*, and *T. t. tuancus* as junior synonyms of *T. t. tana*.

Our findings have implications for the conservation of *T. tana*, which currently is listed as a species of "Least Concern" on the *IUCN Red List of Threatened Species* (Cassola 2016). Some maps of *T. tana* do not reflect the full extent of its geographic range (Cassola 2016; Hawkins 2018), lacking localities in southwestern Borneo and in the Palembang region in southeastern Sumatra (Fig. 1; Corbet and Hill 1992). Understanding the complete distribution is necessary to adequately assess the conservation status of both subspecies. Furthermore, our revision of the infraspecific taxonomy of *T. tana* will better inform decisions about which areas of diversity to prioritize and protect, as these two subspecies appear to represent evolutionarily independent populations facing unique threats. For example, while logging is widespread on both islands, Sumatra faces higher rates of primary forest loss (Margono et al. 2014). Bornean deforestation is driven primarily by oil palm production, whereas pulp wood is an almost equal contributor on Sumatra (Miettinen et al. 2016). Thus, Sumatran *T. t. tana* and Bornean *T. t. speciosa* may require separate conservation interventions, and their recognition as distinct subspecies will provide a basis for management decisions (Patton and Conroy 2017).

The Large Treeshrew's geographic range falls entirely within the Sundaland biodiversity hotspot. Sundaland concentrates 16% of all vertebrates on only 0.4% of Earth's surface, but anthropogenic impacts have reduced native vegetation to only 7.8% of its original cover (Myers et al. 2000), threatening the survival of rainforest species such as *T. tana*. Despite the rich biodiversity of this region, there is a severe lack of research on it relative to many other, less-threatened areas (Sodhi et al. 2004). Our study highlights the importance of investigating taxonomic variation and ecogeographic patterns to improve our understanding of mammalian diversity in this critical region. Given that the most vulnerable populations are likely on offshore islands represented by small samples (e.g., see Fig. 4), our analyses also stress the value of future biological surveys on these islands to provide larger samples for taxonomic studies of insular mammals.

Conclusions

We find little support for the 15 subspecies of *Tupaia tana* currently recognized primarily on the basis of minor pelage variation. In contrast, morphometric differentiation between the two mainland populations on Sumatra and Borneo is sufficient to recognize them as *T. t. tana* on Sumatra and *T. t. speciosa* on Borneo. The names *Tupaia cervicalis* Miller, 1903; *Tana lingae* Lyon, 1913; *Tana cervicalis masae* Lyon, 1913; *Tana tana nainggolani* Sody, 1936; and *Tana tana tuancus* Lyon, 1913 are junior synonyms of *Tupaia tana tana* Raffles, 1821. The names *Tupaia tana banguei* Chasen and Kloss, 1932; *Tana tana besara* Lyon, 1913; *Tupaia bunoae* Miller, 1900; *Tupaia tana chrysura* Günther, 1876; *Tana tana griswoldi* Coolidge, 1938; *Tupaia tana kelabit* Davis, 1958; *Tupaia tana kretami* Davis, 1962; *Tupaia tana nitida* Chasen, 1933; *Tana paitana* Lyon, 1913; *Tupaia sirhassenensis* Miller, 1901; and *Tana tana utara* Lyon, 1913 are junior synonyms of *Tupaia tana speciosa* (Wagner, 1841).

Offshore island populations of *T. t. tana* show little obvious variation in size relative to the mainland Sumatran population. In contrast, offshore populations of *T. t. speciosa* average smaller body size than the mainland population on Borneo. The recognition of *T. t. tana* and *T. t. speciosa* as distinct subspecies, and the revision of the Large Treeshrew's range, suggest that the conservation priorities of this species should be reassessed.

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Supplementary Data

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

Supplementary Data SD1.—Original measurements from the skull and manus of the *Tupaia tana* specimens used in this study, and corresponding summary statistics.

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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 Natural History, Chicago (FMNH); Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Tupaia tana banguei Chasen and Kloss, 1932 ($n = 6$).—MALAYSIA: Borneo: Sabah, Banguey [Banggi] Island (type locality; NHMUK 47.1494—holotype); Banggi Peak (FMNH 141344, 141346); Wak-Wak (FMNH 140934, 140935, 140936).

Tupaia tana bunoae Miller, 1900 ($n = 4$).—INDONESIA: Tambelan Archipelago: Benua Island (type locality) (USNM 101640—holotype, 101641); Tambelan Island (USNM 101653, 101654).

Tupaia tana sirhassenensis Miller, 1901 ($n = 4$).—INDONESIA: Riau Archipelago, Sirhassen [Serasan Island] (type locality) (NHMUK 94.9.28.4; USNM 104711, 104712—holotype, 104713).

Tupaia tana besara (Lyon, 1913) ($n = 3$).—INDONESIA: Borneo: Kapuas River (type locality; USNM 142247—holotype); Landak (AMNH M-106884, M-106993).

Tupaia tana chrysura Günther, 1876 ($n = 2$).—MALAYSIA: Borneo: Labuan Island (NHMUK 93.4.1.2); mainland Borneo opposite Labuan Island (type locality; NHMUK 76.5.2.19—holotype).

Tupaia tana kelabit Davis, 1958 ($n = 1$).—MALAYSIA: Borneo: Sarawak, Pa Umur [Pa Umor] (type locality; FMNH 88368—holotype).

Tupaia tana kretami Davis, 1962 ($n = 13$).—MALAYSIA: Borneo: Sabah: Kinabatangan District, Little Kretam River (type locality) (FMNH 68788, 68789, 68790, 68791, 68793, 68794—holotype, 68795, 68796, 68797, 68798); Deramakot Forest Reserve (FMNH 85071, 85072, 85073).

Tupaia tana nitida Chasen, 1933 ($n = 10$).—MALAYSIA: Borneo: Sarawak, Kuching (FMNH 80086, 80087, 80090, 80091, 80092, 80093); Paku (NHMUK 55.691); Samarahan (NHMUK 55.692, 55.693, 55.694).

Tupaia tana paitana (Lyon, 1913) ($n = 47$).—MALAYSIA: Borneo: Sabah, no locality (USNM 396660, 396661, 396663, 396671); Paitan River (type locality; NHMUK 93.4.1.1—holotype); Sandakan

(FMNH 33031, 33032, 33033); Sapagaya Forest Reserve (FMNH 68799, 76801, 76802, 76803, 76805, 76807, 76808, 76809, 76810, 76811, 76812, 76813, 76892); Morok Forest (USNM 488029, 488031, 488033, 488035, 488039, 488043, 488050); Ranau (USNM 300911, 317184); Nalapak (USNM 488049); Kinabalu Park (USNM 449965, 449966, 449968, 449969, 488024, 488025, 488026, 488027, 488028, 488030, 488037, 488040, 488046, 488047, 488051); Nabong Forest (USNM 488032).

Tupaia tana utara (Lyon, 1913) (*n* = 30).—MALAYSIA: Borneo: Sarawak, Mount Dulit (type locality) (NHMUK 55.695, 55.696, 92.2.7.4, 99.12.9.5—holotype); Belanian (MCZ 8726); Baram (USNM 83938); Mount Mulu (NHMUK 94.6.2.1); Kapit (USNM 311455, 311456); Sut (FMNH 88591); Tapuh (USNM 311454); Tinjar River (NHMUK 51.166); Mount Penrisen (NHMUK 90.6.25.2); Kuching (NHMUK 71.2602). Sabah: no locality (USNM 19224, 34943); Beaufort Forest Reserve (NHMUK 71.2604); Kinabatangan River (USNM 19187); Suanalamba River (USNM 19202); Tawau (NHMUK 71.2594, 71.2598, 71.2599, 71.2600, 71.2601, 71.2605, 71.2606); Kalabakan (NHMUK 71.2589, 71.2590, 71.2592). INDONESIA: Borneo: Karanginton, Martapoeia River (NHMUK 10.4.5.74).

Tupaia tana tana Raffles, 1821 (*n* = 76).—INDONESIA: Sumatra, no locality (NHMUK 77.3.4.1, 79.7.2.2); Bencoolen [Bengkulu] (type locality; NHMUK 95.3.21.4—holotype); Kumbong (NHMUK 19.11.5.13); Sandaran (NHMUK 19.11.5.14, 19.11.5.15); Korinchi (NHMUK 19.11.5.16); Boekit Sanggoel [Bukit Sanggul] (AMNH M-106477, M-106479, M-106481, M-106482, M-106483, M-106485, M-106486, M-106488, M-106489, M-106490, M-106491); Loebock Linggan [Lubuklinggau] (AMNH M-102164); Deli River (USNM 174612); Palembang (AMNH M-102511, M-102515, M-102516, M-102517, M-102519, M-102523, M-102525); Lampung (AMNH M-102829, M-102830, M-102831, M-102832, M-102833, M-102834, M-102835, M-102836, M-102838, M-102839, M-102840, M-102841, M-102842, M-102843; NHMUK 81.3.15.3, 81.3.15.4); Pajo (NHMUK 79.6.28.14); Mount Dempo (AMNH M-106476, M-106478); Kalianda (AMNH M-102853, M-102854). Borneo, Matan River (USNM 145574); Riam (AMNH M-106103); Saratok River (USNM 151885); Pamukan Bay (USNM 154341); Balik Papan Bay (USNM 154340); Talisaian Mountain (USNM 176412); Djambajan River (USNM 199158); Menganne River (USNM 197201); Tandjong Seglu (USNM 197199, 197200); Karangan River, Gunong Batu (USNM 198045, 198046, 198047, 198048); Pelawan River (USNM 198049); Domaring (USNM 176411); Segah River (USNM 176408, 176409, 176410); Birang River (USNM 176403, 176405, 176406, 176407); Mara (AMNH M-103409, M-103410, M-103411); Peleben (AMNH M-103891, M-103895).

Tupaia tana cervicalis Miller, 1903 (*n* = 2).—INDONESIA: Batu Islands: Tana Bala [Tanahbala Island] (type locality) (USNM 121753, 121754—holotype).

Tupaia tana lingae (Lyon, 1913) (*n* = 1).—INDONESIA: Lingga Archipelago, Lingga Island (type locality; USNM 101597—holotype).

Tupaia tana masae (Lyon, 1913) (*n* = 2).—INDONESIA: Batu Islands: Tana Masa [Tanahmasa Island] (type locality) (NHMUK 7.6.18.6, USNM 121835—holotype).

Tupaia tana tuancus (Lyon, 1913) (*n* = 2).—INDONESIA: Banyak Islands: Tuangku Island (type locality) (USNM 114412—holotype, 114413).