Island history affects faunal composition: the treeshrews (Mammalia: Scandentia: Tupaiidae) from the Mentawai and Batu Islands, Indonesia

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The Mentawai and Batu Island groups off the west coast of Sumatra have a complicated geological and biogeographical history. The Batu Islands have shared a connection with the Sumatran 'mainland' during periods of lowered sea level, whereas the Mentawai Islands, despite being a similar distance from Sumatra, have remained isolated from Sumatra, and probably from the Batu Islands as well. These contrasting historical relationships to Sumatra have influenced the compositions of the respective mammalian faunas of these island groups. Treeshrews (Scandentia, Tupaiidae) from these islands have, at various times in their history, been recognized as geographically circumscribed populations of a broadly distributed *Tupaia glis*, subspecies, or distinct species. We used multivariate analyses of measurements from the skull and hands to compare the island populations from Siberut (Mentawai Islands) and Tanahbala (Batu Islands) with the geographically adjacent species from the southern Mentawai Islands (*T. chrysogaster*) and Sumatra (*T. ferruginea*). Results from both the skull and manus of the Siberut population show that it is most similar to *T. chrysogaster*, whereas the Tanahbala population is more similar to *T. ferruginea*, confirming predictions based on island history. These results are further corroborated by mammae counts. Based on these lines of evidence, we include the Siberut population in *T. chrysogaster* and the Tanahbala population in *T. ferruginea*. Our conclusions expand the known distributions of both the Mentawai and Sumatran species. The larger geographical range of the endangered *T. chrysogaster* has conservation implications for this Mentawai endemic, so populations and habitat should be re-evaluated on each of the islands it inhabits. However, until such a re-evaluation is conducted, we recommend that the *IUCN Red List* status of this species be changed from 'Endangered' to 'Data Deficient'.   Published 2013. This article is a U.S. Government work and is in the public domain in the USA, *Biological Journal of the Linnean Society*, 2014, **111**, 290–304.

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INTRODUCTION

The Mentawai Islands off the west coast of Sumatra are notable for their mammalian diversity and endemism (Banks, 1961; Heaney, 1986; Wilting *et al.*, 2012). The four major islands in this group (from north to south: Siberut, Sipora, North Pagai, and South Pagai; Fig. 1) have a cumulative area of less than 6000 km², yet they are home to 17 endemic mammalian species and a larger number of
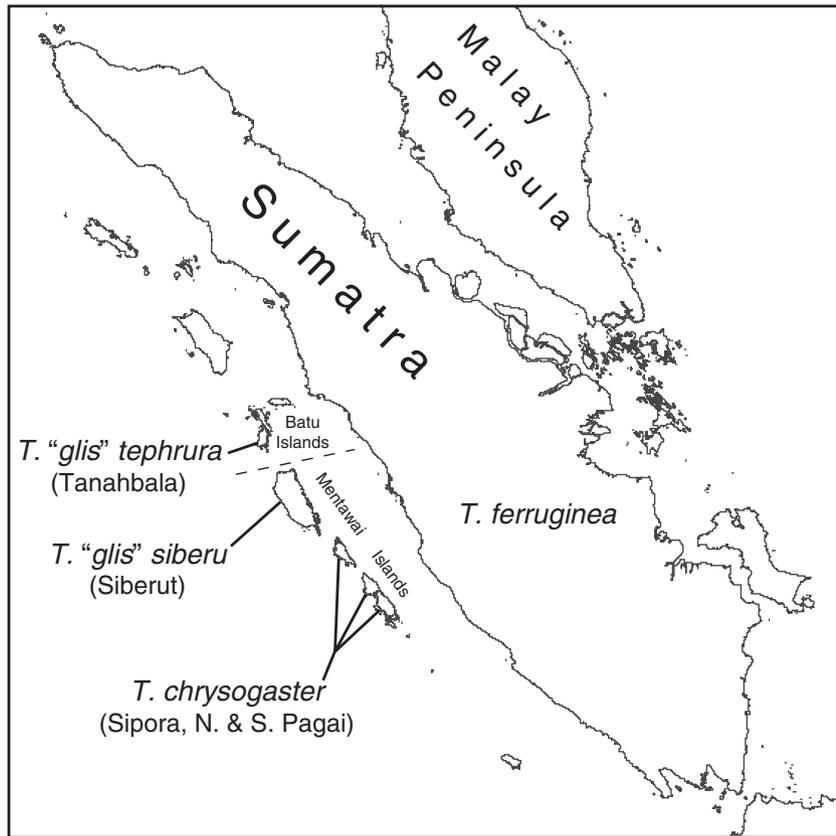
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Figure 1. Map of Sumatra, southern peninsular Malaysia, and surrounding islands showing approximate ranges of the treeshrews *Tupaia chrysogaster* and *T. 'glis' siberu* (= *T. chrysogaster*) in the Mentawai Islands, *T. ferruginea* on Sumatra, and *T. 'glis' tephrura* (= *T. ferruginea*) in the Batu Islands.

subspecies (Corbet & Hill, 1992; Wilson & Reeder, 2005; Wilting *et al.*, 2012); there are ten endemic rodents (four murids, three squirrels, and three flying squirrels), five primates (two macaques, two colobine monkeys, and one gibbon), one treeshrew, and one bat (Wilting *et al.*, 2012). Although the Mentawai Islands are only about 85–130 km from the coast of Sumatra, they have been separated from this landmass since the mid-Pleistocene by the deep Mentawai Basin, which reaches depths of about 1500 m (Wilting *et al.*, 2012) and probably contributes to the high level of endemism. Despite the close proximity of Sumatra, the closest relatives of many Mentawai mammal species reside on Borneo, Peninsular Malaysia, or Java, and this pattern may be explained by local extinctions on Sumatra (Wilting *et al.*, 2012). In contrast to the Mentawai Islands, the more northerly Batu Islands (Pini, Tanahmasa, and Tanahbala; Fig. 1) are separated from Sumatra by a shallow sea and were connected to this landmass during Pleistocene glacial maxima, when global sea level was lower (Voris, 2000; Sathiamurthy & Voris, 2006; Wilting *et al.*, 2012).

The treeshrews (Scandentia, Tupaiidae) from the islands off the west coast of Sumatra have a complicated taxonomic history. The Mentawai (or golden-bellied) treeshrew, *Tupaia chrysogaster* Miller, 1903, is endemic to the Mentawai Islands, but is only known from the southern islands of Sipora, North Pagai, and South Pagai (Fig. 1). This taxon was recognized as a distinct species by Lyon (1913) in his monographic revision of treeshrews, but the name was later synonymized with *T. glis* (Diard, 1820) by Chasen (1940), and it remained in synonymy (e.g. Corbet & Hill, 1992) until Wilson (1993) determined that it represents a separate species. It is currently recognized as distinct from *T. glis* (Helgen, 2005), and this distinction is supported by molecular (Roberts *et al.*, 2011) and morphological (Olson, Sargis & Martin, 2004; Sargis *et al.*, 2013a) evidence. Like many other mammals from the Mentawai Islands, the sister taxon of *T. chrysogaster* is from the more distant island of Borneo rather than nearby Sumatra (Roberts *et al.*, 2011); specifically, *T. chrysogaster* is more closely related to *T. longipes* (Thomas, 1893) from Borneo than to *T. ferruginea* Raffles, 1821

(formerly *T. glis*; see Sargis *et al.*, 2013a) from Sumatra (Roberts *et al.*, 2011). This pattern may be explained by extinction of the *T. chrysogaster*–*T. longipes* clade on Sumatra and subsequent re-colonization of Sumatra by *T. glis* from the Malay Peninsula (Roberts *et al.*, 2011; Wilting *et al.*, 2012). In recognizing *T. chrysogaster*, Wilson (1993: 132) noted that it '[m]ay also include *siberu* and possibly *tephrura*, both currently in the synonymy of *glis*.' Despite this statement, both taxa have remained in synonymy with *T. glis* (Helgen, 2005).

Like *T. chrysogaster*, *T. glis siberu* Chasen & Kloss, 1928 is from the Mentawai Islands, but its range is restricted to the northern island of Siberut (Fig. 1). Although they included this subspecies in *T. glis*, Chasen & Kloss (1928) noted similarities in pelage coloration and craniodental morphology with what they called *T. glis chrysogaster* from the southern Mentawai Islands. Hence, their recognition of *T. glis siberu* and *T. glis chrysogaster* as separate subspecies divided the treeshrews from the Mentawai Islands, with the former only on the northernmost island and the latter on the three southern islands. A similar pattern is seen in some endemic primates, with *Macaca siberu*, *Presbytis potenziani siberu*, and *Simias concolor siberu* on Siberut and *M. pagensis*, *P. potenziani potenziani*, and *S. concolor concolor* occupying the three southern islands (Roos *et al.*, 2003; Whittaker, Ting & Melnick, 2006; Whittaker, 2009), although no such pattern of genetic differentiation has been identified among the populations of *Hylobates klossii* (Whittaker, 2009). Based on the similarities noted between *T. 'glis' siberu* and *T. chrysogaster*, and on the long-term separation of all the Mentawai Islands from Sumatra (see above), we hypothesized that *T. 'glis' siberu* should be more similar to *T. chrysogaster* than to *T. ferruginea* from Sumatra.

Tupaia tephrura Miller, 1903 was recognized as a distinct species by Lyon (1913) based on pelage coloration, but was later considered a subspecies of *T. glis* by Chasen (1940). This treeshrew is only known from Tanahbala (Fig. 1), which, like the other Batu Islands, was connected to Sumatra during the Pleistocene glacial maxima (see above). Hence, we hypothesized that *T. 'glis' tephrura* should be more similar to *T. ferruginea* from Sumatra than to *T. 'glis' siberu* or *T. chrysogaster* from the Mentawai Islands. The presence of different species in the Batu and Mentawai (including Siberut) Island groups mirrors patterns seen in primates, with *Macaca fascicularis* (Tanahbala, Tanahmasa) and *Presbytis melalophos* (Pini) in the Batu Islands (Fooden, 1995; Groves, 2001) and *M. siberu*, *M. pagensis*, and *P. potenziani* in the Mentawai Islands. Like *M. fascicularis* and *P. melalophos*,

Sundamys muelleri, Müller's giant Sunda rat, is present on Sumatra and in the Batu Islands (all three in this case), but absent from the Mentawai Islands (Musser & Newcomb, 1983).

In this article, we report the results of multivariate analyses of the manus and skull, which we used to assess morphological variation among treeshrews from the islands off the west coast of Sumatra. Specifically, we compared *T. 'glis' siberu* from Siberut and *T. 'glis' tephrura* from Tanahbala to *T. chrysogaster* from the three southern Mentawai Islands and *T. ferruginea* from Sumatra. Based on the palaeogeography of the region (see above), we predicted that *T. 'glis' siberu* would be most similar to *T. chrysogaster*, whereas *T. 'glis' tephrura* would be more similar to *T. ferruginea*.

MATERIAL AND METHODS
MANUS

For analyses of the hands, we used measurements obtained from digital X-ray images of dried study skins of 31 specimens of *T. chrysogaster* ($N = 13$), *T. ferruginea* ($N = 14$), *T. 'glis' siberu* ($N = 3$), and *T. 'glis' tephrura* ($N = 1$). Most of these specimens were used in previous analyses conducted by Sargis *et al.* (2013a, b), but here we added the holotypes of *T. chrysogaster* (USNM 121572), *T. glis siberu* (BMNH 28.11.2.3), and *T. tephrura* (USNM 121752) (see Appendix 1 for the list of specimens examined). Hands of the type specimens from the United States National Museum of Natural History (USNM) were X-rayed using a Kevex-Varian (Palo Alto, CA, USA) digital X-ray system in the USNM following the procedure of Sargis *et al.* (2013a, b) (see also Woodman & Morgan, 2005; Woodman & Stephens, 2010). The holotype of *T. glis siberu* was X-rayed at The Natural History Museum (BMNH) in London. The resulting digital images were transferred to Adobe Photoshop CS4 Extended (version 11.0.2, Adobe Systems Inc., San Jose, CA, USA), trimmed, converted to positive images, and measured by N.C.M. with the custom Measurement Scale in the Analysis menu. Measurements were taken from either the right or left side, and supplemented, where necessary and possible, by measurements from the image of the other side. We recorded the following measurements from each of the five rays of the manus (38 total), with the exception that depths (dorsopalmar distances) of bones were substituted for widths (mediolateral distances) in ray I because of its orientation in the images: 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 (see Sargis *et al*., 2013a: fig. 1). A numeral before an abbreviation designates the ray (e.g. 4MW represents the width of metacarpal IV). All measurements are in millimetres and are rounded to the nearest 0.01 mm. Summary statistics include mean, standard deviation, and total range (Table 1).

We carried out principal components analyses (PCA) on combinations of variables from individuals of the four taxa to determine how they vary in manus proportions. Because specimens of *T. 'glis' siberu* and *T. 'glis' tephrura* were the focus of our study, yet had the smallest sample sizes, we attempted to maximize their representation in our analyses. This considerably limited the variables available and reduced the number of individuals of *T. chrysogaster* and *T. ferruginea*. Our PCA model included four width variables (1MW, 4MW, 4PPW, 4MPW) (Table 2). To determine the overall similarity of the manus among all four taxa, we performed a cluster analysis (unweighted pair-group method with arithmetic average, UPGMA) on the 18 variable means from all five rays available for all four taxa. The phenogram from this analysis is presented with Euclidean distances.

SKULL

For our analyses of the cranium and mandible, we recorded the same 22 measurements (Table 3) used by Sargis *et al*. (2013b) and Sargis, Campbell & Olson (2013c) in their study of treeshrews from Java and the Palawan faunal region. These measurements were taken to the nearest 0.01 mm using digital calipers. Our craniodental sample included the same specimen of *T. 'glis' tephrura* ($N = 1$) from the manus analyses, and larger samples of *T. chrysogaster* ($N = 25$), *T. ferruginea* ($N = 63$), and *T. 'glis' siberu* ($N = 4$), including the holotypes of all four taxa. Ninety-three adult skulls (those with fully erupted permanent dentition) were included in this portion of the study (see Appendix 1). Summary craniodental statistics are presented in Table 4.

One PCA of skull variables included seven cranial variables and the other included three cranial and three mandibular variables (Table 5); several variables were excluded from these analyses to allow the inclusion of specimens, particularly from *T. 'glis' siberu* and *T. 'glis' tephrura*, that were missing data as a result of breakage. We also conducted cluster analyses (UPGMA) of taxon means that included: (1) 21 skull variables [lacrimal breadth (LB) excluded]; and (2) a combination of 21 skull variables and 18 manus variables for a total of 39 skeletal variables.

RESULTS

MANUS

Our PCA model for the manus included four width variables (1MW, 4MW, 4PPW, 4MPW). These load strongly on factor axis 1, indicating a size axis representing the widths of the bones of the hand (Table 2); the first factor axis accounts for more than 57% of the total variation. The second factor axis, which represents more than 20% of the total variation, is influenced by 4MPW contrasted with a negatively weighted 1MW. In the resulting plot of factor scores on these two axes (Fig. 2A), there is overlap between *T. chrysogaster* and *T. ferruginea*, although the former averages wider hand bones than the latter. The holotype of *T. 'glis' tephrura is centrally located within the morphospace of* T. ferruginea*, indicating narrower hand bones than in any* T. chrysogaster*. In contrast, two specimens of* T. 'glis' siberu *plot well within the morphospace of* T. chrysogaster *and have wider hand bones than all but one* T. ferruginea*. The third specimen of* T. 'glis' siberu *has wider hand bones than any other individual in our analysis.*

The cluster analysis of 18 variables from the manus indicates that the manus proportions are most similar between *T. chrysogaster* and *T. 'glis' siberu* (Fig. 2B). In contrast, the Tanahbala population, *T. 'glis' tephrura*, is most similar to *T. ferruginea*.

SKULL

Our analyses of skull variables resulted in two models: one PCA with seven cranial variables and the second with three cranial and three mandibular variables (Table 5). In the first analysis, factor 1 is a size vector that accounts for 86.5% of the variation. The second factor represents least interorbital breadth (LIB) and explains 9.7% of the variation (Table 5). The *T. 'glis' tephrura* holotype plots among *T. ferruginea* specimens in the upper left quadrant, and *T. 'glis' siberu* is nested in the morphospace occupied by *T. chrysogaster* in the lower right quadrant (Fig. 3A). In the second PCA, factor 1 is again a size vector that is responsible for 74% of the variation. Factor 2 represents mandibular height (MH) and mandibular condyle height (MCH), and accounts for 12.6% of the variation (Table 5). As in the previous analysis, *T. 'glis' siberu* is nested in the region circumscribed by *T. chrysogaster* in positive morphospace along factor 1, although *T. 'glis' tephrura* plots just outside the morphospace occupied by *T. ferruginea* in the lower left quadrant (Fig. 3B).

Our two cluster analyses of taxon means of 21 craniodental variables and 39 variables combined from the skull and manus produced the same topology; therefore, only the phenogram from the analysis

Table 1. Measurements (mm) of bones in the manus of four taxa of *Tupaia*. Statistics are mean ± SD, range of measurements, and sample size in parentheses. Because of its orientation in the X-rays, depth was measured for ray I; width was measured for the other four rays (see 'Material and Methods')

	Metacarpal length (ML)	Metacarpal depth/width (MD/MW)	Proximal phalanx length (PPL)	Proximal phalanx depth/width (PPD/PPW)	Middle phalanx length (MPL)	Middle phalanx width (MPW)	Distal phalanx length (DPL)	Distal phalanx depth/width (DPD/DPW)
Ray I								
T. chrysogaster	4.56 ± 0.28; 4.09–5.02; (13)	0.70 ± 0.05; 0.61–0.79; (13)	3.45 ± 0.32; 2.77–3.93; (12)	0.69 ± 0.06; 0.61–0.80; (12)	–	–	2.54 ± 0.16; 2.25–2.77; (10)	1.24 ± 0.13; 1.07–1.45; (12)
T. 'glis' siberu	4.87 ± 0.27; 4.66–5.17; (3)	0.71 ± 0.09; 0.65–0.81; (3)	3.78; 3.76–3.79; (2)	0.72; 0.65–0.79; (2)	–	–	2.92; 2.91–2.93; (2)	1.30 ± 0.32; 1.08–1.67; (3)
T. ferruginea	4.62 ± 0.30; 3.91–5.02; (14)	0.62 ± 0.05; 0.52–0.72; (14)	3.59 ± 0.15; 3.30–3.86; (14)	0.64 ± 0.05; 0.57–0.72; (14)	–	–	2.45 ± 0.20; 1.98–2.73; (12)	1.21 ± 0.17; 0.96–1.45; (13)
T. 'glis' tephrura	–; (0)	0.55; (1)	3.14; (1)	0.63; (1)	–	–	–; (0)	–; (0)
Ray II								
T. chrysogaster	8.42 ± 0.62; 7.33–9.39; (11)	0.83 ± 0.07; 0.66–0.91; (9)	4.89 ± 0.21; 4.61–5.35; (12)	0.75 ± 0.05; 0.67–0.85; (9)	2.82 ± 0.15; 2.61–3.01; (9)	0.79 ± 0.04; 0.75–0.86; (5)	2.62 ± 0.34; 1.85–3.16; (12)	1.11 ± 0.05; 1.06–1.18; (7)
T. 'glis' siberu	8.69; 8.45–8.92; (2)	0.75; 0.73–0.77; (2)	5.00 ± 0.01; 5.00–5.01; (2)	0.71; (1)	2.78; 2.60–2.95; (2)	0.78; 0.76–0.80; (2)	2.82; 2.72–2.91; (2)	1.08; (1)
T. ferruginea	8.19 ± 0.59; 6.88–8.97; (14)	0.75 ± 0.05; 0.67–0.82; (11)	5.04 ± 0.31; 4.35–5.54; (14)	0.72 ± 0.07; 0.63–0.89; (12)	2.86 ± 0.21; 2.36–3.13; (11)	0.73 ± 0.04; 0.67–0.79; (9)	1.98 ± 0.27; 1.56–2.39; (12)	1.02 ± 0.06; 0.95–1.09; (8)
T. 'glis' tephrura	–; (0)	0.79; (1)	–; (0)	0.62; (1)	–; (0)	–; (0)	2.39; (1)	1.02; (1)
Ray III								
T. chrysogaster	10.46 ± 0.62; 9.55–11.70; (11)	0.83 ± 0.05; 0.77–0.90; (11)	5.12 ± 0.19; 4.79–5.42; (11)	0.78 ± 0.04; 0.71–0.82; (8)	3.06 ± 0.17; 2.82–3.37; (10)	0.72 ± 0.03; 0.67–0.77; (7)	2.51 ± 0.30; 2.27–3.04; (12)	1.12 ± 0.06; 1.04–1.18; (5)
T. 'glis' siberu	10.31 ± 0.32; 9.95–10.57; (3)	0.85 ± 0.01; 0.84–0.86; (3)	5.18; 5.11–5.24; (2)	0.82 ± 0.08; 0.73–0.88; (3)	2.99 ± 0.27; 2.80–3.18; (2)	0.79; 0.77–0.81; (2)	2.65; 2.33–2.97; (2)	1.12; 1.10–1.13; (2)

T. ferruginea	10.44 ± 0.63 9.53–11.81 (13)	0.79 ± 0.06 0.68–0.89 (11)	5.24 ± 0.28 4.77–5.90 (14)	0.74 ± 0.04 0.66–0.80 (14)	3.34 ± 0.20 3.09–3.70 (11)	0.71 ± 0.05 0.66–0.83 (11)	2.03 ± 0.31 1.49–2.45 (11)
T. 'glis' tephrura	– (0)	– (0)	– (0)	0.69 (1)	– (0)	– (0)	2.49 (1)
Ray IV							
T. chrysogaster	9.51 ± 0.19 9.15–9.81 (8)	0.82 ± 0.06 0.68–0.88 (8)	5.01 ± 0.21 4.70–5.42 (13)	0.78 ± 0.06 0.71–0.89 (10)	3.12 ± 0.19 2.86–3.40 (9)	0.72 ± 0.05 0.66–0.79 (7)	2.60 ± 0.24 2.24–2.95 (12)
T. 'glis' siberu	9.63 9.42–9.85 (2)	0.86 ± 0.05 0.81–0.91 (3)	4.92 ± 0.09 4.83–5.01 (3)	0.83 ± 0.01 0.82–0.83 (3)	2.73 2.67–2.79 (2)	0.72 ± 0.07 0.67–0.80 (3)	2.43 ± 0.65 1.97–2.89 (2)
T. ferruginea	9.08 ± 0.55 8.06–9.80 (8)	0.78 ± 0.05 0.71–0.87 (7)	5.12 ± 0.28 4.67–5.65 (14)	0.74 ± 0.05 0.66–0.86 (13)	3.34 ± 0.22 3.00–3.88 (12)	0.71 ± 0.07 0.56–0.82 (11)	2.13 ± 0.33 1.57–2.82 (11)
T. 'glis' tephrura	8.64 (1)	0.80 (1)	– (0)	0.74 (1)	– (0)	0.67 (1)	2.54 (1)
Ray V							
T. chrysogaster	5.86 ± 0.32 5.36–6.28 (8)	0.85 ± 0.09 0.72–1.00 (7)	4.10 ± 0.16 3.77–4.41 (13)	0.71 ± 0.06 0.63–0.81 (12)	2.27 (1)	0.78 ± 0.05 0.71–0.84 (5)	2.17 ± 0.29 1.63–2.58 (12)
T. 'glis' siberu	6.18 6.14–6.22 (2)	0.71 ± 0.03 0.69–0.74 (3)	4.02 ± 0.17 3.86–4.20 (3)	0.68 0.67–0.69 (2)	– (1)	0.71 0.67–0.75 (2)	1.95 ± 0.23 1.73–2.18 (3)
T. ferruginea	5.83 ± 0.37 5.10–6.36 (12)	0.75 ± 0.08 0.60–0.85 (10)	4.13 ± 0.27 3.80–4.61 (14)	0.70 ± 0.05 0.64–0.80 (12)	2.30 ± 0.17 2.06–2.53 (10)	0.68 ± 0.04 0.62–0.75 (8)	2.00 ± 0.21 1.62–2.32 (14)
T. 'glis' tephrura	6.19 (1)	0.78 (1)	– (0)	0.70 (1)	– (0)	– (0)	– (0)

Additional (rightmost) column:

T. ferruginea	1.06 ± 0.07 0.90–1.14 (8)
T. 'glis' tephrura	1.02 (1)
T. chrysogaster	1.05 ± 0.10 0.94–1.13 (3)
T. 'glis' siberu	– (0)
T. ferruginea	0.97 ± 0.05 0.90–1.05 (6)
T. 'glis' tephrura	1.00 (1)
T. chrysogaster	1.00 ± 0.04 0.94–1.05 (5)
T. 'glis' siberu	1.02 1.01–1.03 (2)
T. ferruginea	0.98 ± 0.09 0.84–1.15 (8)
T. 'glis' tephrura	– (0)

Table 2. Component loadings from principal components analysis of four variables from the manus (Fig. 2). Abbreviations for variables are defined in 'Material and Methods.' Loadings in bold type are discussed in the text

	Axis		
	1	2	3
4MW	0.855	−0.225	−0.052
4PPW	0.790	0.196	−0.538
4MPW	0.633	**0.673**	0.383
1MW	0.734	**−0.529**	0.310
Eigenvalues	2.295	0.821	0.534
Percentage of total variance explained	57.369	20.535	13.356

of skull variables is shown in Figure 3. In both analyses, *T. 'glis' siberu* is most similar to *T. chrysogaster* and *T. 'glis' tephrura* is most similar to *T. ferruginea* (Fig. 3C).

DISCUSSION

Our morphometric analyses of the manus and skull yielded congruent results regarding the *Tupaia* populations from Sumatra, Tanahbala, Siberut, and the other three Mentawai Islands. As hypothesized on the basis of the history of the geographical relationships among these islands, *T. 'glis' tephrura* from Tanahbala is morphologically most similar to *T. ferruginea* from Sumatra (Figs 2 and 3) rather than to *T. chrysogaster* from the Mentawai Islands. This morphometric similarity is further supported by the mammary formulae of 4 (two pairs of abdominal mammae) in both *T. 'glis' tephrura* and *T. ferruginea* (Sargis *et al*., 2013a), which is in contrast with the lower count of 2 (one pair) in *T. chrysogaster* (Sargis *et al*., 2013a) and *T. 'glis' siberu* (see below). Hence, the Tanahbala population is most appropriately included in *T. ferruginea*, with *T. tephrura* Miller, 1903 as a synonym of this species (Appendix 1). Our inclusion of *T. tephrura* within *T. ferruginea* differs from several classifications that included both of these taxa in *T. glis* (e.g. Chasen, 1940; Corbet & Hill, 1992; Wilson, 1993; Helgen, 2005), as well as Lyon's (1913) classification of *T. tephrura* as a distinct species based on pelage coloration. Previously, we (Sargis *et al*., 2013a) considered *T. ferruginea* to be restricted to Sumatra, so our inclusion of the Tanahbala population in *T. ferruginea* expands the geographical range of this species. The absence of this taxon from the intervening Batu Islands of Tanahmasa and Pini may be the result of local extinctions or incomplete collecting on these islands. Like

T. ferruginea, *Presbytis melalophos* is also endemic to Sumatra and only one of the Batu Islands, but the latter is present on Pini rather than Tanahbala (see above; Groves, 2001).

We hypothesized that *T. 'glis' siberu* from the northern Mentawai Island of Siberut would prove to be most similar to *T. chrysogaster* from the three southern Mentawai Islands, and both cranial and postcranial morphology substantiated this prediction (Figs 2 and 3). In addition to the morphometric similarities of their skulls and hands, *T. 'glis' siberu* also appears to share the same mammae count of 2 with *T. chrysogaster* (see Sargis *et al*., 2013a; for *T. 'glis' siberu*, this count was coded on the only known female specimen of this taxon, USNM 252329). Finally, as Chasen & Kloss (1928) noted when they first described *T. glis siberu*, the orange-rufous underparts of this taxon are similar to those of *T. chrysogaster*, the golden-bellied treeshrew. Based on all of these similarities, the Siberut population is best classified with the other Mentawai populations as *T. chrysogaster*, and *T. glis siberu* Chasen & Kloss, 1928 should be treated as a junior synonym of this species (Appendix 1).

With the inclusion of the population from Siberut Island in *T. chrysogaster*, the geographic range of this species includes the four major Mentawai Islands: Siberut, Sipora, North Pagai, and South Pagai. This expanded distribution is more similar to that of other species of Euarchontoglires (Euarchonta [Scandentia, Primates, Dermoptera] + Glires [Rodentia, Lagomorpha]; Murphy *et al*., 2001) found in the Mentawai Islands, most of which are present on Siberut and at least one of the three southern islands (Wilting *et al*., 2012). As noted above, three endemic primate species (*H. klossii*, *P. potenziani*, and *S. concolor*) have distributions that, like that of *T. chrysogaster*, range throughout all four major islands. Although some authors recognize separate subspecies of *P. potenziani* and *S. concolor* on Siberut vs. the three southern islands based on pelage coloration (see Roos *et al*., 2003; Whittaker *et al*., 2006), no genetic distinction has been documented among the populations of *H. klossii* (Whittaker, 2009). Similarly, six of the 11 species of rodents in the Mentawai Islands are found on all four major islands; these include three endemic rats (*Leopoldamys siporanus*, *Maxomys pagensis*, and *Rattus lugens*) and three endemic squirrels (*Callosciurus melanogaster*, *Lariscus obscurus*, and *Sundasciurus fraterculus*) (Wilting *et al*., 2012). Three other species are present on Siberut and at least one of the three southern islands: one endemic mouse (*Chiropodomys karlkoopmani*) and two flying squirrels (*Petaurista petaurista* and the endemic *Petinomys lugens*) (Wilting *et al*., 2012). The two remaining endemic

Table 3. Measurement descriptions (and abbreviations) following Sargis *et al*. (2013b, c). Upper-case abbreviations for teeth (i.e. I, C, P, M) refer to maxillary and premaxillary teeth; lower-case abbreviations (i, c, p, m) refer to mandibular teeth

(1)	Condylo-premaxillary length (CPL): greatest distance between rostral surface of premaxilla and caudal surface of occipital condyle
(2)	Condylo-incisive length (CIL): greatest distance between anterior-most surface of I1 and caudal surface of occipital condyle
(3)	Upper toothrow length (UTL): greatest distance between anterior-most surface of I1 and posterior-most surface of M3
(4)	Maxillary toothrow length (MTL): greatest distance between anterior-most surface of C1 and posterior-most surface of M3
(5)	Epipterygoid–premaxillary length (EPL): greatest distance between rostral surface of premaxilla and caudal surface of epipterygoid process
(6)	Palato-premaxillary length (PPL): greatest distance between rostral surface of premaxilla and caudal surface of palatine
(7)	Epipterygoid breadth (EB): greatest distance between lateral points of epipterygoid processes
(8)	Mastoid breadth (MB): greatest distance between lateral apices of mastoid portion of petrosal
(9)	Lacrimal breadth (LB): greatest distance between lateral apices of lacrimal tubercles
(10)	Least interorbital breadth (LIB): least distance between the orbits
(11)	Zygomatic breadth (ZB): greatest distance between lateral surfaces of zygomatic arch
(12)	Braincase breadth (BB): greatest breadth of braincase
(13)	Lambdoid–premaxillary length (LPL): greatest distance between rostral surface of premaxilla and caudal surface of lambdoid crest
(14)	Condylo-nasal length (CNL): greatest distance between rostral surface of nasal and caudal surface of occipital condyle
(15)	Postorbital bar–premaxillary length (PBPL): greatest distance between rostral surface of premaxilla and caudal surface of postorbital bar
(16)	Lacrimal tubercle–premaxillary length (LTPL): greatest distance between rostral surface of premaxilla and caudal surface of lacrimal tubercle
(17)	Lambdoid crest height (LCH): greatest distance from apex (or apices if bilobate) of lambdoid crest to both ventral apices of occipital condyles (i.e. along midline)
(18)	Mandibular height (MH): greatest distance between coronoid and angular processes of mandible
(19)	Mandibular condyle height (MCH): greatest distance between mandibular condyle and angular process of mandible
(20)	Mandibular condyle width (MCW): greatest distance between medial and lateral surfaces of mandibular condyle
(21)	Mandibular condylo-incisive length (MCIL): greatest distance between anterior-most surface of i1 and caudal surface of mandibular condyle
(22)	Lower toothrow length (LTL): greatest distance between anterior-most surface of i1 and posterior-most surface of m3

flying squirrel species (*Hylopetes sipora* and *Iomys sipora*) are restricted to the southern islands. None of the rodents as currently recognized are endemic to Siberut alone (Wilting *et al*., 2012). The endemic bat (*Hipposideros breviceps*) is also restricted to a southern island (North Pagai; Wilting *et al*., 2012). Although exceptions to this pattern exist (e.g. *M. siberu* on Siberut and *M. pagensis* on the three southern islands; Ziegler *et al*., 2007), there is no clear biogeographical break for species of Euarchontoglires between Siberut and the three southern islands. Molecular data from all four island populations will be required to test for more subtle population differences within *T. chrysogaster*, but, on the basis of morphology, its pattern of distribution most closely resembles that of the majority of primates and rodents.

The inclusion of the Siberut population in *T. chrysogaster* has implications for its conservation status. *Tupaia chrysogaster* is one of only two treeshrew species currently categorized as 'Endangered' based on criterion B1ab(iii) ver. 3.1 (Meijaard & MacKinnon, 2008) of the *IUCN Red List of Threatened Species* (IUCN, 2013), which refers to an extent of occurrence less than 5000 km² that is fragmented or composed of five or fewer locations and is declining in area and/or habitat quality. This species is reported to inhabit lowland forest that is being lost (Meijaard & MacKinnon, 2008), and its previous, more restricted distribution on Sipora (601 km²), North

Table 4. Craniodental measurements (mm) of selected species of *Tupaia*. Statistics are mean ± SD, range of measurements, and sample size in parentheses. See Table 3 for measurement abbreviations and descriptions

	(1) CPL	(2) CIL	(3) UTL	(4) MTL	(5) EPL	(6) PPL	(7) EB	(8) MB
Tupaia chrysogaster	50.12 ± 1.30 47.99–52.66 (19)	49.36 ± 1.20 47.20–51.60 (18)	28.59 ± 0.75 27.27–29.99 (20)	19.79 ± 0.56 18.90–20.91 (22)	37.13 ± 1.14 34.81–38.78 (12)	30.54 ± 0.91 29.11–32.58 (21)	12.26 ± 0.77 11.51–13.56 (9)	18.57 ± 0.41 17.51–19.23 (21)
Tupaia ferruginea	48.59 ± 1.02 46.84–50.93 (46)	47.92 ± 1.00 46.22–50.38 (46)	27.32 ± 0.62 25.65–29.03 (58)	19.03 ± 0.44 18.23–19.93 (59)	35.21 ± 0.99 33.14–37.19 (39)	28.99 ± 0.71 27.70–30.83 (50)	11.95 ± 0.67 9.77–12.71 (21)	18.17 ± 0.52 17.32–19.42 (46)
Tupaia 'glis' siberu	50.42 ± 0.85 49.44–50.95 (3)	50.01 ± 0.86 49.02–50.59 (3)	29.34 ± 0.28 29.15–29.66 (3)	20.52 ± 0.34 20.22–20.89 (3)	37.74 ± 0.92 36.96–38.75 (3)	31.76 ± 0.47 31.43–32.09 (2)	12.54 (1)	19.17 ± 0.21 19.02–19.32 (2)
Tupaia 'glis' tephrura	48.36 (1)	47.84 (1)	27.48 (1)	18.93 (1)	35.27 (1)	29.25 (1)	11.72 (1)	18.1 (1)

	(9) LB	(10) LIB	(11) ZB	(12) BB	(13) LPL	(14) CNL	(15) PBPL
Tupaia chrysogaster	19.35 ± 0.58 18.66–21.08 (18)	14.53 ± 0.51 13.51–15.57 (21)	26.77 ± 0.55 25.36–27.95 (20)	19.80 ± 0.39 19.07–20.34 (20)	54.43 ± 1.35 52.20–57.50 (19)	49.20 ± 1.18 47.09–51.45 (19)	37.50 ± 0.99 35.20–39.15 (20)
Tupaia ferruginea	18.71 ± 0.62 17.16–20.00 (47)	14.62 ± 0.63 11.99–15.70 (58)	25.57 ± 0.92 21.55–27.14 (48)	19.66 ± 0.53 17.93–20.61 (47)	51.79 ± 1.63 44.29–54.15 (42)	47.01 ± 1.02 44.67–49.08 (40)	34.91 ± 1.34 27.62–37.71 (56)
Tupaia 'glis' siberu	19.43 ± 0.50 19.07–19.78 (2)	14.86 ± 0.33 14.49–15.10 (3)	26.54 (1)	19.96 ± 0.72 19.45–20.47 (2)	54.88 ± 1.32 53.36–55.74 (3)	49.54 ± 0.05 49.50–49.57 (2)	37.77 ± 1.05 36.77–38.86 (3)
Tupaia 'glis' tephrura		14.95 (1)	25.2 (1)	19.77 (1)	52.04 (1)	46.31 (1)	35.08 (1)

	(16) LTPL	(17) LCH	(18) MH	(19) MCH	(20) MCW	(21) MCIL	(22) LTL
Tupaia chrysogaster	26.06 ± 0.93 23.91–27.82 (21)	13.28 ± 0.37 12.63–14.28 (21)	14.58 ± 0.68 13.38–16.12 (24)	9.57 ± 0.44 8.64–10.63 (24)	3.67 ± 0.18 3.34–4.01 (24)	40.62 ± 1.07 38.51–43.72 (20)	27.28 ± 0.76 26.36–29.40 (19)
Tupaia ferruginea	23.93 ± 1.06 18.30–26.40 (58)	12.43 ± 0.32 11.69–13.03 (45)	13.99 ± 0.66 11.82–15.34 (60)	9.33 ± 0.46 8.23–10.25 (61)	3.17 ± 0.25 2.52–3.69 (61)	38.32 ± 0.83 36.60–40.54 (59)	25.68 ± 0.91 20.14–27.00 (57)
Tupaia 'glis' siberu	26.40 ± 0.67 25.61–27.25 (4)	13.26 ± 0.46 12.93–13.58 (2)	15.16 ± 0.34 14.80–15.46 (3)	9.83 ± 0.25 9.56–10.04 (3)	3.62 ± 0.18 3.49–3.82 (3)	41.19 ± 0.60 40.76–41.61 (2)	27.70 ± 0.34 27.46–27.94 (2)
Tupaia 'glis' tephrura	23.73 (1)	12.22 (1)	13.27 (1)	8.25 (1)	3.1 (1)	38.38 (1)	26.02 (1)

Table 5. Component loadings from principal components analysis (PCA) of skulls (Fig. 3). Abbreviations for variables are defined in Table 3. Loadings in bold type are discussed in the text

(A) PCA of 7 cranial variables (Fig. 3A)

	Axis	
	1	2
(1) CPL	0.980	−0.014
(2) CIL	0.971	−0.050
(5) EPL	0.975	−0.081
(10) LIB	0.608	**0.793**
(13) LPL	0.978	−0.091
(15) PBPL	0.972	−0.125
(16) LTPL	0.964	−0.135
Eigenvalues	6.052	0.680
Percentage of total variance explained	86.458	9.714

(B) PCA of 3 cranial and 3 mandibular variables (Fig. 3B)

	Axis	
	1	2
(3) UTL	0.933	−0.274
(4) MTL	0.878	−0.236
(16) LTPL	0.925	−0.197
(18) MH	0.867	**0.376**
(19) MCH	0.732	**0.640**
(20) MCW	0.807	−0.186
Eigenvalues	4.437	0.755
Percentage of total variance explained	73.952	12.584

Pagai (622 km²), and South Pagai (900 km²) totalled a maximum of only about 2123 km² (http://islands.unep.ch/isldir.htm; Dahl, 1991). The addition of the population from Siberut (3829 km²; http://islands.unep.ch/isldir.htm; Dahl, 1991) to this species nearly triples its potential range to 5952 km², which slightly surpasses the 5000 km² limit on the 'Endangered' category (see above), but is well below 20 000 km², one criterion for being classified as 'Vulnerable' (IUCN, 2013). Although this larger range, which includes Siberut National Park (see Whittaker, 2009), signifies an increased potential area for the preservation of this species, the presumed forest habitat of *T. chrysogaster* continues to be threatened by logging (Meijaard & MacKinnon, 2008). However, we are unaware of any published or unpublished studies of any aspect of the ecology or habitat require-

ments or preferences of this species. Neither the description of *T. chrysogaster* nor that of *T. glis siberu* included any information along these lines, and the collecting localities of the known specimens are imprecise, indicating only the island from which they were collected (see Appendix 1). Morphologically similar continental congeners, such as *T. belangeri*, have been described as 'highly adaptable' and are known to inhabit agricultural plantations and other anthropogenically modified habitats (Han, Duckworth & Molur, 2008). The same is thought to be true of *T. glis* (Han, 2008), and even some island endemics, such as *T. palawanensis* (Esselstyn, Widmann & Heaney, 2004; Gonzalez, Widmann & Heaney, 2008). Although the expanded but still restricted insular distribution of *T. chrysogaster*, as we now recognize it, supports a heightened conservation status relative to other species of *Tupaia*, most of which are ranked as 'Least Concern' (IUCN, 2013), we nonetheless recommend a revised *IUCN Red List* classification of 'Data Deficient' until additional information on the basic ecology and natural history of *T. chrysogaster* becomes available.

The impact of taxonomy on conservation strategies has been noted repeatedly in the literature (e.g. Meijaard & Nijman, 2003; Mace, 2004; Agnarsson & Kuntner, 2007), and the problem of taxonomic inflation has been highlighted in some previous papers (e.g. Isaac, Mallet & Mace, 2004; Mace, 2004). In our previous studies (Sargis *et al.*, 2013a, b), we have elevated some taxa to species because they were morphometrically distinct (morphologically diagnosable) from the species with which they were synonymized. Recognizing such taxa as distinct species certainly has potential conservation implications, especially for small island populations. Hence, we suggested that the conservation status of these populations should be re-assessed because the level to which they are threatened may be *increased* compared with their current listing on the *IUCN Red List of Threatened Species* (IUCN, 2013; Sargis *et al.*, 2013a, b). However, in the current case of including the Siberut population in *T. chrysogaster*, a re-evaluation of conservation status may be necessary because it is possible that the level of threat to this species is *decreased* because of the expansion of its recognized range to Siberut Island, especially given the presence of Siberut National Park on that island (see Whittaker, 2009). In this case, we have not elevated *T. 'glis' tephrura* or *T. 'glis' siberu* to species status, but removing them from synonymy with *T. glis* and reclassifying these populations in *T. ferruginea* and *T. chrysogaster*, respectively, changes our understanding of their biogeographic limits and may have consequences for the conservation status of these taxa. Some treeshrews, like
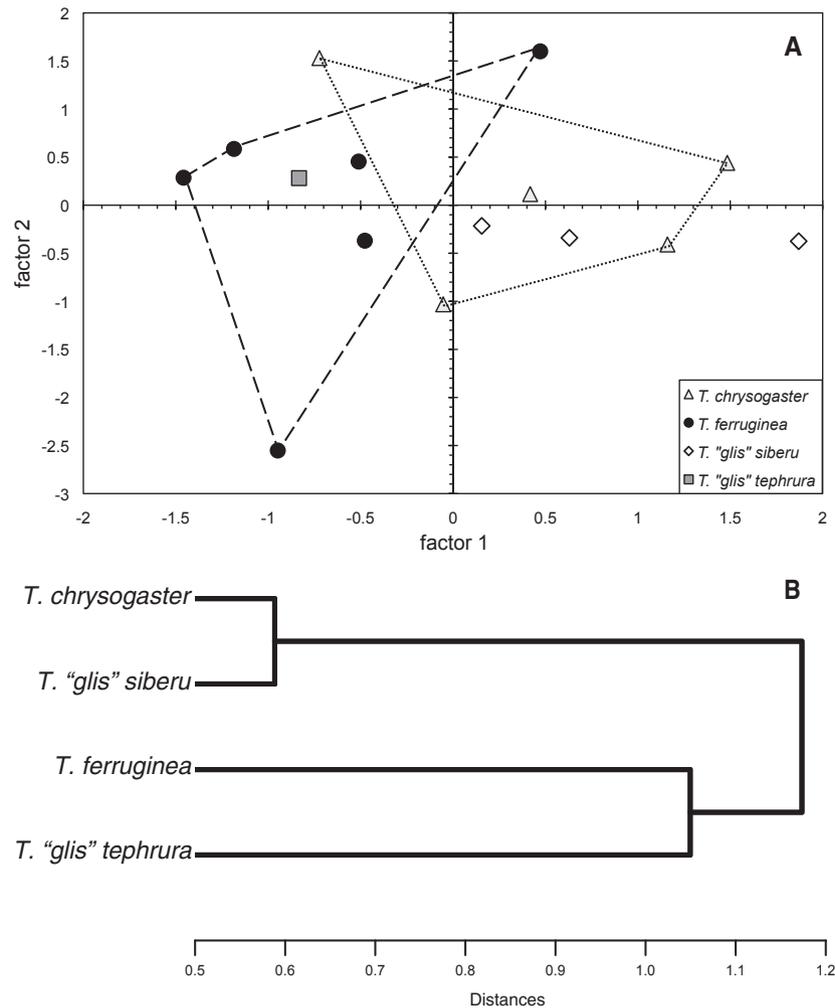
Figure 2. Plots illustrating results of manus analyses. A, Plot of factor scores on the first two factor axes from principal components analysis (PCA) of four manus variables from rays I and IV (Table 2). B, Phenogram from cluster analysis of 18 variables from all five rays. *T. 'glis' siberu* is most similar to *T. chrysogaster*, whereas *T. 'glis' tephrura* is most similar to *T. ferruginea*.

primates (Brandon-Jones *et al*., 2004; Mace, 2004), have certainly been over-lumped in previous classifications (e.g. Chasen, 1940), and only through careful taxonomic revision using modern morphological and molecular methods will we be able to construct an accurate picture of species diversity, geographic ranges, and conservation priorities.
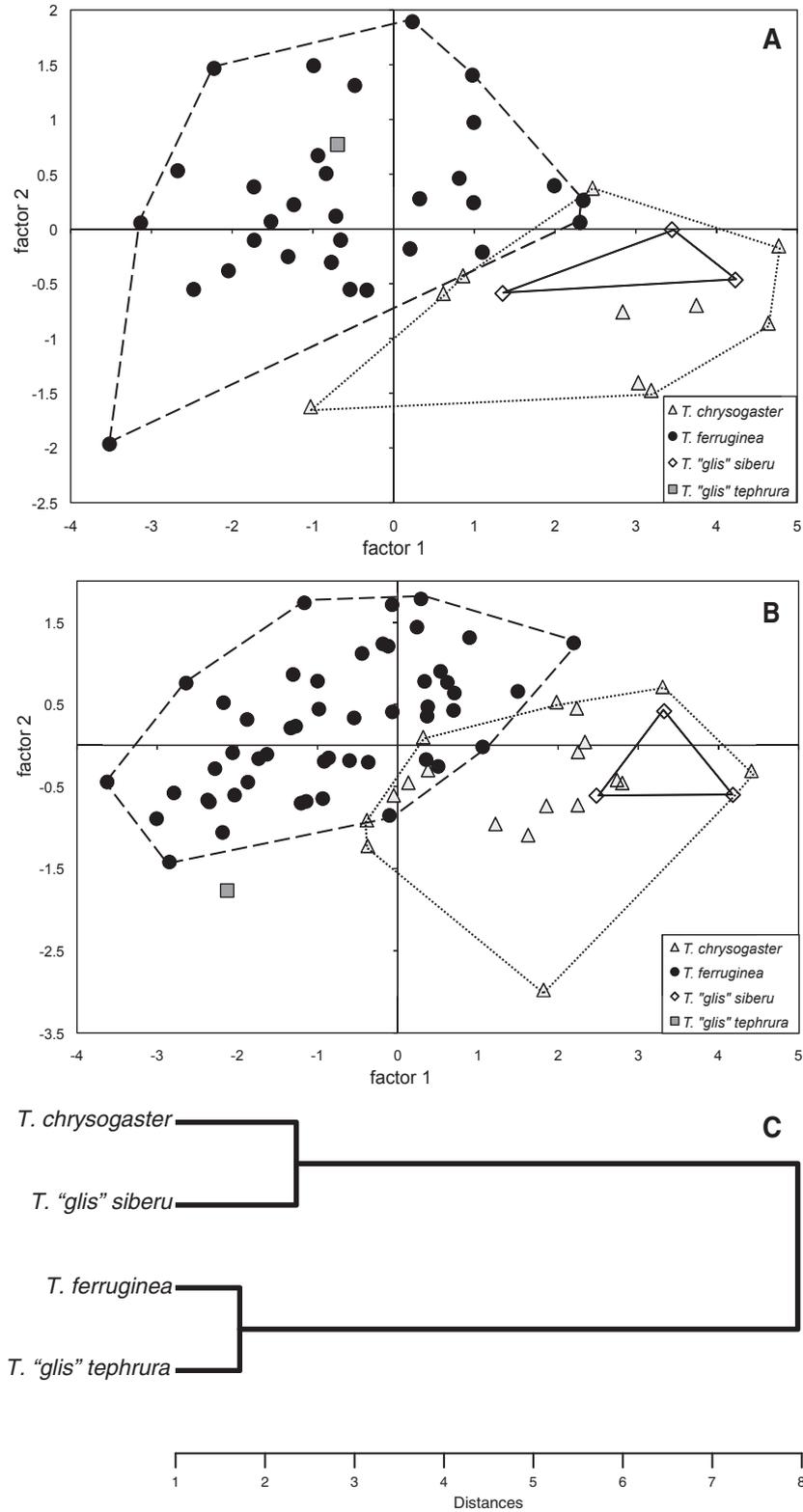
Figure 3. Plots illustrating results of skull analyses. A, Plot of factor scores on the first two axes from principal components analysis (PCA) of seven cranial variables (Table 5). B, Plot of factor scores on the first two axes from PCA of three cranial and three mandibular variables (Table 5). C, Phenogram from cluster analysis of 21 skull variables. *T. 'glis' siberu* is most similar to *T. chrysogaster*, whereas *T. 'glis' tephrura* is most similar to *T. ferruginea*.

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APPENDIX 1

SPECIMENS EXAMINED

Specimens from the following institutions (with abbreviations) were included in this study: American Museum of Natural History (AMNH), New York, NY, USA; The Natural History Museum (BMNH), London, UK; Field Museum of Natural History (FMNH), Chicago, IL, USA; Los Angeles County Museum of Natural History (LACM), Los Angeles, CA, USA; Museum of Comparative Zoology at Harvard University (MCZ), Cambridge, MA, USA; Museum of Vertebrate Zoology at University of California (MVZ), Berkeley, CA, USA; Naturhistorisches Museum Basel (NMB), Basel, Switzerland; Naturhistorisches Museum Wien (NMW), Vienna, Austria; Nationaal Natuurhistorisch Museum (RMNH), Leiden, The Netherlands; United States National Museum of Natural History, Smithsonian Institution (USNM), Washington DC, USA; Museum für Naturkunde (ZMB), Berlin, Germany; Zoologisk Museum University of Copenhagen (ZMUC), Copenhagen, Denmark.

Specimens used in both the manus and skull analyses are indicated with an asterisk (*), and holotypes of the four taxa analysed in this study are in italic type. Specimens used for the samples of T. 'glis' siberu and T. 'glis' tephrura are listed in a separate paragraph under T. chrysogaster and T. ferruginea, respectively.

Tupaia chrysogaster (N = 25). – INDONESIA: Mentawai Islands: Pagai Utara (North Pagai) Island (AMNH 103093, 103094, 103097, 103098, 103100, 103102, 103103, 103106, 103316; RMNH 34235; USNM 121571*, *121572** – holotype of *T. chrysogaster* Miller, 1903, 121573*, 121575*); Pagai Selatan (South Pagai) Island (USNM 121577*, 121579*); Sipora Island (BMNH 28.11.2.4; USNM 252330*–252333*, 252334, 252335*, 252337*, 252338*).

Siberut Island (N = 4) (*BMNH 28.11.2.3** – holotype of *T. glis siberu* Chasen & Kloss, 1928, 89.207; USNM 252328*, 252329*).

Tupaia ferruginea (N = 63). – INDONESIA: Sumatra: no locality (MCZ 6276; ZMB 11460, 87172; ZMUC 19); Bencoolen [Bengkulu] (*BMNH 79.11.21.573* – holotype of *T. ferruginea* Raffles, 1821); Rimbo Pengadang (Lebong), Bengkulen [Bengkulu] (RMNH 12602); Tarussan Bay (USNM 141074*); Loh

Sidoh Bay (USNM 114152*, 114153*); Aru Bay (FMNH 43835; USNM 143329*, 143333*); Tapanuli Bay (USNM 114548*, 114549*, 114553); Langsa, Atjeh [Aceh] (RMNH 34183, 34185); Perlak, Atjeh [Aceh] (FMNH 47123–47125; RMNH 34163, 34165–34167, 34169, 34171–34177, 34180–34182, 44290; USNM 257593*, 257594*, 257595*, 257596*); Little Siak River (USNM 144204*, 144205*, 144209*); Indragiri (NMB 2992, 10005); Indragiri River (USNM 174610); Lower Langkat (BMNH 4.4.1.4, 4.6.9.1; NMB 10004); Lampongs [Lampung] (RMNH 15634–15637, 15639, 15640); Giesting, Lampoengs (RMNH 34186); Panhalan [Pangkalan] Brandan (ZMB 33979); Padangse Bovenlanden (Haut Padang; RMNH 36112); Ketambe Research Station, Leuser National Park, 400 m, Aceh (MVZ 192187); Seolah Dras, Korinchi Valley (BMNH 19.11.5.17); Deli (LACM 52185); Pajo (BMNH 79.6.28.15); Paja, Bahong, Deli, Langsa (NMW 4540).

Batu Islands (*N* = 1): Tana Bala [Tanahbala] Island (*USNM 121752** – holotype of *T. tephrura* Miller, 1903).