Biological Journal of the Linnean Society, 2017, **120**, 286–312. With 5 figures.

Skeletal variation and taxonomic boundaries among mainland and island populations of the common treeshrew (Mammalia: Scandentia: Tupaiidae)

ERIC J. SARGIS[1,2,3]*, NEAL WOODMAN[4], NATALIE C. MORNINGSTAR[1], TIFFANY N. BELL[2] and LINK E. OLSON[5]

[1]*Department of Anthropology, Yale University, P.O. Box 208277, New Haven, CT 06520, USA*
[2]*Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, CT 06520, USA*
[3]*Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT 06520, USA*
[4]*United States Geological Survey, Patuxent Wildlife Research Center, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA*
[5]*University of Alaska Museum, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

Received 12 May 2016; revised 8 July 2016; accepted for publication 8 July 2016

Treeshrews (order Scandentia) include 23 currently recognized species of small-bodied mammals from South and Southeast Asia. The taxonomy of the common treeshrew, *Tupaia glis*, which inhabits the Malay Peninsula south of the Isthmus of Kra, as well as a variety of offshore islands, has an extremely complicated history resulting from its wide distribution and subtly variable pelage. In our ongoing investigation of species boundaries in *Tupaia*, we compared island and mainland populations of *T. glis* using multivariate analyses. Specifically, we compared the skull and hand morphology of 13 island populations, most of which have been recognized as separate species or subspecies, to that of the mainland population. Island populations generally average smaller body size than those on the mainland, but none of the island populations are sufficiently distinct from the mainland population to warrant species recognition. This has important conservation implications for this widespread and morphologically variable species. It also highlights the potential role that ecogeographic explanations can play in understanding intraspecific variation, a role that should be considered in taxonomic studies and investigated further in *T. glis* and other treeshrews. Published 2016. This article has been contributed to by a US Government employee and their work is in the public domain in the USA, *Biological Journal of the Linnean Society*, 2017, **120**, 286–312.

KEYWORDS: cranium – hand – mandible – manus – morphology – rays – skull – Southeast Asia – taxonomy – *Tupaia glis*.

INTRODUCTION

Treeshrews (order Scandentia) are small-bodied (< 315 g; Sargis, 2002) mammals, endemic to South and Southeast Asia. The first formally described species was *Tupaia glis* (Diard, 1820), the common treeshrew. A second species, *Tupaia ferruginea* Raffles, 1821, was described soon after and serves as the type species for the genus *Tupaia* Raffles, 1821. Since its discovery, *T. glis* has had a complex taxonomic history that includes periods of splitting and lumping, which has led to widely variable estimates of diversity, misidentification and misallocation of taxa, and general confusion regarding this and closely related species (Sargis *et al.*, 2013a). One result is that *T. glis* has been treated as a poorly defined 'wastebasket' taxon encompassing as many as 27 synonyms (Helgen, 2005). In our previous analyses of *T. glis*, we recognized three populations previously synonymized with *T. glis* as distinct species: *T. ferruginea* Raffles, 1821 from Sumatra and the Batu island of Tanahbala; *T. discolor* Lyon, 1906 from Bangka; and *T. hypochrysa* (Thomas, 1895) from Java (Sargis *et al.*, 2013a; fig. 9; 2013b: fig. 1). We

*Corresponding author. E-mail: eric.sargis@yale.edu

subsequently demonstrated that the Siberut Island population attributed to *T. glis* is instead conspecific with the Mentawai treeshrew, *T. chrysogaster* Miller, 1903 (Sargis *et al.*, 2014a). These changes in our understanding of *T. glis* greatly reduced its known geographic range, restricting it to the Malay Peninsula south of the Isthmus of Kra, the purported contact zone with its sister species *T. belangeri* (Wagner, 1841) (Helgen, 2005; Olson, Sargis & Martin, 2005; Roberts *et al.*, 2011), and adjacent offshore islands (Fig. 1).

The type locality for *T. glis* is Penang Island, along the west coast of the Malay Peninsula (Fig. 1). As Lyon (1913: 41) stated, '[i]t is perhaps a slight misfortune that the earliest name applied to the species was given to one of the insular races and not to the real parent form occurring on the large land masses.' He distinguished the Penang Island population, *T. glis glis*, from two mainland populations on the Malay Peninsula: *T. glis ferruginea*, which he conceived as occupying the adjacent mainland south to Singapore (and Sumatra), and *T. lacernata wilkinsoni* Robinson & Kloss, 1911; from the middle of the Malay Peninsula just north of Penang Island to the Isthmus of Kra. As noted above, *T. ferruginea* is now

Figure 1. Map of the Malay Peninsula, Sumatra, and surrounding islands showing localities discussed in the text.

recognized as a distinct species restricted to Sumatra and Tanahbala (Sargis *et al.*, 2013a, 2014a). The description of *Tupaia lacernata* Thomas & Wroughton, 1909 was based on another island population (Langkawi Island), and the name is a junior synonym of *T. glis* (Chasen, 1940; Corbet & Hill, 1992; Wilson, 1993; Helgen, 2005). The type locality for *T. g. wilkinsoni* is Ko-Khau, Thailand on the Malay Peninsula; this is the oldest available name for the mainland population of *T. glis*, so we use this name herein to refer to the mainland population of the common treeshrew from the Malay Peninsula south of the Isthmus of Kra (see Appendix 1).

In addition to *T. g. glis* from the western island of Penang, Lyon (1913) recognized subspecies of *T. glis* from the eastern islands of Aur (*T. g. pulonis* Miller, 1903), Pemanggil (*T. g. pemangilis* Lyon, 1911), and Tioman (*T. g. sordida* Miller, 1900), and the southern island of Batam (*T. g. batamana* Lyon, 1907) (Fig. 1). He classified the populations from the western islands as subspecies of *T. lacernata*, including those from Langkawi and Terutau (*T. l. lacernata* Thomas & Wroughton, 1909) and the Butang Islands of Adang and Rawi (*T. l. raviana* Lyon, 1911) (Lyon, 1913). All of these names are now treated as synonyms of *T. glis* (Helgen, 2005). Although Lyon (1913) considered most of the island populations as distinct subspecies, he recognized the population from the southern island of Bintan as a distinct species, *T. castanea* Miller, 1903.

Since Lyon's (1907, 1911, 1913) work, populations from other islands near the Malay Peninsula have been treated in a variety of ways. The population from the western island of Ta Li Bong was described as a subspecies of *T. glis*, *T. g. umbratilis* Chasen, 1940, whereas that from the southern island of Mapur was classified as a subspecies of *T. castanea*, *T. c. redacta* Robinson, 1916. Traditionally, taxonomic distinctions in the *T. glis* species complex were largely based on differences in body size and pelage coloration (Lyon, 1913; Hill, 1960, Steele, 1983) rather than specific osteological features or morphometric shape differences. For example, the original descriptions of six island taxa (*T. g. glis, T. g. pemangilis, T. g. sordida, T. l. lacernata, T. g. umbratilis,* and *T. c. redacta*) referred to their smaller body or skull size compared to the mainland populations. In contrast, *T. g. batamana* from Batam was described as having a 'heavier skull' (Lyon, 1913: 46) and *T. castanea* from Bintan as having similar body size to mainland *T. glis* (Lyon, 1913: 90). Although Endo *et al.* (1999, 2000a,b,c) investigated geographic variation in the skull of *T. glis*, those studies focused entirely on variation among the mainland populations, and island populations have mostly been ignored. As part of a taxonomic re-appraisal of these island populations, we compared the skull and hand morphology of island and mainland populations in a series of multivariate analyses to assess possible size and shape differences among these populations.

MATERIALS AND METHODS

Herein we recognize *Tupaia glis* as circumscribed by Helgen (2005), but with the exception of those populations we previously showed to be distinct (*T. ferruginea* from Sumatra and Tanahbala; *T. discolor* from Bangka; *T. hypochrysa* from Java; and *T. chrysogaster* from the Mentawai Islands, including Siberut; Sargis *et al.*, 2013a,b, 2014a). To evaluate morphological variation within and among populations of *T. glis*, we recorded 38 manus and 22 craniomandibular measurements employed in previous studies of treeshrews (Sargis *et al.*, 2013a,b, 2014a; Sargis, Campbell & Olson, 2014b). All measurements are in millimetres and are rounded to the nearest 0.01 mm. Summary statistics include mean, standard deviation, and range. We also conducted a cursory qualitative examination of the pelage of 62 specimens representing the mainland and 12 island populations to assess variation among several proposed taxa, which were originally designated based primarily on pelage differences.

Manus

We X-rayed the right and left manus of 89 study skins of *Tupaia glis* adults (those with fully erupted permanent dentition) (see Appendix 1) using 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) in the Division of Fishes, National Museum of Natural History (USNM), Washington, DC. Digital images were constructed using Varian Medical Systems Image Viewing and Acquisition software (VIVA version 2.0; Waltham, Massachusetts) and transferred to Adobe Photoshop CS4 Extended (version 11.0.2; Adobe Systems Inc., San Jose, CA, USA), where they were converted to positive images and measured with the Custom Measurement Scale (see Woodman & Morgan, 2005; Woodman & Stephens, 2010; Sargis *et al.*, 2013a,b, 2014a). Measurements were taken from the most complete image of either the right or left side and supplemented where necessary with measurements from the other side. We use the term ‘ray’ to refer to that part of the manus with the metacarpal plus the phalanges (Woodman & Stephens, 2010). We recorded the following measurements from all five rays, with the exception that depths (dorsopalmar distances) of bones were substituted for widths (mediolateral distances) in ray I because of its 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). Summary statistics from the manus are presented in Table 1.

Specimens examined included 23 *T. glis* from Penang Island (the type locality), 39 from mainland peninsular Malaysia, and 27 from Singapore and 11 nearshore islands to the west, east, and south of the Malay Peninsula. These specimens are listed in Appendix 1.

Skull

For our analyses of the cranium and mandible, 22 measurements (Table 2; Sargis *et al.*, 2013b, 2014a, b) were recorded from 260 adult specimens (see Appendix 1) using digital calipers. Our sample includes all specimens of *T. glis glis* used in the manus analyses, and larger samples of all the other populations, including the holotypes of ten species or subspecies. Summary statistics from the skulls are presented in Table 3.

Specimens examined included 23 *T. glis* from Penang Island (the type locality), 95 from mainland peninsular Malaysia, and 142 from Singapore and 11 nearshore islands to the west, east, and south of the Malay Peninsula. These specimens are listed in Appendix 1.

Morphological variation among mainland and island populations

The mainland and island populations of *T. glis* included in our study have each been recognized at times as subspecies or species (e.g., Lyon, 1913; Appendix 1). We examined the potential variation between mainland and island populations using a four-stage approach: (1) We first looked for possible differentiation between the type population of *T. glis* on Penang Island and the mainland population from the southern Malay Peninsula. Next, we compared the mainland population with populations from three geographically defined groups of islands at different latitudes with distinct geological histories (Fig. 1): (2) to the west of the Malay Peninsula (Penang, Adang, Rawi, Langkawi, Terutau, and Ta Li Bong); (3) to the east of the peninsula (Aur, Pemanggil, and Tioman); and (4) to the south of the peninsula (Batam, Bintan, Mapur, and Singapore).

Table 1. Manus measurements (mm) from selected populations of *Tupaia glis*. Statistics are mean ± standard deviation (SD), range, and sample size in parentheses. See 'Materials and Methods' for measurement abbreviations and descriptions

Taxon	Island	1ML	1MD	1PPL	1PPD	1DPL	1DPD
Peninsular Malaysia							
'*T. g. wilkinsoni*'		4.46 ± 0.21	0.61 ± 0.05	3.55 ± 0.17	0.64 ± 0.04	2.40 ± 0.15	1.18 ± 0.14
		4.06–4.94	0.54–0.70	3.23–3.98	0.52–0.71	2.16–2.74	0.88–1.47
		(39)	(38)	(37)	(38)	(35)	(33)
Western islands							
T. g. glis	Penang	4.49 ± 0.34	0.57 ± 0.04	3.42 ± 0.21	0.60 ± 0.04	2.50 ± 0.14	1.15 ± 0.14
		4.05–5.81	0.50–0.69	2.99–3.95	0.51–0.67	2.24–2.75	1.01–1.46
		(22)	(22)	(22)	(20)	(19)	(13)
'*T. g. raviana*'	Adang	4.24	0.55	3.48	0.67	2.37	1.27
		(1)	(1)	(1)	(1)	(1)	(1)
'*T. g. raviana*'	Rawi	4.40	0.65	3.39	0.67	—	1.39
		(1)	(1)	(1)	(1)		(1)
'*T. g. lacernata*'	Langkawi	4.01	0.62	3.30	0.60	2.26	1.22
		3.94–4.08	0.60–0.63	3.28–3.32	0.54–0.65	2.20–2.32	
		(2)	(2)	(2)	(2)	(2)	(1)
'*T. g. lacernata*'	Terutau	4.15 ± 0.18	0.55 ± 0.04	3.26 ± 0.17	0.60 ± 0.05	2.29 ± 0.20	1.01 ± 0.10
		3.91–4.34	0.49–0.59	3.11–3.48	0.52–0.65	2.16–2.52	0.93–1.14
		(4)	(4)	(4)	(4)	(3)	(4)
'*T. g. umbratilis*'	Ta Li Bong	4.16	0.58	3.14	0.63	2.25	0.94
		(1)	(1)	(1)	(1)	(1)	(1)
Eastern islands							
'*T. g. pulonis*'	Aur	4.19	0.66	3.50	0.63	2.78	1.41
		(1)	(1)	(1)	(1)	(1)	(1)
'*T. g. pemangilis*'	Pemanggil	3.97	0.58	3.35	0.68	2.38	1.27
		(1)	(1)	(1)	(1)	(1)	(1)
'*T. g. sordida*'	Tioman	4.17 ± 0.20	0.58 ± 0.05	3.31 ± 0.18	0.58 ± 0.05	2.39 ± 0.12	1.01 ± 0.09
		3.69–4.37	0.51–0.67	2.90–3.55	0.50–0.64	2.15–2.54	0.89–1.11
		(10)	(10)	(10)	(10)	(10)	(10)
Southern islands							
'*T. g. batamana*'	Batam	4.16	0.63	3.54	0.70	2.76	0.99
		3.59–4.73	0.62–0.64	3.46–3.62	0.69–0.71		0.93–1.04
		(2)	(2)	(2)	(2)	(1)	(2)
T. g. castanea	Bintan	4.53	0.58	3.39	0.71	2.93	1.22
		4.42–4.63	0.56–0.60	3.36–3.42	0.66–0.76		
		(2)	(2)	(2)	(2)	(1)	(1)
'*T. g. redacta*'	Mapur	5.05	0.58	2.83	0.59	2.07	—
		(1)	(1)	(1)	(1)	(1)	
T. glis	Singapore	4.43	0.61	3.11	0.58	2.34	1.17
		(1)	(1)	(1)	(1)	(1)	(1)

Table 1. *Continued*

Taxon	Island	2ML	2MW	2PPL	2PPW	2MPL	2MPW	2DPL	2DPW
Peninsular Malaysia									
‘*T. g. wilkinsoni*’		7.97 ± 0.41 7.11–9.11 (38)	0.76 ± 0.05 0.65–0.86 (38)	4.89 ± 0.21 4.30–5.35 (34)	0.70 ± 0.05 0.56–0.80 (36)	2.96 ± 0.25 2.78–3.14 (2)	0.73 ± 0.03 0.68–0.82 (23)	2.37 ± 0.27 1.79–2.77 (28)	1.01 ± 0.05 0.89–1.10 (17)
Western islands									
T. g. glis	Penang	7.89 ± 0.45 7.02–8.90 (20)	0.72 ± 0.04 0.61–0.80 (23)	4.65 ± 0.16 4.20–4.96 (16)	0.68 ± 0.03 0.63–0.74 (22)	–	0.66 ± 0.04 0.59–0.71 (18)	2.37 ± 0.23 2.00–2.67 (10)	1.00 ± 0.07 0.94–1.14 (11)
‘*T. g. raviana*’	Adang	7.41 (1)	0.76 (1)	4.77 (1)	–	2.96 (1)	–	2.45 (1)	–
‘*T. g. raviana*’	Rawi	–	0.75 (1)	4.83 (1)	0.78 (1)	–	–	–	–
‘*T. g. lacernata*’	Langkawi	7.70 7.65–7.74 (2)	0.76 0.72–0.80 (2)	4.53 4.41–4.64 (2)	0.72 0.71–0.72 (2)	2.57 2.46–2.68 (2)	0.71 (1)	1.80 1.79–1.80 (2)	0.87 (1)
‘*T. g. lacernata*’	Terutau	7.43 ± 0.43 7.18–8.07 (4)	0.79 0.73–0.84 (2)	4.64 ± 0.02 4.62–4.67 (4)	0.70 ± 0.02 0.67–0.72 (4)	2.76 ± 0.14 2.66–2.92 (3)	0.62 0.60–0.64 (2)	2.15 ± 0.35 1.65–2.46 (4)	0.97 0.95–0.99 (2)
‘*T. g. umbratilis*’	Ta Li Bong	7.60 (1)	0.71 (1)	4.69 (1)	0.69 (1)	2.75 (1)	0.67 (1)	2.10 (1)	0.99 (1)
Eastern islands									
‘*T. g. pulonis*’	Aur	7.36 (1)	0.72 (1)	5.09 (1)	0.70 (1)	—	—	—	—
‘*T. g. pemangilis*’	Pemanggil	7.26 (1)	0.69 (1)	4.84 (1)	0.65 (1)	—	—	2.41 (1)	—
‘*T. g. sordida*’	Tioman	7.38 ± 0.32 6.91–7.84 (10)	0.69 ± 0.03 0.66–0.75 (10)	4.51 ± 0.18 4.11–4.76 (10)	0.67 ± 0.05 0.57–0.72 (8)	2.71 ± 0.23 2.32–3.20 (10)	0.67 ± 0.08 0.56–0.82 (7)	2.11 ± 0.25 1.82–2.41 (9)	0.98 ± 0.08 0.94–1.07 (3)
Southern islands									
‘*T. g. batamana*’	Batam	7.24 (1)	0.81 0.78–0.83 (2)	5.15 4.85–5.45 (2)	0.76 0.73–0.78 (2)	2.92 (1)	0.73 0.69–0.77 (2)	2.41 (1)	—
T. g. castanea	Bintan	7.71 7.60–7.82 (2)	0.75 0.68–0.82 (2)	4.99 4.97–5.01 (2)	0.76 0.74–0.77 (2)	2.71 (1)	0.77 (1)	2.48 2.44–2.51 (2)	1.23 (1)
‘*T. g. redacta*’	Mapur	6.74 (1)	0.73 (1)	4.45 (1)	0.71 (1)	—	—	—	—
T. glis	Singapore	7.71 (1)	0.80 (1)	4.43 (1)	0.68 (1)	2.87 (1)	0.67 (1)	—	—

Table 1. *Continued*

Taxon	Island	3ML	3MW	3PPL	3PPW	3MPL	3MPW	3DPL	3DPW
Peninsular Malaysia									
'T. g. wilkinsoni'		9.82 ± 0.49	0.81 ± 0.05	5.16 ± 0.19	0.77 ± 0.04	3.28 ± 0.23	0.71 ± 0.04	2.42 ± 0.37	1.05 ± 0.13
		8.78–10.83	0.69–0.90	4.78–5.54	0.66–0.85	3.11–3.44	0.58–0.80	1.37–2.86	0.94–1.60
		(36)	(34)	(36)	(39)	(2)	(28)	(31)	(26)
Western islands									
T. g. glis	Penang	9.66 ± 0.39	0.74 ± 0.03	4.82 ± 0.27	0.71 ± 0.04	3.57	0.66 ± 0.05	2.53 ± 0.26	1.03 ± 0.07
		8.96–10.65	0.67–0.80	4.07–5.26	0.58–0.78		0.58–0.73	1.80–2.99	0.94–1.15
		(22)	(23)	(16)	(23)	(1)	(15)	(15)	(11)
'T. g. raviana'	Adang	—	0.70	4.96	0.73	3.63	0.74	1.89	—
			(1)	(1)	(1)	(1)	(1)	(1)	
'T. g. raviana'	Rawi	10.03	0.83	5.27	0.76	—	0.72	—	—
		(1)	(1)	(1)	(1)		(1)		
'T. g. lacernata'	Langkawi	9.32	0.80	4.84	0.73	2.80	0.67	1.84	0.92
		9.14–9.50	0.78–0.81	4.70–4.97	0.70–0.76	2.45–3.14	0.65–0.69	1.61–2.06	
		(2)	(2)	(2)	(2)	(2)	(2)	(2)	(1)
'T. g. lacernata'	Terutau	8.99	0.75 ± 0.05	4.84 ± 0.10	0.71 ± 0.05	3.08 ± 0.08	0.68 ± 0.11	2.00	1.07
		8.90–9.07	0.71–0.81	4.70–4.95	0.65–0.75	2.99–3.15	0.61–0.81	1.99–2.00	1.05–1.09
		(2)	(4)	(4)	(4)	(3)	(3)	(2)	(2)
'T. g. umbratilis'	Ta Li Bong	9.61	0.70	4.96	0.81	2.68	0.67	1.73	1.16
		(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Eastern islands									
'T. g. pulonis'	Aur	9.66	0.85	5.46	0.76	–	–	2.98	–
		(1)	(1)	(1)	(1)			(1)	
'T. g. pemangilis'	Pemanggil	8.79	0.68	5.14	0.75	—	0.67	2.46	0.99
		(1)	(1)	(1)	(1)		(1)	(1)	(1)
'T. g. sordida'	Tioman	9.24 ± 0.49	0.73 ± 0.03	4.52 ± 0.28	0.72 ± 0.05	2.97 ± 0.15	0.64 ± 0.03	2.01 ± 0.28	1.06 ± 0.13
		8.65–9.96	0.68–0.77	4.05–4.92	0.65–0.81	2.75–3.18	0.59–0.70	1.70–2.52	0.91–1.13
		(10)	(8)	(10)	(10)	(10)	(9)	(8)	(3)
Southern islands									
'T. g. batamana'	Batam	8.60	0.82	4.94	0.80	3.02	0.69	2.45	1.01
			0.79–0.84		0.76–0.84			2.26–2.64	
		(1)	(2)	(1)	(2)	(1)	(1)	(2)	(1)
T. g. castanea	Bintan	10.09	0.86	5.31	0.82	3.44	0.74	2.02	1.17
		10.05–10.13		5.26–5.36	0.81–0.82		0.72–0.75	1.91–2.12	1.10–1.23
		(2)	(1)	(2)	(2)	(1)	(2)	(2)	(2)
'T. g. redacta'	Mapur	9.10	0.70	4.80	0.62	2.56			
		(1)	(1)	(1)	(1)	(1)			
T. glis	Singapore	9.37	0.79	4.73	0.74	2.73	0.74	2.43	1.03
		(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)

Table 1. *Continued*

Taxon	Island	4ML	4MW	4PPL	4PPW	4MPL	4MPW	4DPL	4DPW
Peninsular Malaysia									
'*T. g. wilkinsoni*'		9.03 ± 0.45 8.10–10.15 (33)	0.81 ± 0.04 0.71–0.90 (36)	4.98 ± 0.19 4.52–5.39 (35)	0.75 ± 0.04 0.66–0.84 (37)	3.36 ± 0.17 3.17–3.49 (3)	0.70 ± 0.04 0.58–0.77 (24)	2.51 ± 0.28 1.71–3.12 (27)	1.04 ± 0.07 0.98–1.21 (12)
Western islands									
T. g. glis	Penang	8.86 ± 0.47 7.70–9.80 (23)	0.75 ± 0.03 0.69–0.81 (23)	4.70 ± 0.19 4.32–5.03 (18)	0.70 ± 0.03 0.65–0.76 (23)	3.51 (1)	0.65 ± 0.04 0.60–0.74 (15)	2.45 ± 0.20 2.12–2.75 (13)	0.99 ± 0.11 0.93–1.19 (5)
'*T. g. raviana*'	Adang	9.08 (1)	—	4.90 (1)	—	3.63 (1)	—	2.18 (1)	—
'*T. g. raviana*'	Rawi	9.88 (1)	0.92 (1)	5.32 (1)	0.73 (1)	—	—	—	—
'*T. g. lacernata*'	Langkawi	8.47 (1)	0.86 (1)	4.65 4.56–4.73 (2)	0.70 0.68–0.72 (2)	2.82 2.72–2.92 (2)	0.65 0.62–0.68 (2)	2.02 1.72–2.32 (2)	—
'*T. g. lacernata*'	Terutau	8.39 ± 0.35 8.03–8.84 (4)	0.75 ± 0.07 0.69–0.84 (4)	4.81 ± 0.13 4.66–4.96 (4)	0.71 ± 0.02 0.69–0.73 (4)	2.94 ± 0.25 2.66–3.14 (3)	0.63 0.61–0.64 (2)	1.98 1.81–2.15 (2)	0.92 0.88–0.96 (2)
'*T. g. umbratilis*'	Ta Li Bong	8.80 (1)	0.74 (1)	4.79 (1)	0.69 (1)	3.00 (1)	0.60 (1)	2.01 (1)	1.03 (1)
Eastern islands									
'*T. g. pulonis*'	Aur	8.63 (1)	—	5.37 (1)	0.73 (1)	—	—	2.79 (1)	—
'*T. g. pemangilis*'	Pemanggil	7.80 (1)	0.73 (1)	4.94 (1)	0.75 (1)	—	0.64 (1)	2.37 (1)	0.99 (1)
'*T. g. sordida*'	Tioman	8.39 ± 0.45 7.73–9.09 (7)	0.74 ± 0.05 0.67–0.78 (7)	4.50 ± 0.30 4.09–4.98 (10)	0.69 ± 0.05 0.62–0.77 (10)	2.97 ± 0.23 2.73–3.47 (10)	0.62 ± 0.05 0.56–0.69 (8)	2.24 ± 0.27 1.81–2.75 (8)	0.93 ± 0.06 0.88–1.00 (5)
Southern islands									
'*T. g. batamana*'	Batam	9.00 8.16–9.84 (2)	0.82 0.76–0.87 (2)	4.99 (1)	0.81 0.78–0.83 (2)	3.29 (1)	0.77 (1)	2.49 (1)	1.09 (1)
T. g. castanea	Bintan	8.95 8.61–9.29 (2)	0.88 (1)	5.10 5.08–5.12 (2)	0.79 0.78–0.80 (2)	3.33 (1)	0.77 (1)	2.20 (1)	—
'*T. g. redacta*'	Mapur	8.34 (1)	0.64 (1)	4.59 (1)	0.75 (1)	2.35 (1)	—	—	—
T. glis	Singapore	8.49 (1)	0.75 (1)	4.58 (1)	0.73 (1)	2.85 (1)	0.68 (1)	2.31 (1)	—

Table 1. *Continued*

Taxon	Island	5ML	5MW	5PPL	5PPW	5MPL	5MPW	5DPL	5DPW
Peninsular Malaysia									
'*T. g. wilkinsoni*'		5.82 ± 0.31	0.78 ± 0.07	4.16 ± 0.22	0.71 ± 0.04	—	0.69 ± 0.05	1.95 ± 0.28	0.94 ± 0.05
		5.09–6.65	0.65–0.93	3.77–4.95	0.60–0.78		0.59–0.80	0.99–2.34	0.83–1.09
		(38)	(38)	(35)	(38)		(29)	(33)	(27)
Western islands									
T. g. glis	Penang	5.71 ± 0.32	0.71 ± 0.07	3.95 ± 0.12	0.66 ± 0.04	—	0.61 ± 0.03	2.07 ± 0.24	0.97 ± 0.06
		4.69–6.26	0.54–0.83	3.69–4.14	0.59–0.72		0.57–0.68	1.58–2.51	0.88–1.05
		(22)	(22)	(17)	(21)		(13)	(17)	(11)
'*T. g. raviana*'	Adang	—	0.73	4.23	0.60	2.11	—	2.35	—
			(1)	(1)	(1)	(1)		(1)	
'*T. g. raviana*'	Rawi	6.21	0.93	4.48	0.78	—	0.74	2.19	1.02
		(1)	(1)	(1)	(1)		(1)	(1)	(1)
'*T. g. lacernata*'	Langkawi	5.69	0.79	3.89	0.70	2.10	0.61	1.87	0.81
		5.66–5.72	0.78–0.80	3.72–3.99	0.69–0.71			1.84–1.90	
		(2)	(2)	(2)	(2)	(1)	(1)	(2)	(1)
'*T. g. lacernata*'	Terutau	5.43 ± 0.42	0.70	3.91 ± 0.10	0.66 ± 0.05	2.24	—	1.90 ± 0.28	0.89
		5.10–6.03	0.62–0.78	3.78–4.01	0.61–0.70	2.15–2.33		1.71–2.22	0.88–0.90
		(4)	(2)	(4)	(3)	(2)		(3)	(2)
'*T. g. umbratilis*'	Ta Li Bong	5.53	0.79	3.76	0.73	1.75	0.75	1.39	—
		(1)	(1)	(1)	(1)	(1)	(1)	(1)	
Eastern islands									
'*T. g. pulonis*'	Aur	—	—	4.68	0.75	—	—	2.54	—
				(1)	(1)			(1)	
'*T. g. pemangilis*'	Pemanggil	4.86	0.81	3.73	0.66	—	—	—	—
		(1)	(1)	(1)	(1)				
'*T. g. sordida*'	Tioman	5.36 ± 0.31	0.69 ± 0.09	3.81 ± 0.20	0.67 ± 0.04	2.19 ± 0.12	0.62 ± 0.05	1.90 ± 0.22	0.95 ± 0.03
		4.98–5.98	0.59–0.80	3.49–4.02	0.59–0.73	2.01–2.32	0.54–0.71	1.55–2.18	0.91–0.97
		(9)	(8)	(10)	(9)	(7)	(9)	(7)	(4)
Southern islands									
'*T. g. batamana*'	Batam	5.73	0.70	4.20	0.71	2.27	—	1.85	1.01
		5.30–6.16	0.55–0.85						
		(2)	(2)	(1)	(1)	(1)		(1)	(1)
T. g. castanea	Bintan	5.56	0.79	3.95	0.73	2.09	—	2.11	1.11
					0.71–0.74			1.94–2.28	1.04–1.18
		(1)	(1)	(1)	(2)	(1)		(2)	(2)
'*T. g. redacta*'	Mapur	5.48	0.53	3.84	—	—	—	—	—
		(1)	(1)	(1)					
T. glis	Singapore	5.35	0.64	3.74	0.69	2.27	0.64	2.06	—
		(1)	(1)	(1)	(1)	(1)	(1)	(1)	

To study overall variation among mainland and island populations, we conducted independent principal components analyses (PCA) of variables from the manus and skull. At each stage, we attempted to maximize the number of individuals included in our analyses while minimizing missing data. This situation often resulted in different numbers and combinations of variables in the final models.

To assess morphological similarity among the western, eastern, and southern island populations, we performed hierarchical cluster analyses (UPGMA) on all available skull and manus variables. Phenograms from these analyses are presented with Euclidean distances.

1 *Penang Island* – To assess overall variation between Penang Island and mainland specimens, we performed a PCA on: (a) eight manus variables (1MW, 1PPW, 3MW, 4MW, 3PPW, 4PPW, 5PPW, 5MW) and (b) nine skull variables (six cranial and three mandibular; Table 4). Several variables were excluded from analyses to allow the inclusion of specimens that were missing data due to breakage.
2 *Western islands* – In investigating populations from islands west of the Malay Peninsula, we conducted a PCA on: (a) six manus variables (1ML, 1PPL, 1PPW, 1MW, 3MW, 3PPW) and (b) 12 skull variables (nine cranial and three mandibular; Table 5). We also performed cluster analyses of taxon means that included: (a) all 22 skull variables and (b) a combination of the 22 skull variables and 30 manus variables for a total of 52 skeletal variables.
3 *Eastern islands* – This stage included a PCA of: (a) 10 manus variables (1ML, 1MW, 1PPL, 1PPW, 2ML, 2MW, 3ML, 3PPL, 3PPW, 4PPW) and (b) 13 skull variables (nine cranial and four mandibular; Table 6). Our cluster analyses of taxon means included: (a) all 22 skull variables and (b) a combination of the 22 skull variables and 21 manus variables for a total of 43 skeletal variables.
4 *Southern islands* – Our study of the southern islands included a PCA of: (a) nine manus variables (1ML, 1MW, 1PPL, 1PPW, 2MW, 2PPL, 2PPW, 3PPW, 4PPW) and (b) 12 skull variables (nine cranial and three mandibular; Table 7). The cluster analyses of taxon means included: (a) 19 skull variables (lacrimal breadth [LB], least interorbital breadth [LIB], and braincase breadth [BB] excluded) and (b) a combination of the 19 skull variables and 22 manus variables for a total of 41 skeletal variables.

RESULTS

PENANG ISLAND

Manus

A plot of the first two components from a PCA of eight manus variables from the Penang (*T. glis glis*) and mainland (‘*T. glis wilkinsoni*’) populations is shown in Fig. 2a. The first component (PC1), which represents overall size, accounts for more than 60% of the variation in the model (Table 8). Along this axis, the two populations show some separation, but with wide overlap among the larger individuals in the Penang population and the smallest individuals from the mainland population. The two populations overlap completely on the second component axis (PC2), which accounts for nearly 13% of the variation and represents a contrast between 1PPW and 5MW (Table 8). This PCA included only width variables, and it reflects the average narrower bones of the rays of the island form compared to the mainland population (Table 1). This analysis shows the greatest separation of any of the analyses of these two populations, although the general pattern is the same for PCA of length and width variables from individual rays (not shown), with individuals from Penang Island always among the smallest individuals and often representing a subset of the mainland population.

Skull

This PCA included nine of the 22 skull variables. Factor 1 is a size vector that accounts for more than 68% of the variation. Factor 2 represents a contrast between mandibular condyle width (MCW) and two negatively weighted length variables (condylonasal length [CNL] and condylopremaxillary length [CPL]); the second factor explains more than 9% of the variation (Table 4). In the plot of these two factors (Fig. 2b), the populations from the mainland and Penang Island overlap almost completely on PC2. Along PC1, there is overlap between the two populations, but most of the mainland individuals plot in positive morphospace, whereas all of the Penang individuals plot in negative morphospace, demonstrating the smaller size of the latter relative to the former.

WESTERN ISLANDS

Manus

A plot of scores on the first two axes of a PCA of six variables from populations from the mainland, Penang, and the other western islands is shown in Fig. 3a. The first principle component, accounting for more than 43% of the variation, represents size,

Table 2. Measurement descriptions (and abbreviations) following Sargis *et al.* (2013b, 2014a,b)

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

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.

although width variables more greatly influence this component than do length variables (Table 9). Most individuals from islands plot low on this axis, whereas those from the mainland generally plot higher, although there is considerable overlap among the largest island individuals and the smallest mainland individuals. One Penang specimen and another from Butang plot particularly high on this axis, indicating that they are larger than most other island individuals. The second component accounts for about 23% of the variation and represents a contrast of 3PPW with 1ML and 1PPL (Table 9). Although individuals from the islands overlap extensively on this axis, Penang individuals generally plot lower, whereas individuals from the other islands all plot higher. This suggests the potential for variation in the proportions of individual bones of the hand among island populations.

Skull

The PCA for this island group included 12 of the 22 variables. The first factor represents size and is responsible for nearly 72% of the variation. The second factor, accounting for more than 10% of the variation, represents maxillary toothrow length (MTL) contrasted with mandibular condyle width (MCW), mandibular condyle height (MCH), and zygomatic breadth (ZB) (Table 5). The plot of these two factors is shown in Fig. 3b. For PC1, most of the mainland individuals plot in the two right quadrants, whereas nearly all of the island individuals fall into the two left quadrants, indicating smaller body size on islands. Only two individuals each from the Butang Islands (‘*T. g. raviana*’) and Langkawi-Terutau (‘*T. g. lacernata*’) plot in the upper right quadrant with mainland individuals. On PC2, only the population from the Butang Islands is restricted to positive morphospace.

Table 3. Craniodental measurements (mm) from selected populations of *Tupaia glis*. Statistics are mean ± standard deviation (SD), range, and sample size in parentheses. See Table 2 for measurement abbreviations and descriptions

Taxon	Island	1) CPL	2) CIL	3) UTL	4) MTL	5) EPL	6) PPL	7) EB
Peninsular Malaysia								
'*Tupaia g. wilkinsoni*'		48.42 ± 1.29 45.25–51.57 (82)	47.74 ± 1.23 44.51–50.07 (75)	27.38 ± 0.68 25.80–28.87 (74)	18.82 ± 0.48 17.89–19.94 (73)	35.35 ± 1.06 32.85–38.00 (77)	29.21 ± 0.84 27.33–31.24 (85)	11.67 ± 0.51 10.71–12.60 (56)
Western islands								
Tupaia g. glis	Penang	46.39 ± 0.93 44.45–48.36 (21)	45.91 ± 0.93 44.15–47.82 (17)	26.44 ± 0.57 25.59–27.85 (15)	18.20 ± 0.50 17.09–18.92 (19)	34.02 ± 0.62 33.22–35.66 (16)	27.91 ± 0.59 26.63–28.99 (19)	10.96 ± 0.53 9.72–11.91 (13)
'*Tupaia g. raviana*'	Adang	46.89 ± 1.27 45.20–48.20 (4)	46.75 (1)	26.75 ± 0.39 26.47–27.02 (2)	18.44 ± 0.33 18.02–18.79 (5)	33.55 ± 0.96 32.25–34.53 (4)	27.92 ± 0.49 27.24–28.58 (5)	10.64 ± 0.45 10.09–11.14 (4)
'*Tupaia g. raviana*'	Rawi	46.09 ± 0.06 46.04–46.13 (2)	45.37 ± 0.18 45.24–45.50 (2)	25.75 ± 0.19 25.61–25.88 (2)	17.67 ± 0.11 17.55–17.76 (3)	32.98 ± 0.04 32.95–33.01 (2)	27.30 ± 0.15 27.14–27.44 (3)	11.18 ± 0.17 11.06–11.30 (2)
'*Tupaia g. lacernata*'	Langkawi	46.78 ± 0.78 45.40–48.02 (21)	46.24 ± 0.76 44.89–47.52 (20)	26.85 ± 0.52 25.75–27.61 (20)	18.23 ± 0.46 17.27–19.33 (19)	34.20 ± 0.65 33.38–35.31 (14)	28.30 ± 0.61 27.05–29.37 (23)	11.52 ± 0.83 9.77–12.83 (12)
'*Tupaia g. lacernata*'	Terutau	45.41 ± 0.63 44.31–46.54 (17)	44.95 ± 0.62 43.77–45.82 (16)	26.15 ± 0.39 25.18–26.86 (17)	17.99 ± 0.43 17.42–18.90 (20)	33.38 ± 0.43 32.72–34.17 (17)	27.71 ± 0.50 26.45–28.29 (19)	11.11 ± 0.33 10.58–11.74 (15)
'*Tupaia g. umbratilis*'	Ta Li Bong	45.75 ± 0.83 44.36–46.87 (6)	45.07 ± 0.74 43.92–45.97 (6)	26.37 ± 0.41 25.63–26.69 (6)	17.86 ± 0.41 17.18–18.24 (6)	34.07 ± 0.93 32.53–34.84 (5)	27.90 ± 0.58 27.07–28.44 (6)	11.60 ± 0.52 10.82–12.10 (5)
Eastern islands								
'*Tupaia g. pulonis*'	Aur	47.93 ± 0.37 47.37–48.48 (6)	47.34 ± 0.47 46.82–47.75 (3)	26.90 ± 0.22 26.66–27.10 (3)	18.62 ± 0.19 18.36–18.82 (4)	35.30 ± 0.36 34.59–35.69 (7)	28.70 ± 0.39 28.14–29.09 (7)	12.48 ± 0.41 11.94–13.07 (5)
'*Tupaia g. pemangilis*'	Pemanggil	46.72 ± 1.28 44.97–48.05 (4)	45.74 ± 2.27 44.13–47.34 (2)	26.36 ± 1.46 25.32–27.39 (2)	17.70 (1)	34.31 ± 1.08 32.85–35.47 (4)	28.06 ± 1.03 26.96–28.99 (3)	11.51 ± 0.88 10.88–12.13 (2)
'*Tupaia g. sordida*'	Tioman	45.76 ± 0.93 43.56–47.03 (21)	45.07 ± 0.87 43.16–46.30 (19)	25.78 ± 0.48 24.97–26.63 (14)	17.95 ± 0.42 17.13–18.56 (14)	33.39 ± 0.97 31.75–34.78 (17)	27.49 ± 0.69 26.24–28.47 (19)	11.29 ± 0.72 10.48–12.55 (11)

Table 3. *Continued*

Taxon	Island	1) CPL	2) CIL	3) UTL	4) MTL	5) EPL	6) PPL	7) EB
Southern islands								
'*Tupaia g. batamana*'	Batam	49.24 ± 1.14 46.67–51.33 (17)	48.78 ± 1.15 46.20–51.12 (17)	28.18 ± 0.69 27.09–29.62 (16)	19.56 ± 0.59 18.73–20.90 (16)	36.05 ± 0.94 34.34–37.58 (15)	29.74 ± 0.80 28.12–31.25 (17)	11.74 ± 0.35 11.21–12.43 (14)
Tupaia g. castanea	Bintan	49.86 ± 0.65 48.89–50.75 (6)	49.19 ± 0.62 48.26–50.01 (5)	27.78 ± 0.48 27.14–28.45 (5)	19.10 ± 0.48 18.37–19.83 (6)	36.43 ± 0.78 34.98–37.33 (6)	29.77 ± 0.61 28.96–30.58 (6)	12.15 ± 0.36 11.68–12.59 (5)
'*Tupaia g. redacta*'	Mapur	47.24 (1)	46.64 (1)	25.73 (1)	17.97 (1)	34.13 (1)	28.00 (1)	11.62 (1)
Tupaia glis	Singapore	48.19 ± 1.23 45.76–50.36 (16)	47.73 ± 1.34 45.17–50.01 (15)	27.79 ± 0.70 26.39–28.85 (18)	19.07 ± 0.48 18.01–19.83 (20)	34.78 ± 0.97 32.97–36.55 (16)	29.40 ± 0.73 27.96–30.44 (17)	11.12 ± 0.46 10.41–12.18 (13)

Taxon	Island	8) MB	9) LB	10) LIB	11) ZB	12) BB	13) LPL
Peninsular Malaysia							
'*Tupaia g. wilkinsoni*'		18.19 ± 0.51 17.13–19.43 (78)	19.12 ± 0.78 17.54–20.75 (76)	14.65 ± 0.73 13.10–16.46 (88)	25.76 ± 1.13 22.76–28.29 (81)	19.59 ± 0.42 18.57–20.44 (81)	51.94 ± 1.34 48.98–55.05 (80)
Western islands							
Tupaia g. glis	Penang	17.62 ± 0.47 17.00–18.76 (19)	18.34 ± 0.48 17.41–19.27 (19)	13.84 ± 0.44 12.90–14.60 (21)	24.70 ± 0.63 23.77–25.69 (20)	18.91 ± 0.44 17.84–19.88 (21)	49.86 ± 0.99 48.05–51.25 (18)
'*Tupaia g. raviana*'	Adang	18.30 ± 0.35 18.05–18.54 (2)	18.39 ± 0.25 18.14–18.63 (4)	14.19 ± 0.15 14.02–14.34 (5)	25.33 ± 0.49 24.85–26.15 (5)	18.65 ± 0.30 18.37–18.97 (3)	50.11 ± 1.96 48.21–52.12 (3)
'*Tupaia g. raviana*'	Rawi	17.62 ± 0.07 17.57–17.67 (2)	18.84 ± 0.58 18.44–19.50 (3)	14.66 ± 0.49 14.28–15.21 (3)	25.24 ± 0.50 24.84–25.80 (3)	18.66 ± 0.07 18.61–18.71 (2)	49.43 ± 0.16 49.31–49.54 (2)
'*Tupaia g. lacernata*'	Langkawi	17.84 ± 0.35 17.14–18.39 (19)	18.51 ± 0.54 17.07–19.38 (24)	14.14 ± 0.52 13.23–15.28 (23)	24.77 ± 0.73 23.31–26.00 (20)	18.72 ± 0.31 18.07–19.54 (20)	50.27 ± 0.80 49.01–51.25 (19)
'*Tupaia g. lacernata*'	Terutau	17.79 ± 0.31 17.35–18.52 (20)	18.16 ± 0.41 17.53–18.84 (17)	13.72 ± 0.53 12.48–14.46 (22)	24.32 ± 0.63 23.26–25.73 (19)	18.49 ± 0.40 17.79–19.09 (17)	49.28 ± 0.72 47.74–50.34 (15)
'*Tupaia g. umbratilis*'	Ta Li Bong	17.91 ± 0.47 17.14–18.35 (5)	17.63 ± 0.34 17.18–17.99 (6)	13.54 ± 0.23 13.29–13.89 (6)	24.10 ± 0.22 23.71–24.31 (6)	19.01 ± 0.16 18.89–19.30 (5)	49.16 ± 0.75 48.03–50.16 (6)

Table 3. *Continued*

Taxon	Island	8) MB	9) LB	10) LIB	11) ZB	12) BB	13) LPL
Eastern islands							
‘*Tupaia g. pulonis*’	Aur	18.78 ± 0.32 18.39–19.16 (5)	19.80 ± 0.40 19.46–20.52 (7)	15.40 ± 0.39 15.01–15.99 (7)	26.50 ± 0.68 25.55–27.29 (6)	19.53 ± 0.31 19.16–19.95 (6)	51.64 ± 0.51 51.01–52.11 (5)
‘*Tupaia g. pemangilis*’	Pemanggil	18.02 ± 0.72 17.18–18.63 (4)	18.12 ± 0.84 17.17–18.78 (3)	14.05 ± 0.84 12.93–14.81 (4)	24.82 ± 1.89 23.48–26.15 (2)	19.22 ± 0.46 18.80–19.64 (4)	50.07 ± 1.31 48.14–51.03 (4)
‘*Tupaia g. sordida*’	Tioman	17.67 ± 0.40 16.99–18.40 (21)	18.29 ± 0.59 17.47–19.51 (18)	14.28 ± 0.63 13.44–15.37 (22)	24.89 ± 0.74 23.74–26.62 (21)	19.11 ± 0.35 18.31–19.64 (21)	48.90 ± 0.97 47.08–50.21 (21)
Southern islands							
‘*Tupaia g. batamana*’	Batam	18.40 ± 0.45 17.58–19.28 (17)	19.78 ± 0.53 19.19–20.94 (9)	14.84 ± 0.35 14.26–15.44 (17)	26.91 ± 0.86 25.80–28.69 (16)	19.40 ± 0.38 18.79–20.20 (17)	52.80 ± 1.14 50.40–54.88 (17)
Tupaia g. castanea	Bintan	18.67 ± 0.47 17.89–19.17 (7)	19.62 ± 0.57 18.59–20.17 (7)	15.17 ± 0.55 14.38–15.79 (6)	26.36 ± 0.55 25.48–27.09 (6)	19.48 ± 0.53 18.73–20.33 (7)	53.62 ± 0.68 52.69–54.60 (6)
‘*Tupaia g. redacta*’	Mapur	18.26 (1)			24.94 (1)		50.76 (1)
Tupaia glis	Singapore	18.01 ± 0.32 17.20–18.47 (15)	18.96 ± 0.67 18.00–20.78 (16)	14.48 ± 0.49 13.78–15.43 (18)	25.18 ± 0.80 23.77–26.95 (15)	19.18 ± 0.44 18.38–19.83 (18)	51.39 ± 1.29 49.06–53.24 (15)

Taxon	Island	14) CNL	15) PBPL	16) LTPL	17) LCH	18) MH	19) MCH
Peninsular Malaysia							
‘*Tupaia g. wilkinsoni*’		46.74 ± 1.41 44.01–51.32 (82)	35.39 ± 0.97 33.09–37.84 (88)	24.29 ± 0.87 22.35–26.45 (88)	12.67 ± 0.44 11.71–13.50 (78)	13.88 ± 0.72 12.19–15.48 (86)	9.13 ± 0.54 8.04–10.29 (89)
Western islands							
Tupaia g. glis	Penang	44.80 ± 0.82 42.88–46.44 (20)	34.01 ± 0.75 32.53–35.59 (20)	23.38 ± 0.59 21.84–24.74 (19)	11.99 ± 0.27 11.49–12.39 (18)	13.06 ± 0.51 12.14–14.08 (22)	8.80 ± 0.38 8.05–9.51 (22)
‘*Tupaia g. raviana*’	Adang	45.27 ± 1.30 43.40–46.40 (4)	34.08 ± 0.78 32.89–35.08 (5)	23.45 ± 0.64 22.41–24.19 (5)	12.34 ± 0.07 12.28–12.42 (3)	14.31 ± 0.18 14.05–14.52 (5)	9.38 ± 0.17 9.16–9.56 (5)
‘*Tupaia g. raviana*’	Rawi	43.91 ± 0.09 43.84–43.97 (2)	33.34 ± 0.11 33.21–33.40 (3)	22.66 ± 0.08 22.58–22.74 (3)	12.04 ± 0.32 11.81–12.26 (2)	13.20 ± 0.55 12.81–13.83 (3)	8.72 ± 0.46 8.19–9.01 (3)

Table 3. *Continued*

Taxon	Island	14) CNL	15) PBPL	16) LTPL	17) LCH	18) MH	19) MCH
'*Tupaia g. lacernata*'	Langkawi	45.06 ± 0.78 43.96–46.53 (21)	34.25 ± 0.69 33.03–35.34 (23)	23.55 ± 0.63 22.46–24.80 (24)	12.24 ± 0.33 11.58–13.05 (20)	13.43 ± 0.53 12.31–14.51 (22)	8.92 ± 0.35 8.34–9.60 (24)
'*Tupaia g. lacernata*'	Terutau	43.55 ± 0.76 42.08–44.76 (18)	33.58 ± 0.52 32.44–34.40 (19)	22.73 ± 0.51 21.58–23.45 (18)	12.03 ± 0.24 11.63–12.43 (18)	13.20 ± 0.51 12.25–14.07 (21)	8.69 ± 0.38 7.82–9.43 (22)
'*Tupaia g. umbratilis*'	Ta Li Bong	44.00 ± 0.87 42.92–45.20 (6)	33.46 ± 0.53 33.00–34.34 (6)	22.76 ± 0.54 22.29–23.66 (6)	11.69 ± 0.14 11.47–11.85 (5)	12.87 ± 0.44 12.04–13.20 (6)	8.71 ± 0.33 8.21–9.11 (6)
Eastern islands							
'*Tupaia g. pulonis*'	Aur	46.03 ± 0.48 45.25–46.71 (6)	35.07 ± 0.31 34.52–35.44 (7)	24.10 ± 0.13 23.84–24.24 (7)	12.45 ± 0.21 12.16–12.66 (5)	13.57 ± 0.25 13.30–13.98 (7)	8.65 ± 0.12 8.53–8.81 (7)
'*Tupaia g. pemangilis*'	Pemanggil	44.61 ± 1.47 43.35–46.25 (4)	34.13 ± 0.98 32.76–35.10 (4)	23.04 ± 0.75 21.96–23.66 (4)	12.46 ± 0.31 12.00–12.68 (4)	13.12 ± 0.59 12.24–13.55 (4)	8.58 ± 0.39 8.00–8.84 (4)
'*Tupaia g. sordida*'	Tioman	44.01 ± 0.99 41.91–45.49 (21)	33.31 ± 0.76 31.91–34.72 (21)	22.68 ± 0.81 21.08–24.15 (20)	12.21 ± 0.36 11.65–13.06 (21)	13.26 ± 0.60 12.31–14.52 (21)	8.70 ± 0.51 7.82–9.49 (21)
Southern islands							
'*Tupaia g. batamana*'	Batam	47.61 ± 1.03 45.30–49.13 (17)	36.19 ± 0.82 34.45–37.74 (17)	25.04 ± 0.65 24.15–26.31 (13)	12.62 ± 0.44 11.95–13.25 (17)	14.32 ± 0.55 13.48–15.20 (16)	9.45 ± 0.43 8.81–10.36 (16)
Tupaia g. castanea	Bintan	48.11 ± 1.06 46.09–49.07 (7)	36.31 ± 0.50 35.44–36.90 (6)	25.29 ± 0.49 24.46–26.01 (7)	12.93 ± 0.26 12.43–13.22 (7)	14.47 ± 0.63 13.72–15.39 (7)	9.70 ± 0.62 8.83–10.48 (7)
'*Tupaia g. redacta*'	Mapur	45.78 (1)	34.64 (1)	23.34 (1)	11.98 (1)	14.07 (1)	9.45 (1)
Tupaia glis	Singapore	46.44 ± 1.25 43.96–48.15 (17)	35.57 ± 0.92 33.89–36.99 (19)	24.38 ± 0.82 22.80–25.51 (18)	12.40 ± 0.38 11.83–13.27 (16)	13.26 ± 0.50 12.24–14.42 (19)	8.86 ± 0.41 7.96–9.50 (20)

Table 3. *Continued*

Taxon	Island	20) MCW	21) MCIL	22) LTL
Peninsular Malaysia				
'*Tupaia g. wilkinsoni*'		3.31 ± 0.25 2.50–3.87 (90)	38.45 ± 1.02 35.71–40.84 (85)	25.82 ± 0.58 24.35–27.22 (83)
Western islands				
Tupaia g. glis	Penang	3.17 ± 0.25 2.77–3.55 (22)	36.72 ± 0.71 35.16–37.61 (17)	24.84 ± 0.50 23.79–25.59 (17)
'*Tupaia g. raviana*'	Adang	3.24 ± 0.15 3.12–3.50 (5)	37.39 ± 0.49 36.90–38.00 (4)	24.92 ± 0.29 24.62–25.20 (4)
'*Tupaia g. raviana*'	Rawi	3.05 ± 0.25 2.91–3.34 (3)	36.24 (1)	
'*Tupaia g. lacernata*'	Langkawi	3.09 ± 0.19 2.80–3.46 (25)	37.09 ± 0.68 35.65–38.11 (23)	25.25 ± 0.45 24.52–26.08 (23)
'*Tupaia g. lacernata*'	Terutau	3.05 ± 0.23 2.59–3.35 (22)	36.00 ± 0.53 34.95–36.77 (15)	24.51 ± 0.36 23.90–24.89 (13)
'*Tupaia g. umbratilis*'	Ta Li Bong	3.00 ± 0.23 2.59–3.27 (6)	36.30 ± 0.49 35.45–36.89 (6)	24.98 ± 0.40 24.21–25.27 (6)
Eastern islands				
'*Tupaia g. pulonis*'	Aur	3.14 ± 0.09 2.97–3.23 (7)	38.35 ± 0.36 37.68–38.69 (6)	25.78 ± 0.39 25.42–26.35 (5)
'*Tupaia g. pemangilis*'	Pemanggil	2.99 ± 0.14 2.81–3.14 (4)	37.18 ± 1.09 35.68–38.30 (4)	24.82 ± 0.69 24.04–25.37 (3)
'*Tupaia g. sordida*'	Tioman	3.09 ± 0.18 2.86–3.46 (21)	36.38 ± 0.83 34.83–37.74 (20)	24.52 ± 0.55 23.77–25.86 (18)
Southern islands				
'*Tupaia g. batamana*'	Batam	3.41 ± 0.30 2.97–3.97 (17)	39.13 ± 0.95 37.12–41.00 (16)	26.46 ± 0.63 25.27–27.69 (16)

Table 3. *Continued*

Taxon	Island	20) MCW	21) MCIL	22) LTL
Tupaia g. castanea	Bintan	3.48 ± 0.17 3.28–3.78 (7)	39.22 ± 0.87 37.98–40.12 (6)	26.23 ± 0.66 25.37–26.98 (4)
'Tupaia g. redacta'	Mapur	3.20 (1)	37.47 (1)	23.99 (1)
Tupaia glis	Singapore	3.19 ± 0.19 2.86–3.57 (19)	38.35 ± 0.97 36.34–39.97 (18)	26.27 ± 0.59 24.98–27.07 (18)

Table 4. Component loadings and eigenvalues from principal components analysis of nine variables from the skull of populations from the Malay Peninsula and Penang Island (Fig. 2b)

	Axis	
	1	2
(1) CPL	0.900	**−0.308**
(10) LIB	0.854	0.118
(11) ZB	0.861	0.225
(12) BB	0.681	−0.289
(14) CNL	0.845	**−0.388**
(15) PBPL	0.917	−0.214
(18) MH	0.862	0.116
(19) MCH	0.777	0.260
(20) MCW	0.698	**0.575**
Eigenvalues	6.135	0.851
Percent of total		
Variance explained	68.171	9.454

Abbreviations for variables are defined in Table 2. Loadings in bold type are discussed in the text.

Table 5. Component loadings and eigenvalues from principal components analysis of 12 variables from the skull of populations from the Malay Peninsula and the western islands (Fig. 3b)

	Axis	
	1	2
(1) CPL	0.944	−0.259
(4) MTL	0.754	**−0.493**
(6) PPL	0.914	−0.288
(9) LB	0.830	0.274
(10) LIB	0.827	0.291
(11) ZB	0.852	**0.321**
(14) CNL	0.898	−0.298
(15) PBPL	0.957	−0.193
(16) LTPL	0.942	−0.210
(18) MH	0.788	0.280
(19) MCH	0.707	**0.357**
(20) MCW	0.707	**0.446**
Eigenvalues	8.624	1.231
Percent of total		
Variance explained	71.865	10.254

Abbreviations for variables are defined in Table 2. Loadings in bold type are discussed in the text.

Cluster analyses

We carried out two cluster analyses using taxon means of the: (a) 22 skull variables; and (b) 52 combined skull and manus variables. Because the two

Table 6. Component loadings and eigenvalues from principal components analysis of 13 variables from the skull of populations from the Malay Peninsula and the eastern islands (Fig. 4b)

	Axis	
	1	2
(1) CPL	0.958	−0.249
(5) EPL	0.960	−0.161
(6) PPL	0.930	−0.276
(9) LB	0.791	0.293
(10) LIB	0.720	**0.340**
(12) BB	0.631	0.158
(14) CNL	0.895	−0.271
(15) PBPL	0.964	−0.181
(16) LTPL	0.956	−0.177
(18) MH	0.797	**0.358**
(19) MCH	0.728	**0.452**
(20) MCW	0.700	**0.377**
(21) MCIL	0.933	−0.232
Eigenvalues	9.415	1.057
Percent of total variance explained	72.419	8.134

Abbreviations for variables are defined in Table 2. Loadings in bold type are discussed in the text.

Table 7. Component loadings and eigenvalues from principal components analysis of 12 variables from the skull of populations from the Malay Peninsula and the southern islands (Fig. 5b)

	Axis	
	1	2
(1) CPL	0.959	−0.217
(5) EPL	0.953	−0.125
(6) PPL	0.905	**−0.316**
(8) MB	0.689	0.232
(13) LPL	0.970	−0.087
(14) CNL	0.882	−0.205
(15) PBPL	0.936	−0.252
(16) LTPL	0.930	−0.242
(17) LCH	0.687	0.177
(18) MH	0.752	**0.525**
(19) MCH	0.693	**0.600**
(20) MCW	0.669	**0.369**
Eigenvalues	8.547	1.192
Percent of total Variance explained	71.224	9.934

Abbreviations for variables are defined in Table 2. Loadings in bold type are discussed in the text.

Table 8. Component loadings and eigenvalues from principal components analysis of eight variables from the manus of populations from the Malay Peninsula and Penang Island (Fig. 2a)

	Axis	
	1	2
3MW	0.906	0.087
4MW	0.889	−0.223
3PPW	0.848	0.167
4PPW	0.842	0.078
5PPW	0.831	−0.258
5MW	0.682	**−0.564**
1MW	0.585	0.249
1PPW	0.521	**0.701**
Eigenvalues	4.810	1.029
Percent of total Variance explained	60.1	12.9

Abbreviations for variables are defined in 'Materials and Methods'. Loadings in bold type are discussed in the text.

analyses yielded the same topology, only the dendrogram from the former is shown in Fig. 3c. In both analyses, the population from Langkawi-Terutau ('*T. g. lacernata*') is most similar to the one from Ta Li Bong ('*T. g. umbratilis*'), and the one from Penang (*T. glis glis*) is the next most similar. The population from the Butang Islands ('*T. g. raviana*'), the most geographically isolated of the western islands (Fig. 1), is more similar morphologically to the other island populations than it is to the mainland population (Fig. 3c).

Eastern islands

Manus

A plot of scores on the first two axes of a PCA of ten variables from populations from the mainland and the eastern islands is shown in Fig. 4a. The first principle component, representing size, accounts for about half of the total variance (Table 10). With the exception of the first metacarpal and in contrast to the patterns seen in the previous analyses (see above), length variables influence this axis more than width variables. On this axis, most of the mainland specimens have positive scores (larger hands), whereas all of the island specimens have negative scores (smaller hands). There is overlap between the smallest mainland specimens and the largest island specimens, but most of this difference is a result of the single individual from Aur Island, which is the largest island specimen in this analysis. The second component, accounting for < 15% of the variance, represents a contrast between several width (3PPW, 1MD, 4PPW) and length (1ML, 1PPL) variables (Table 10). This component does little to discriminate any of the populations.

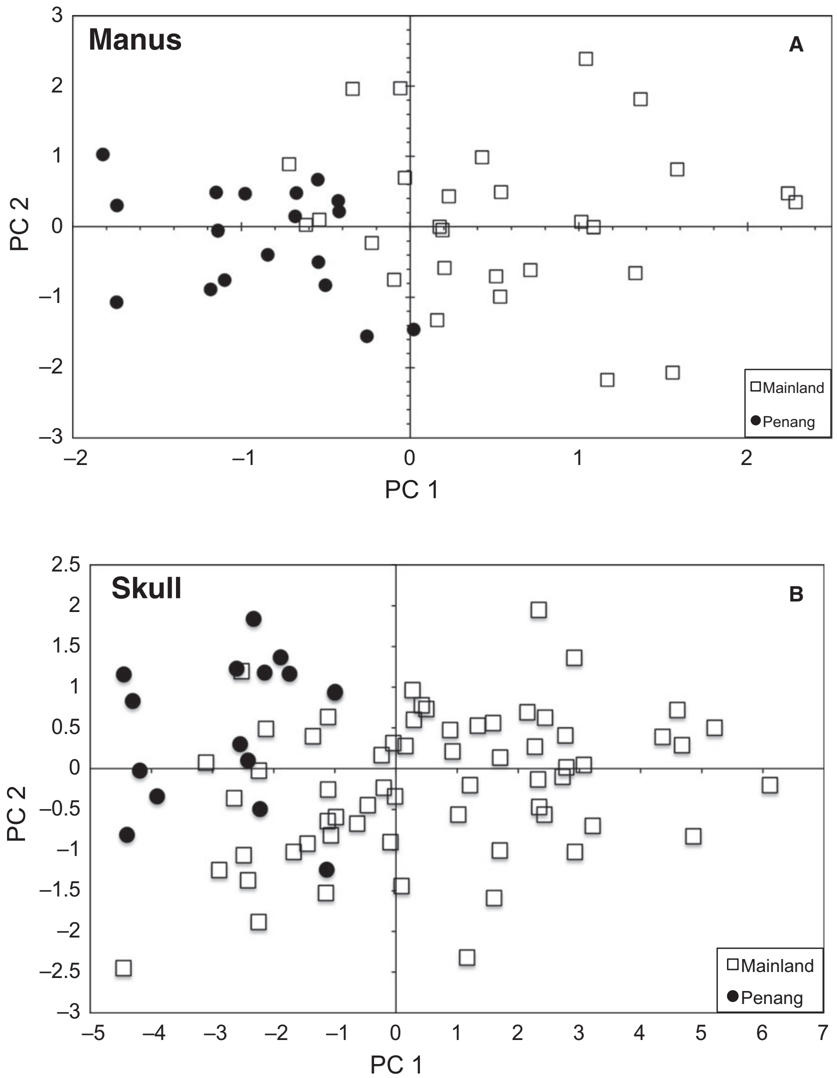

Figure 2. Plots illustrating results of principal components analyses (PCA) comparing *T. glis* individuals from the Malay Peninsula to those from Penang Island. A, Plot of factor scores on the first two axes from PCA of eight hand variables (Table 8). B, Plot of factor scores on the first two axes from PCA of six cranial and three mandibular variables (Table 4). *T. glis* individuals from Penang Island are generally smaller than those from the mainland.

Skull

For these islands, 13 of the 22 variables were included in the PCA. Factor 1 is a size vector representing more than 72% of the variation. Factor 2 explains more than 8% of the variation and represents mandibular condyle height (MCH), mandibular condyle width (MCW), mandibular height (MH), and least interorbital breadth (LIB) (Table 6). In the plot of these two factors (Fig. 4b), most of the mainland individuals plot in positive morphospace along PC1, but almost all of the island individuals plot in negative morphospace, signifying smaller body size in the island populations; only three individuals from Aur Island ('*T. g. pulonis*') plot in the two right quadrants. The island populations are relatively well separated along PC2, with individuals from Pemanggil Island ('*T. g. pemangilis*') restricted to the lower left quadrant, those from Tioman Island ('*T. g. sordida*') mostly in the upper left quadrant, and those from Aur Island overlapping the other two in the centre.

Cluster analyses

Our two cluster analyses of taxon means included: (a) 22 skull variables; and (b) 43 combined skull and manus variables. Both produced the same

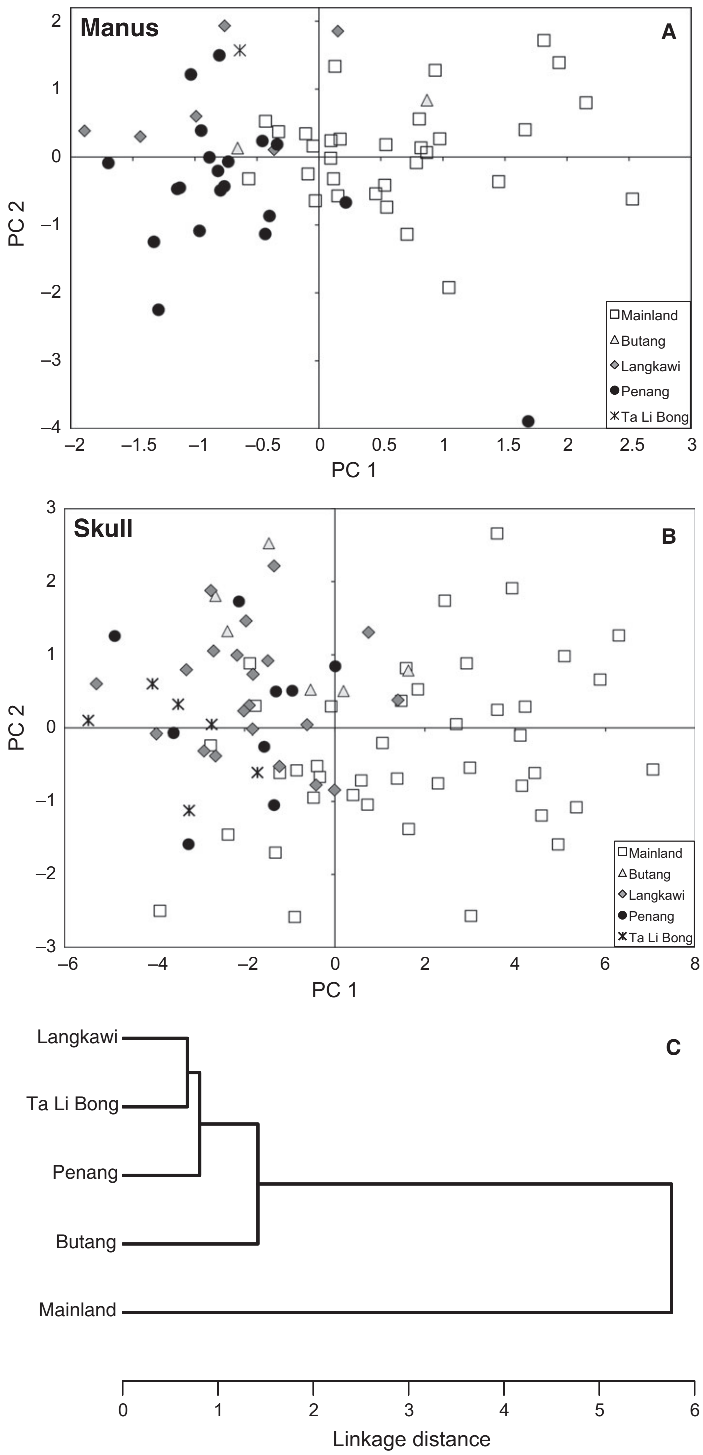

Figure 3. Plots illustrating results of analyses comparing *T. glis* individuals from the Malay Peninsula to those from the western islands. A, Plot of factor scores on the first two axes from PCA of six hand variables (Table 9). B, Plot of factor scores on the first two axes from PCA of nine cranial and three mandibular variables (Table 5). *T. glis* individuals from the western islands are generally smaller than those from the mainland. C, Phenogram from cluster analysis of 22 skull variables. The island populations are more similar to one another than any is to the mainland population. Butang refers to Adang and Rawi Islands ('*T. glis raviana*'); Langkawi refers to Langkawi and Terutau Islands ('*T. glis lacernata*').

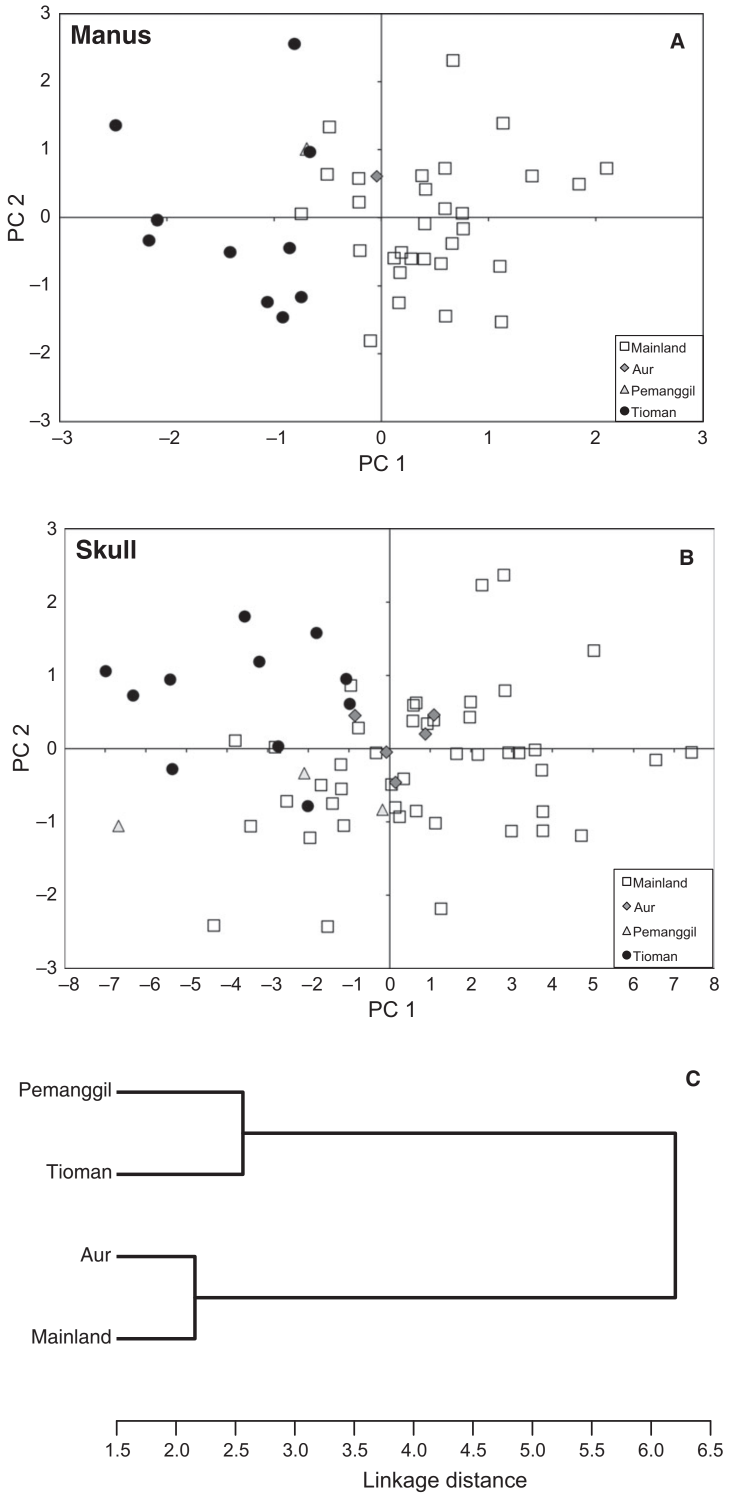

Figure 4. Plots illustrating results of analyses comparing *T. glis* individuals from the Malay Peninsula to those from the eastern islands. A, Plot of factor scores on the first two axes from PCA of ten hand variables (Table 10). B, Plot of factor scores on the first two axes from PCA of nine cranial and four mandibular variables (Table 6). *T. glis* individuals from the eastern islands are generally smaller than those from the mainland. C, Phenogram from cluster analysis of 22 skull variables. The population from Aur Island is more similar to the mainland population than to the other two island populations.

topology, so only the dendrogram from the former is shown in Fig. 4c. In both analyses, the population from Pemanggil (‘*T. g. pemangilis*’) is most similar to that from Tioman (‘*T. g. sordida*’). Surprisingly, the population from Aur (‘*T. g. pulonis*’) is more similar to the mainland population than it is to the other island populations (Fig. 4c).

SOUTHERN ISLANDS

Manus

A plot of scores on the first two axes of a PCA of nine variables from populations from the mainland, Singapore, and the southern islands is shown in Fig. 5a. Most of the variables contribute substantially to PC1, which generally represents size, although it is most influenced by widths of the proximal phalanges. This component accounts for more than 41% of the total variance (Table 11). The second component, accounting for nearly 17% of the variance, represents three negatively weighted length variables (1PPL, 2PPL, 1ML) contrasted with a width variable (2MW) (Table 11). Neither component clearly discriminates any of the island populations from the mainland population, and the specimens are intermingled in morphospace. The specimens from Batam and Bintan are larger than the average for the mainland population, with positive scores along the PC1 axis, whereas the population from Mapur is represented by the smallest individual in the analysis. The individual from Singapore is also among the smaller specimens, but it is barely distinguishable from the mainland population.

Table 9. Component loadings and eigenvalues from principal components analysis of six variables from the manus of populations from the Malay Peninsula and the western islands (Fig. 3a).

	Axis	
	1	2
3MW	0.843	0.239
3PPW	0.734	**0.434**
1MW	0.682	0.118
1PPW	0.627	0.198
1PPL	0.563	**−0.676**
1ML	0.432	**−0.796**
Eigenvalues	2.612	1.389
Percent of total Variance explained	43.5	23.2

Abbreviations for variables are defined in ‘Materials and Methods’. Loadings in bold type are discussed in the text.

Skull

This PCA included 12 of the 22 skull variables. The first factor represents size and accounts for over 71% of the variation. The second factor explains nearly 10% of the variation, and it represents mandibular condyle height (MCH), mandibular height (MH), and mandibular condyle width (MCW) contrasted with palato—premaxillary length (PPL) (Table 7). The plot of these two factors is shown in Fig. 5b. On PC1, the mainland individuals are nearly equally divided between positive and negative morphospace. All of the individuals from Bintan Island (‘*T. g. castanea*’) and most of the individuals from Batam Island (‘*T. g. batamana*’) plot in positive morphospace, whereas the single individual from Mapur Island (‘*T. g. redacta*’) and most of the individuals from Singapore fall in negative morphospace. Along PC2, the mainland, Batam, and Singapore individuals are nearly equally divided between the upper and lower quadrants, whereas the single Mapur individual and most of the Bintan individuals plot in the upper two quadrants.

Cluster analyses

The two cluster analyses of taxon means included: (a) 19 skull variables; and (b) 41 combined skull and manus variables. Both yielded the same topology, so only the dendrogram from the former is shown in Fig. 5c. The dendrogram shows that the population from Batam (‘*T. g. batamana*’) is most similar to that from the adjacent island of Bintan (‘*T. g. castanea*’).

Table 10. Component loadings and eigenvalues from principal components analysis of ten variables from the manus of populations from the Malay Peninsula and the eastern islands (Fig. 4a).

	Axis	
	1	2
3PPL	0.859	−0.209
2ML	0.759	−0.315
1PPL	0.740	**−0.403**
3ML	0.734	−0.288
3PPW	0.721	**0.519**
4PPW	0.717	**0.476**
1PPW	0.713	0.177
2MW	0.698	0.314
1ML	0.692	**−0.435**
1MD	0.328	**0.514**
Eigenvalues	5.017	1.468
Percent of total Variance explained	50.2	14.7

Abbreviations for variables are defined in ‘Materials and Methods’. Loadings in bold type are discussed in the text.

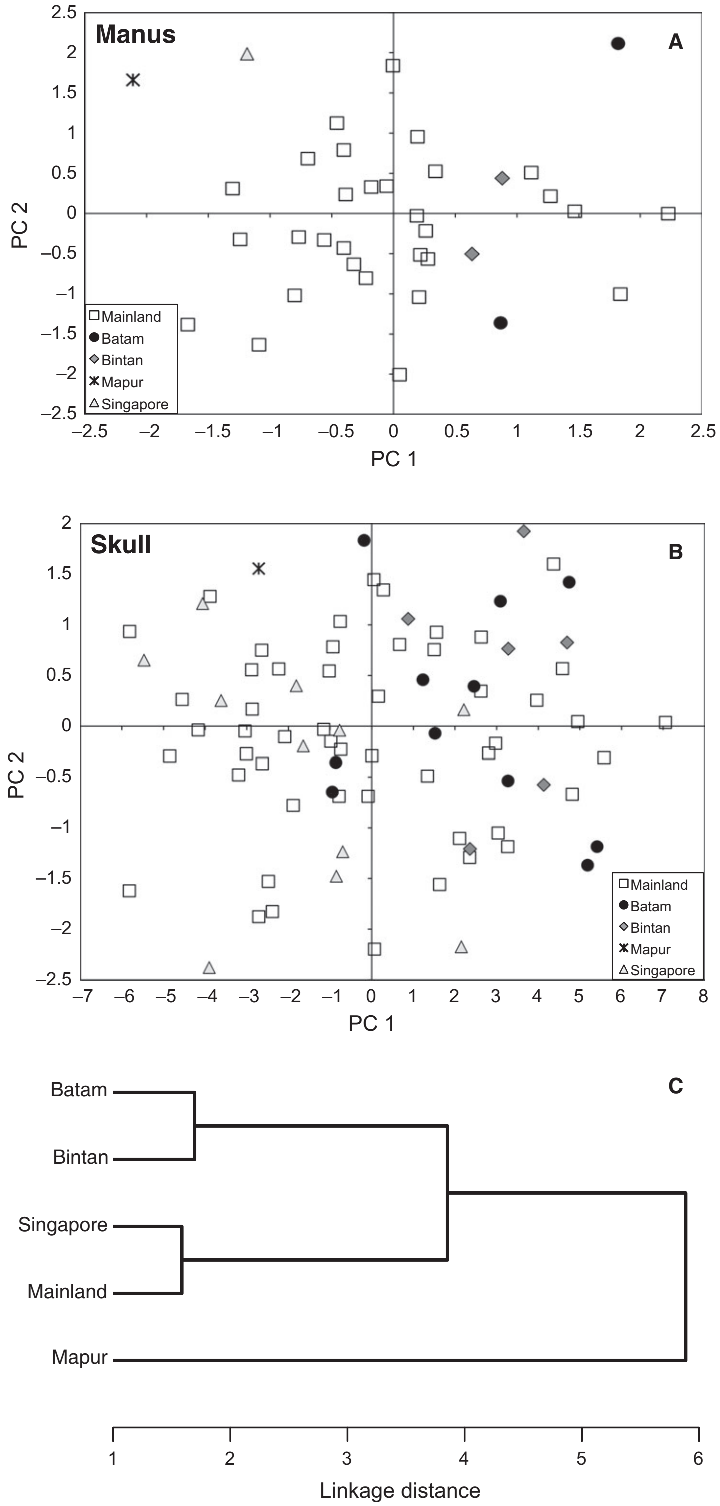

Figure 5. Plots illustrating results of analyses comparing *T. glis* individuals from the Malay Peninsula to those from the southern islands. A, Plot of factor scores on the first two axes from PCA of nine hand variables (Table 11). B, Plot of factor scores on the first two axes from PCA of nine cranial and three mandibular variables (Table 7). *T. glis* individuals from Mapur and Singapore islands are generally smaller than those from the mainland, but this is not the case for those from Batam and Bintan islands. C, Phenogram from cluster analysis of 19 skull variables. The population from Singapore is more similar to the mainland population than to the other three island populations.

Not surprisingly, the population from Singapore is most similar to the mainland population. The individual from Mapur ('*T. g. redacta*'), the most isolated of the southern islands (Fig. 1), represents the most morphologically distinct population in this analysis (Fig. 5c), but this population is only represented by a single specimen in our study.

DISCUSSION

Taxonomic implications

Lyon (1913) recognized some mainland and Penang Island populations of *T. glis* as distinct species (see 'Introduction') whose primary distinguishing features were subtle differences in pelage coloration. Chasen (1940) classified all of these populations as *T. glis*, but continued to recognize them as subspecies, again based on pelage. Our inspections of 62 study skins led us to conclude that variation in pelage coloration among individuals on Penang Island is not exclusive to this population, and it represents a subset of the total variation in pelage exhibited within the mainland *T. glis* population. These minor differences in pelage are insufficient to warrant taxonomic separation in light of previous work demonstrating the latitudinally clinal nature of pelage variation in both mainland and island populations of treeshrews (Hill, 1960). With one particular exception, the subtle variations in pelage coloration that were used to characterize island populations can be found within the variation present in the mainland population.

Table 11. Component loadings and eigenvalues from principal components analysis of nine variables from the manus of populations from the Malay Peninsula and the southern islands (Fig. 5a).

	Axis	
	1	2
2PPW	0.885	0.228
3PPW	0.833	0.011
4PPW	0.808	0.265
1PPW	0.638	−0.215
2PPL	0.625	**−0.654**
2MW	0.609	**0.438**
1MW	0.454	0.124
1PPL	0.409	**−0.699**
1ML	−0.174	**−0.476**
Eigenvalues	3.700	1.518
Percent of total Variance explained	41.1	16.9

Abbreviations for variables are defined in 'Materials and Methods'. Loadings in bold type are discussed in the text.

Moreover, some of the variation in pelage that we observed likely results from age and/or seasonal molt. For example, the dorsal pelage of five specimens of *T. glis* from Tioman Island ('*T. g. sordida*') collected in October 1899 and October 1900 is subtly darker and less grizzled than that of seven specimens collected in August 1970. The difference between these two samples is more apparent than those separating some recognized subspecies (e.g., Lyon, 1913).

Our morphological comparisons of the mainland and Penang Island populations revealed that average body size is smaller in the island population (Fig. 2). There is extensive overlap in size, however, between the smallest mainland individuals and the largest Penang individuals. Given the morphological similarity between these two populations, we see no reason to recognize '*T. glis wilkinsoni*' (mainland) and *T. glis glis* (Penang) as distinct species or subspecies.

Although populations from islands to the west and east of the Malay Peninsula generally average smaller body size than the mainland population, those from some southern islands tend to average larger body size (Fig. 5), indicating a lack of a consistent trend in body size variation. Such inconsistent patterns of body size variation among Southeast Asian islands and island groups have also been noted in crab-eating macaques, *Macaca fascicularis* (Fooden & Albrecht, 1993). Insular populations of common treeshrews may be converging on either small or large body size depending on the local conditions and characteristics of their respective islands (see Heaney, 1978). Island populations are generally identifiable as *T. glis*, and most lack any distinctive morphological differences to distinguish them (Figs. 3–5). For this reason, we do not recognize '*T. g. raviana*' (Adang-Rawi), '*T. g. lacernata*' (Langkawi-Terutau), '*T. g. umbratilis*' (Ta Li Bong), '*T. g. pulonis*' (Aur), '*T. g. pemangilis*' (Pemanggil), '*T. g. sordida*' (Tioman), '*T. g. redacta*' (Mapur), '*T. g. batamana*' (Batam), or the Singapore population as distinct subspecies; we consider these names, like '*T. g. wilkinsoni*' (see above), to be junior synonyms of *T. glis glis*.

The cases of the Bintan ('*T. g. castanea*') and Mapur populations, however, are unique. Although we currently have no evidence from the skull or hand to support their recognition as a taxon distinct from *T. glis*, their ferruginous dorsal pelage and red-orange tail are most similar to those of the ruddy treeshrew, *T. splendidula* Gray, 1865. Lyon (1913: 90—91) considered *T. castanea* from Bintan to be a 'very distinct form' that is 'related to *Tupaia splendidula*,' and Robinson (1916: 63) described *T. castanea redacta* from the adjacent island of Mapur as 'extremely close to *Tupaia castanea*, Miller, but somewhat smaller.' However, Chasen (1940), Wilson (1993), and Helgen

(2005) all classified these island populations as forms of *T. glis*. Additional study of *T. splendidula* is underway, but until it is completed, we consider it best practice to provisionally recognize these distinctive populations from Bintan and Mapur as *T. glis castanea*.

In summary, populations of *T. glis* from nearly all (11 of 13) offshore islands in our study average smaller body size than the mainland population on the Malay Peninsula, the probable source for these island populations. Populations from Batam and Bintan represent exceptions to this pattern; i.e., those from the western and eastern island groups consistently average smaller body size, whereas those from the southern island group show no consistent pattern. Nevertheless, none of the island populations exhibit sufficient morphological differences in the skull or hands, as evidenced in the overlap among island and mainland individuals in morphospace (Figs 2–5), to warrant taxonomic distinction from the mainland population at either the species or subspecies level. Two potential exceptions are the populations from Bintan and Mapur, which have a clearly distinctive pelage that suggests affinity with a species other than *T. glis*. The lack of morphological separation in this study is in sharp contrast to our previous taxonomic studies of treeshrew populations from islands such as Sumatra, Borneo, Bangka, Java, Siberut, Tanahbala, and the Palawan Faunal Region (Sargis *et al.*, 2013a,b, 2014a,b). All of the *T. glis* populations in this study warrant further investigation with molecular evidence to better understand the relationships among them and their evolutionary and biogeographic history.

Although previous taxonomic boundaries for island populations of *T. glis* were partially based on size differences compared to the mainland population (e.g., Lyon, 1913; Robinson, 1916; Chasen, 1940; see above), possible insular variation was not considered in these early classifications. Our conclusions regarding island vs. mainland populations of *T. glis* demonstrate that such patterns must be considered in taxonomic studies and should be explored further as a general phenomenon, especially the intersection of insular variation and species boundaries.

Conservation implications

Tupaia glis was once considered to occupy a broad geographic range that included Sumatra, Java, Bangka, Siberut, and Tanahbala, but our recent taxonomic revisions (Sargis *et al.*, 2013a,b, 2014a) have restricted its range to the Malay Peninsula south of the Isthmus of Kra (~10° N latitude) and several small offshore islands (Fig. 1). In light of this, Sargis *et al.* (2013b) suggested that its status of 'Least Concern' (Han, 2008) on the *IUCN Red List of Threatened Species* should be re-assessed. Our results here indicate that mainland and island populations in general are not taxonomically distinctive, although divergence in body size between mainland and island populations appears to be a frequent occurrence (see above). Furthermore, the fact that *T. glis* is common on the Malay Peninsula (Han, 2008) does not diminish the ecological role of this species in its native island habitats. Moreover, the populations on Bintan and Mapur are unique in being indistinguishable from mainland *T. glis* in their skull and hand morphology while possessing a distinctive pelage coloration that may warrant their recognition as a distinct (and possibly threatened) subspecies, though this requires further investigation in a taxonomic study that includes *T. splendidula* (see above). Finally, the abundance of *T. glis* on the mainland and its presence on offshore islands makes this species valuable for understanding the processes contributing to body size evolution on islands, a topic that we are investigating further in a broader analysis of ecogeographic rules in this species.

ACKNOWLEDGEMENTS

We dedicate this paper to D. Gentry Steele (2/8/41–10/27/14), whose exhaustive and meticulous research on treeshrew morphology and distribution greatly facilitated our work. This research was supported by National Science Foundation grant DEB-0542532/0542725 and an Alaska EPSCoR grant to E.J.S. and L.E.O. Additional support was provided to N.W. from the United States Geological Survey's Patuxent Wildlife Research Center, to N.C.M. from the Yale Peabody Museum of Natural History Summer Internship Program, and to T.N.B. from the Yale College Dean's Research Fellowship in the Sciences and the Richter Summer Fellowship. L.E.O. was supported by an Edward P. Bass Distinguished Visiting Environmental Scholarship from the Yale Institute for Biospheric Studies. We thank the following curators, collection managers, and museums for access to the specimens in their collections: R. Portela-Miguez, L. Tomsett, and P. Jenkins, The Natural History Museum (BMNH), London; J. Cuisin, Muséum national d'Histoire naturelle (MNHN), Paris; C. Conroy and J. Patton, Museum of Vertebrate Zoology at University of California, Berkeley (MVZ); H. van Grouw, Nationaal Natuurhistorisch Museum, Leiden (RMNH); L. Gordon, R. Thorington, K. Helgen, and D. Lunde, United States National Museum of Natural History (USNM), Washington, DC; and L. Heaney and especially the contribution of the late, indisputably eminent B.

Stanley, Field Museum of Natural History (FMNH), Chicago. We are grateful to S. Raredon, Division of Fishes, Museum Support Center, USNM, for assistance with the digital X-ray system and to R. Portela-Miguez, Department of Zoology, BMNH, for X-raying 15 specimens, including two holotypes, that were invaluable to our study. We thank Bob Timm and three anonymous reviewers for valuable comments that improved the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States government.

REFERENCES

Chasen FN. 1940. A handlist of Malaysian mammals. *Bulletin of the Raffles Museum, Singapore* **15:** 1–209.

Corbet GB, Hill JE. 1992. *The mammals of the Indomalayan region: a systematic review*. Oxford: Oxford University Press.

Diard PM. 1820. Report of a meeting of the Asiatic Society for March 10. *Asiatic Journal and Monthly Register* **10:** 477–478.

Endo H, Cuisin J, Nadee N, Nabhitabhata J, Suyanto A, Kawamoto Y, Nishida T, Yamada J. 1999. Geographical variation of the skull morphology of the common tree shrew (*Tupaia glis*). *Journal of Veterinary Medical Science* **61:** 1027–1031.

Endo H, Hayashi Y, Rerkamnuaychoke W, Nadee N, Nabhitabhata J, Kawamoto Y, Hirai H, Kimura J, Nishida T, Yamada J. 2000a. Sympatric distribution of the two morphological types of the common tree shrew in Hat-Yai districts (South Thailand). *Journal of Veterinary Medical Science* **62:** 759–761.

Endo H, Nishiumi I, Hayashi Y, Rashdi ABM, Nadee N, Nabhitabhata J, Kawamoto Y, Kimura J, Nishida T, Yamada J. 2000b. Multivariate analysis in skull osteometry of the common tree shrew from both sides of the Isthmus of Kra in southern Thailand. *Journal of Veterinary Medical Science* **62:** 375–378.

Endo H, Rashdi ABM, Yamagiwa D, Yamada J, Nabhitabhata J 2000c. Principal component analysis of the common tree shrew skulls from Laos, Thailand and Malaysia. In: Matsuura K, ed. *Proceedings of the first and second symposia on collection building and natural history studies in Asia*. Tokyo: National Science Museum Monographs, 171–175.

Fooden J, Albrecht GH. 1993. Latitudinal and insular variation of skull size in crab-eating macaques (Primates, Cercopithecidae: *Macaca fascicularis*). *American Journal of Physical Anthropology* **92:** 521–538.

Gray JE. 1865. Notice of a species of *Tupaia* from Borneo in the collection of the British Museum. *Proceedings of the Zoological Society of London* **1865:** 322.

Han KH. 2008. *Tupaia glis*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 25 September 2013.

Heaney LR. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution* **32:** 29–44.

Helgen KM. 2005. Order Scandentia. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference, 3rd edn*. Baltimore: The Johns Hopkins University Press, 104–109.

Hill JE. 1960. The Robinson collection of Malaysian mammals. *Bulletin of the Raffles Museum, Singapore* **29:** 1–112.

Lyon MW. 1906. Mammals of Banka, Mendanau, and Billiton Islands, between Sumatra and Borneo. *Proceedings of the United States National Museum* **31:** 575–612.

Lyon MW. 1907. Mammals of Batam Island, Rhio Archipelago. *Proceedings of the United States National Museum* **31:** 653–657.

Lyon MW. 1911. Descriptions of four new treeshrews. *Proceedings of the Biological Society of Washington* **24:** 167–170.

Lyon MW. 1913. Treeshrews: an account of the mammalian family Tupaiidae. *Proceedings of the United States National Museum* **45:** 1–188.

Miller GS. 1900. Mammals collected by Dr. W. L. Abbott on islands in the North China Sea. *Proceedings of the Washington Academy of Sciences* **2:** 203–246.

Miller GS. 1903. Seventy new Malayan mammals. *Smithsonian Miscellaneous Collections* **45:** 1–73.

Olson LE, Sargis EJ, Martin RD. 2005. Intraordinal phylogenetics of treeshrews (Mammalia: Scandentia) based on evidence from the mitochondrial 12S rRNA gene. *Molecular Phylogenetics and Evolution* **35:** 656–673.

Raffles TS. 1821. Descriptive catalogue of a zoological collection, made on account of the honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stamford Raffles, Lieutenant-Governor of Fort Marlborough; with additional notices illustrative of the natural history of those countries. *Transactions of the Linnean Society of London* **13:** 239–274.

Roberts TE, Lanier HC, Sargis EJ, Olson LE. 2011. Molecular phylogeny of treeshrews (Mammalia: Scandentia) and the timescale of diversification in Southeast Asia. *Molecular Phylogenetics and Evolution* **60:** 358–372.

Robinson HC. 1916. A collection of mammals and birds from Pulau Panjang or Pulau Mapor, Rhio-Lingga Archipelago. *Journal of the Federated Malay States Museums* **7:** 59–72.

Robinson HC, Kloss CB. 1911. On six new mammals from the Malay Peninsula and adjacent islands. *Journal of the Federated Malay States Museums* **4:** 169–174.

Sargis EJ. 2002. A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. *Mammalia* **66:** 579–598.

Sargis EJ, Woodman N, Reese AT, Olson LE. 2013a. Using hand proportions to test taxonomic boundaries within the *Tupaia glis* species complex (Scandentia, Tupaiidae). *Journal of Mammalogy* **94:** 183–201.

Sargis EJ, Woodman N, Morningstar NC, Reese AT, Olson LE. 2013b. Morphological distinctiveness of Javan

Tupaia hypochrysa (Scandentia, Tupaiidae). *Journal of Mammalogy* **94:** 938–947.

Sargis EJ, Woodman N, Morningstar NC, Reese AT, Olson LE. 2014a. Island history affects faunal composition: the treeshrews (Mammalia: Scandentia: Tupaiidae) from the Mentawai and Batu Islands, Indonesia. *Biological Journal of the Linnean Society* **111:** 290–304.

Sargis EJ, Campbell KK, Olson LE. 2014b. Taxonomic boundaries and craniometric variation in the treeshrews (Scandentia, Tupaiidae) from the Palawan Faunal Region. *Journal of Mammalian Evolution* **21:** 111–123.

Steele DG. 1983. Within-group variation in coat-color characteristics of the common tree shrew, *Tupaia glis* Diard, 1820. *International Journal of Primatology* **4:** 185–200.

Thomas O. 1895. On some mammals collected by Dr. E. Modigliani in Sipora, Mentawei Islands. *Annali. Museuo Civico de Storia Naturale Genoa ser*. 2 **14**: 661–672.

Thomas O, Wroughton RC. 1909. Diagnoses of new mammals collected by Mr. H. C. Robinson in the islands of the Straits of Malacca. *Annals and Magazine of Natural History ser*. 8 **4:** 534–536.

Wagner JA. 1841. Schreber's Saugthiere, Supplementband, 2. *Abtheilung* **1841:**37–44, 553.

Wilson DE. 1993. Order Scandentia. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*, 2nd edn. Washington, D.C.: Smithsonian Institution Press, 131–133.

Woodman N, Morgan JJP. 2005. Skeletal morphology of the forefoot in shrews (Mammalia: Soricidae) of the genus *Cryptotis*, as revealed by digital X-rays. *Journal of Morphology* **266:** 60–73.

Woodman N, Stephens RB. 2010. At the foot of the shrew: manus morphology distinguishes closely-related *Cryptotis goodwini* and *Cryptotis griseoventris* (Mammalia: Soricidae) in Central America. *Biological Journal of the Linnean Society* **99:** 118–134.

APPENDIX 1

Specimens Examined

Specimens of *Tupaia glis* used in this study, organized by sample. As a reference, each sample is accompanied by species or subspecies names [in brackets] with which it has, at times (e.g., Lyon, 1913), been associated. We do not recognize these subspecies as distinguishable units. These specimens are housed in the following institutions: The Natural History Museum, London, United Kingdom (BMNH); Field Museum of Natural History, Chicago, IL (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); Museum of Vertebrate Zoology at University of California, Berkeley (MVZ); Nationaal Natuurhistorisch Museum, Leiden (RMNH); United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Specimens used in both the manus and skull analyses are indicated with an asterisk (*).

MAINLAND

Peninsular Malaysia [*T. ferruginea wilkinsoni* Robinson & Kloss, 1911] (n = 95). MALAYSIA: Johor: Bekok (USNM 487923*, 487925*, 487926*, 487927*, 487928*, 487931*); Endau River (USNM 112575, 112578*, 112580*, 112601*); Pelepak (BMNH 5.12.7.3; USNM 143268, 143269); Sembrong River (USNM 112616*); Tanjong Peniabong (USNM 112658*). Kedah: Kedah Peak (BMNH 55.1271); Kelantan: 'K. Pehi Estate' (BMNH 9.5.9.1). Negeri Sembilan: Ayer Kring (BMNH 55.1252, 55.1254); Gunong Tampin (BMNH 55.1255, 55.1256). Pahang: Gunong Tahan (BMNH 6.10.4.10, 6.10.4.11, 55.1219); Punjum, Kuala Lipis (BMNH 55.1233); Rompin River (USNM 115491*); Tampong Ubai, Kuantan (BMNH 61.1148); Telom River (BMNH 34.7.18.90, 34.7.18.91, 34.7.18.94, 34.7.18.96, 34.7.18.97, 34.7.18.98, 55.1221); Triang (BMNH 55.1231, 55.1232). Perak: Batu Tegor (BMNH 55.1215); Gunong Ijau (BMNH 55.1218); Lenggong (BMNH 55.1213); Maxwell Hill (BMNH 61.1149; USNM 311298*); Taiping (BMNH 55.1214); Temengoh (BMNH 55.1217). Selangor: Ginting Bidai (BMNH 10.10.1.12, 10.10.1.13, 10.10.1.15, 10.10.1.16, 55.1245, 55.1246, 55.1248); Klang Gates (BMNH 55.1249); Kuala Lumpur (BMNH 34.7.18.99; MVZ 116955, 118599, 183625; USNM 152184*, 152185, 487939*, 487946*); Rawang (BMNH 55.1251, 55.1267); Subang (USNM 487943*); Tanjong Duablas (USNM 487940*, 487941, 487942*); Ulu Gombak (BMNH 61.1150; MNHN 1981–185); Ulu Langat (USNM 291264*); Cheras (BMNH 55.1236, 55.1237, 55.1238, 55.1239, 55.1240, 55.1241); Menuang Gasing (BMNH 55.1243, 55.1244). Terengganu: Bukit Besi (USNM 311307*, 311308*, 311309*, 311310*, 311311*); Kuala Brang (USNM 487949*, 487950*, 487951*, 487953*); Tanjong Dungun (USNM 105024*, 105025*, 105026*, 105027*, 105030*, 105031*, 105032*, 105033*, 105034*). THAILAND: Trang: Ko-Khau (BMNH 12.10.7.1*—holotype of *T. ferruginea wilkinsoni*).

WESTERN ISLANDS

Penang Island [type locality for *Tupaia glis* (Diard, 1820)](n = 23). MALAYSIA: Penang: Penang Island (BMNH 12.10.7.9*, 12.10.7.10*, 12.10.7.11*, 12.10.7.12*, 12.10.7.13*, 12.10.7.14*, 55.1207*, 55.1208*, 55.1210*, 55.1211*, 55.1212*, 60.5.4.72*, 79.11.21.687*; FMNH 98454*, 98455*, 98456*, 98459*, 98460*, 98462*, 98468*, 98469*, 98470*; USNM 487954*).

Butang Islands [*T. raviana* Lyon, 1911] (*n* = 8). THAILAND: Satun: Adang Island [= Ko Adang] (BMNH 12.10.22.5, 12.10.22.6, 55.1379, 55.1380; USNM 104354*); Rawi Island (BMNH 12.10.22.4, 55.1378; USNM 104355*—holotype of *T. raviana*).

Langkawi and Terutau Islands [*T. lacernata* Thomas & Wroughton, 1909] (*n* = 49). MALAYSIA: Kedah: Langkawi Island (BMNH 9.11.1.22, 9.11.1.23, 9.11.1.24, 9.11.1.25, 9.11.1.26, 9.11.1.27, 9.11.1.28, 9.11.1.29, 9.11.1.30—holotype of *T. lacernata*, 55.1381, 55.1382, 55.1383, 55.1384, 55.1385, 55.1386, 55.1387, 55.1389, 55.1390, 55.1391, 55.1392, 55.1393; USNM 104353*, 123901*, 311302, 311303, 311306). THAILAND: Satun: Terutau Island (BMNH 9.11.1.14, 9.11.1.15, 9.11.1.16, 9.11.1.17, 9.11.1.18, 9.11.1.19, 9.11.1.20, 55.1394, 55.1395, 55.1396, 55.1397, 55.1398, 55.1399, 55.1400, 55.1401, 55.1402, 55.1403; FMNH 43836; USNM 123981*, 123982*, 123985*, 123987*, 123988).

Ta Li Bong Island [*T. g. umbratilis* Chasen, 1940] (*n* = 6). THAILAND: Trang: 'Telibon' [= Ta Li Bong] Island (BMNH 47.1496—holotype of *T. g. umbratilis*, 55.1374, 55.1375, 55.1376, 55.1377; USNM 83256*).

EASTERN ISLANDS

Aur Island [*T. pulonis* Miller, 1903] (*n* = 7). MALAYSIA: Johor: 'Aor' (= Aur) Island (BMNH 12.10.22.2, 12.10.22.3, 55.1352, 55.1353, 55.1354, 55.1355; USNM 112449*—holotype of *T. pulonis*).

Pemanggil Island [*T. pemangilis* Lyon, 1911] (*n* = 4). MALAYSIA: Johor: Pemanggil Island (BMNH 12.10.22.1, 55.1350, 55.1351; USNM 112499*—holotype of *T. pemangilis*).

Tioman Island [*T. sordida* Miller, 1900] (*n* = 22). MALAYSIA: Pahang: Pekan District, Tioman Island (USNM 101746*, 101747*—holotype of *T. sordida*, 104973*, 104974*, 104975*, 104976*), Kampong Tekek (USNM 487932*, 487933*, 487937*, 487938*), Kampong Ayer Padi (USNM 487934*, 487936*), Juara Bay (BMNH 8.1.25.4, 10.10.1.11, 55.1340, 55.1341, 55.1342, 55.1343, 55.1345, 55.1346, 55.1347, 55.1348).

SOUTHERN ISLANDS

Batam Island [*T. ferruginea batamana* Lyon, 1907] (*n* = 17). INDONESIA: 'Rhio' (= Riau) Archipelago; 'Battam' (= Batam) Island; Senimba Bay (USNM 142151*—holotype of *T. ferruginea batamana*, 142152*, 143252, 143253, 143254, 143255, 143256, 143257); Tanjong Turut (BMNH 9.4.1.114, 9.4.1.115; 9.4.1.116, 9.4.1.117, 9.4.1.118, 9.4.1.119, 9.4.1.120; RMNH 36091, 36092).

Bintan Island [*T. castanea* Miller, 1903] (*n* = 8). INDONESIA: 'Rhio' (= Riau) Archipelago; 'Bintang' (= Bintan) Island (USNM 115607*, 115608*—holotype of *T. castanea*); Sungei Biru (BMNH 9.4.1.101; RMNH 36093, 36094); Pasir Panjang (BMNH 9.4.1.102, 9.4.1.103, 9.4.1.104).

Mapur Island [*T. castanea redacta* Robinson, 1916] (*n* = 1). INDONESIA: 'Rhio' (= Riau) Archipelago; 'Mapor' (= Mapur) Island (BMNH 26.10.19.4* – holotype of *T. castanea redacta*).

Singapore [*T. glis*] (*n* = 20). SINGAPORE (BMNH 9.4.1.105, 9.4.1.106, 9.4.1.107, 9.4.1.108, 9.4.1.109, 9.4.1.110, 9.4.1.111, 55.1257, 55.1258, 55.1260, 55.1261, 55.1262, 55.1263, 55.1264, 55.1265, 55.1266; USNM 105078, 105079, 105080, 124317*).