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Skeletal Variation and Taxonomic Boundaries in the Pen-tailed Treeshrew (Scandentia: Ptilocercidae; *Ptilocercus lowii* Gray, 1848)

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Abstract

The Pen-tailed Treeshrew, *Ptilocercus lowii* Gray, 1848, is a small arboreal mammal from Southeast Asia. It is the only extant species of Ptilocercidae and includes two subspecies: *P. l. lowii* from Borneo and offshore islands, and *P. l. continentis* from the Malay Peninsula, Sumatra, and smaller islands, including the Batu and Mentawai Islands. Intraspecific taxonomic boundaries in *Ptilocercus* have yet to be rigorously evaluated using modern morphological methods, so we investigated the morphometric variation between these subspecies using quantitative cranial and postcranial data obtained from museum specimens. Multivariate analyses revealed limited overlap between *P. l. lowii* and *P. l. continentis* in cranioskeletal morphospace, indicating some divergence of these two lineages. Future studies should incorporate additional morphological and molecular data to further test whether these lineages represent two distinct species. Recognition of two *Ptilocercus* species would have conservation implications for both populations, which should be reevaluated across their separate ranges in light of region-specific threats. Additional biological surveys, particularly from undersampled island populations, will be critical in reassessing the distribution and conservation priorities for *P. lowii*.

Keywords Borneo · Innominate · Morphology · Southeast Asia · Skull · Taxonomy

Introduction

Treeshrews are small-bodied mammals endemic to South and Southeast Asia comprising their own taxonomic order (Scandentia), which is currently subdivided into the families Tupaiidae (22 species in three genera) and the monospecific Ptilocercidae. The Pen-tailed Treeshrew, *Ptilocercus lowii*, is the sole representative of the latter (Helgen 2005; Olson et al. 2005; Roberts et al. 2011; Hawkins 2018; Sargis 2020) and certainly unique among treeshrew species. It is the only nocturnal treeshrew (Emmons 2000), as well as

one of the smallest, averaging ~ 45 g (Sargis 2002a), and one of the only arboreal species (Lim 1967; Muul and Lim 1971; Gould 1978; Emmons 2000). Pen-tailed Treeshrews appear to be less frugivorous than most other treeshrews (Emmons 2000; Selig et al. 2019a), consume large amounts of fermented floral nectar (Wiens et al. 2008), and have a distinctive dentition compared to that of tupaiids (Steele 1973; Butler 1980; Selig et al. 2019a, 2019b, 2020). In addition to its distinct dental morphology, *Ptilocercus* has also been contrasted with tupaiids in its general anatomy (Le Gros Clark 1926), postcranial morphology (Szalay and Drawhorn 1980; Sargis 2001, 2002a, 2002b, 2002c, 2002d, 2004, 2007), and cranial morphology, the latter based on John Wible's seminal studies of the treeshrew skull (Wible and Zeller 1994; Wible 2009, 2011). Given all of the morphological differences between *Ptilocercus* and tupaiids and the similarity of *Ptilocercus* to various outgroups, including colugos, primates, and extinct plesiadapiforms, many have proposed that *Ptilocercus* exhibits the more plesiomorphic condition for many features throughout the skeleton (Le Gros Clark 1926; Butler 1980; Szalay and Drawhorn 1980; Sargis 2001, 2002a, 2002b, 2002c, 2002d, 2004, 2007) as well as for various ecological attributes (Gould 1978;

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Emmons 2000). Finally, *Ptilocercus lowii*, the sole extant species, has been called a "living fossil" because of its similarity to its only described extinct congener, *P. kylin* from the Oligocene of China (Li and Ni 2016). For these reasons, and because of its sister relationship to all other scandentians (Olson et al. 2004, 2005; Roberts et al. 2011), *Ptilocercus* is a critical taxon to include in supraordinal phylogenetic analyses (Wible and Zeller 1994; Sargis 2000, 2002b, 2002c, 2002d, 2004, 2007; Janečka et al. 2007; O'Leary et al. 2013).

In contrast to the longstanding interest in its relevance to higher-level mammalian systematics and primate evolution (e.g., Sargis 2004, 2007; Janečka et al. 2007; O'Leary et al. 2013), *Ptilocercus* has received scant taxonomic attention at the intraspecific level, due in large part to its scarcity in collections as well as its rarity, elusiveness, or possibly both in nature (Lyon 1913; Corbet and Hill 1992; Emmons 2000; Han et al. 2020). Two subspecies are currently recognized: *P. lowii lowii* Gray, 1848 from Borneo and the nearby islands of Labuan and Serasan, and *P. lowii continentis* Thomas, 1910 from the Malay Peninsula and Sumatra as well as the smaller islands of Bangka, Lingga, Karimunbesar, Siberut, and Pini (Fig. 1; Lyon 1913; Chasen 1940; Helgen 2005; Cassola 2016). A paucity of comparative material has

persisted since the species was first described. Nonetheless, Thomas (1910: 426) recognized the first non-Bornean specimen as a distinct subspecies, putatively diagnosable by a handful of mostly integumental characters but otherwise "very similar" to the Bornean form. Lyon (1913) dismissed all but two of Thomas's characters yet upheld his classification, the validity of which Corbet and Hill (1992) later questioned in light of there being too few specimens for rigorous assessment. Although some subsequent taxonomic treatments of *Ptilocercus* have preserved Thomas's (1910) infraspecific classification (e.g., Chasen 1940; Helgen 2005; Hawkins 2018), it has not been re-evaluated in over a century or examined in a biogeographic context.

Apart from Siberut, the Pen-tailed Treeshrew's entire range is believed to have been contiguous during most of the Pleistocene, eventually splitting into different islands about 400,000 years ago due to rising sea levels (Husson et al. 2020). The Mentawai Islands, which include Siberut, have been separated from Sumatra by the deep Mentawai Basin for even longer (Wilting et al. 2012), presumably preventing gene flow between populations of Pen-tailed Treeshrews on Sumatra and Siberut since the mid-Pleistocene (see Sargis et al. 2014a). As is the case in many other Sundaland mammals (Roberts et al.
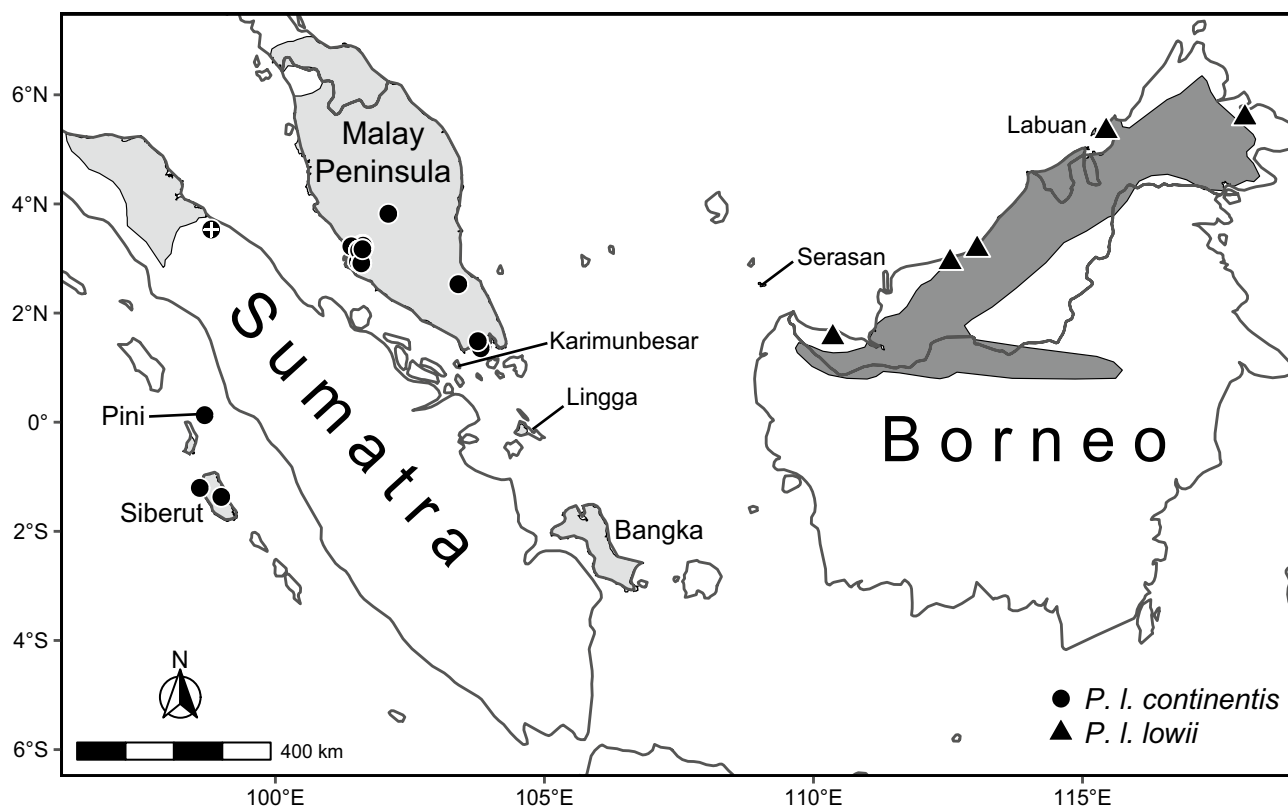

Fig. 1 Map of Sumatra, southern Malay Peninsula, Borneo, and surrounding islands showing collecting localities of specimens included in this study and landmasses discussed in the text. Shaded areas represent IUCN range (Cassola 2016) for *Ptilocercus lowii*, with lighter and darker shading reflecting ranges of *P. l. continentis* and *P. l. lowii*, respectively, as recognized by Chasen (1940). Circle inscribed with white cross indicates a specimen with a damaged skull that was only included in the postcranial dataset

2011; Wilting et al. 2011), *Ptilocercus* populations on different islands have been geographically isolated from one another since the flooding of the Sunda shelf, and overwater dispersal is likely rare in treeshrews (Olson et al. 2005; Roberts et al. 2011). This long-term separation has potential consequences for infraspecific distinctiveness in *P. lowii.*

Historically, inter- and intraspecific treeshrew taxonomy have relied heavily (and in most cases exclusively) on pelage and cranial variation, but the former has proven to be largely subjective and varies seasonally, throughout an individual's lifetime, and over time in storage (Davis et al. 2013). Furthermore, qualitative cranial variation among closely related treeshrews is generally negligible. Craniometric differences have often been implicitly invoked but rarely analyzed quantitatively, at least until relatively recently. Despite the traditional focus on cranial characters in small-mammal (including treeshrew) systematics, we have shown that postcranial data are also useful in both inter- and intraspecific taxonomic circumscription in treeshrews (Sargis et al. 2013a, 2013b, 2014a, 2017; Juman et al. 2021). With that in mind, and in light of the unresolved issues reviewed above, we assessed morphometric variation between *P. l. lowii* and *P. l. continentis* using multivariate analyses of both cranial and postcranial characters, and we evaluated whether these subspecies may warrant species-level recognition; following the general lineage species concept (de Queiroz 1998), we consider morphological differentiation to be one indicator of distinct lineages. We also compared two offshore island populations of *P. l. continentis* (Pini and Siberut) to *P. l. continentis* from the Malay Peninsula and *P. l. lowii* from Borneo. Additionally, we tested for sexual dimorphism in this species to assess whether it resembles other treeshrew species in lacking this trait (Emmons 2000; Woodman et al. 2020; Juman et al. 2021).

Materials and Methods

We analyzed three morphometric datasets (one craniomandibular and two postcranial), each varying in the number of measurements recorded and individuals included due to differences in specimen preparation and geographic representation. This allowed us to assess intraspecific variation and test for morphological distinctiveness between both taxonomically and geographically circumscribed groupings.

Our craniomandibular sample included eight specimens of *P. l. lowii* from mainland Borneo, 34 specimens of *P. l. continentis* from the Malay Peninsula, two specimens of *P. l. continentis* from Siberut, and one specimen of *P. l. continentis* from Pini (Appendix 1, Supplementary Information 1). Although we were able to include the holotype of *P. l. continentis*, the *P. l. lowii* holotype (NHMUK 48.5.12.3) is a dental subadult and was therefore not measured (see

Woodman et al. 2020). Unfortunately, we were unable to inspect any specimens of *Ptilocercus* from Bangka Island. Examined specimens are housed in the following museums: Field Museum of Natural History (FMNH), Chicago, IL; Museum of Comparative Zoology at Harvard University (MCZ), Cambridge, MA; The Natural History Museum (NHMUK), London, UK; Oxford University Museum of Natural History (OUMNH), Oxford, UK; United States National Museum of Natural History (USNM), Washington, DC; and Yale Peabody Museum of Natural History (YPM), New Haven, CT (Appendix 1, Supplementary Information 1).

We recorded 18 craniomandibular measurements (Table 1; Sargis et al. 2013b, 2014a, 2014b, 2017, 2018; Juman et al. 2021) from 43 adult (those with fully erupted permanent dentition; see Woodman et al. 2020) museum specimens (Appendix 1) using Mitutoyo digital calipers that read to 0.01 mm. Because some skulls were broken or damaged, we were unable to record all measurements for all individuals. The CT scans of two additional fluid-preserved specimens (FMNH 57450 and OUMNH ZC-8974) were measured in Avizo Lite 9.7 (Thermo Fisher Scientific/FEI Visualization Sciences Group, Berlin, thermofisher.com). Original measurements (in mm) are provided in Supplementary Information 1. Summary statistics, including mean and standard deviation, are presented in Table 2. We georeferenced 23 specimen localities and generated a locality map using the ggplot2, rnaturalearth, and ggspatial packages in R (R Core Team 2013; Wickham 2016; South 2017; Dunnington 2020) (Fig. 1).

Multivariate analyses were performed on log-transformed (ln) data in R. We conducted principal component analyses (PCA) on correlation matrices with the "princomp" function and discriminant function analyses (DFA) with the MASS package (Venables and Ripley 2002). Plots were created using the ggplot2 package. Variables were selected to maximize the number of individuals that could be included in the analyses (particularly *P. l. lowii* from Borneo and *P. l. continentis* from island populations with smaller sample sizes).

We first tested for sexual size dimorphism by comparing males and females with a cross-validated DFA of six craniomandibular variables (CNL, CPL, LIB, MTL, MCH, MH; see Table 1 for abbreviations) in: (a) the total sample ($n = 20$ males, 17 females) and (b) the *P. l. continentis* sample ($n = 16$ males, 16 females). We also conducted t-tests with skull (condylopremaxillary) length as a response variable and sex as a binary grouping variable in both samples noted above. These analyses were not conducted separately on the *P. l. lowii* sample due to missing data and the small number of specimens.

We then investigated variation between *P. l. lowii* ($n = 8$) and *P. l. continentis* ($n = 34$) using a PCA of six

Table 1 Cranial, mandibular, and innominate measurement descriptions (and abbreviations) following Sargis (2000, 2002c), Sargis et al. (2013b, 2014a, 2014b, 2017, 2018), and Juman et al. (2021). Upper-case abbreviations (i.e., I, C, P, M) refer to maxillary and premaxillary teeth; lowercase abbreviations (i, c, p, m) refer to mandibular teeth

Cranium

Braincase breadth (BB): greatest breadth of braincase

Condyloincisive length (CIL): greatest distance between anterior-most surface of I1 and caudal surface of occipital condyle

Condylonasal length (CNL): greatest distance between rostral surface of nasal and caudal surface of occipital condyle

Condylopremaxillary length (CPL): greatest distance between rostral surface of premaxilla and caudal surface of occipital condyle

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)

Least interorbital breadth (LIB): least distance between the orbital margins

Lambdoid-premaxillary length (LPL): greatest distance between rostral surface of premaxilla and caudal surface of lambdoid crest

Mastoid breadth (MB): greatest distance between lateral apices of mastoid portion of petrosal

Maxillary toothrow length (MTL): greatest distance between anterior-most surface of C1 and posterior-most surface of M3

Postorbital bar-premaxillary length (PBPL): greatest distance between rostral surface of premaxilla and caudal surface of postorbital bar

Palatopremaxillary length (PPL): greatest distance between rostral surface of premaxilla and caudal surface of palatine

Upper toothrow length (UTL): greatest distance between anterior-most surface of I1 and posterior-most surface of M3

Zygomatic breadth (ZB): greatest distance between lateral surfaces of zygomatic arch

Mandible

Lower toothrow length (LTL): greatest distance between anterior-most surface of i1 and posterior-most surface of m3

Mandibular condyle height (MCH): greatest distance between mandibular condyle and angular process of mandible

Mandibular condyloincisive length (MCIL): greatest distance between anterior-most surface of i1 and caudal surface of mandibular condyle

Mandibular condyle width (MCW): greatest distance between medial and lateral surfaces of mandibular condyle

Mandibular height (MH): greatest distance between coronoid and angular processes of mandible

Innominate

Ilium length (ILL): superior edge of ilium (iliac crest) to superior edge of acetabulum

Ilium width (ILW): medial edge to lateral edge along iliac crest

Innominate length (INL): superior edge of ilium (iliac crest) to inferior edge of ischium with ilium and ischium oriented vertically

Ischium length (ISL): inferior edge of acetabulum to inferior edge of ischium

craniomandibular variables (BB, LIB, MTL, PPL, MCH, MH), which maximized the number of specimens that could be included in the analysis. Given the similar sizes of the two subspecies (Table 2), we explored shape differences by standardizing the PCA variables with a body size proxy calculated as the geometric mean of these six measurements for each individual. We further compared *P. l. lowii* (*n* = 8) and *P. l. continentis* (*n* = 34) using a DFA of four craniomandibular variables (LIB, MCH, MCIL, MH) and cross-validated our model with a jackknifing procedure. These four variables were selected because they produced the strongest cross-validated model and included many individuals from both populations.

Finally, we conducted multivariate analyses on a subset of the postcranial dataset from Sargis (2000, 2002b, 2002c; see Supplementary Information 1). We performed a PCA on four innominate variables (ILL, ILW, INL, ISL; see Table 1 for abbreviations) from *P. l. lowii* (*n* = 3) and *P. l. continentis* (*n* = 4), including a specimen of *P. l. continentis* from mainland Sumatra (Fig. 1, Appendix 1). We focused on the innominate bone because this element had adequate samples (minimum of *n* = 3) for both subspecies.

Summary statistics for these innominate variables are presented in Table 2.

To compare the phenetic similarity between the two *Ptilocercus* subspecies and two well-accepted tupaiid tree-shrew species, we conducted a cluster analysis (unweighted pair-group average; UPGMA) in STATISTICA (Version 6.0, StatSoft, Tulsa, OK) on log-transformed (ln) population means of the two *Ptilocercus* subspecies and two *Dendrogale* species using 50 postcranial variables from Sargis (2000, 2002b, 2002c; see Supplementary Information 1). The phenogram from this analysis is presented with Euclidean distances.

Results

We detected no sexual dimorphism in our sample. Linear complete DFA of six craniomandibular variables produced correct sex classification rates of about 65% and 59% for the overall sample and *P. l. continentis* sample, respectively (Table 3). The t-test on condylopremaxillary length by sex was not significant for the overall sample (*t* = 0.484,

Table 2 Summary statistics (in mm) for cranial, mandibular, and innominate variables. Statistics are mean ± standard deviation, range, and sample size in parentheses (abbreviations are defined in Table 1)

Cranium

Taxon	BB	CIL	CNL	CPL	LCH	LIB	LPL
P. l. continentis	14.60 ± 0.37 13.97—15.54 (35)	35.45 ± 0.75 34.09—37.40 (34)	35.67 ± 0.74 34.24—37.46 (36)	36.15 ± 0.75 34.62—38.14 (36)	8.66 ± 0.23 8.20—9.05 (34)	8.18 ± 0.32 7.57—9.36 (36)	37.30 ± 0.72 35.59—39.07 (34)
P. l. lowii	14.47 ± 0.30 13.78—14.70 (8)	35.16 ± 0.82 34.59—36.54 (5)	35.27 ± 0.81 34.49—36.48 (5)	35.89 ± 0.83 35.22—37.24 (5)	8.73 ± 0.31 8.47—9.22 (5)	8.35 ± 0.33 7.80—8.91 (8)	37.28 ± 1.26 35.95—39.16 (8)

Taxon	MB	MTL	PBPL	PPL	UTL	ZB	
P. l. continentis	15.40 ± 0.26 14.82—15.94 (36)	12.48 ± 0.27 11.90—12.95 (37)	21.81 ± 0.51 20.74—22.97 (36)	18.12 ± 0.67 15.18—19.39 (36)	17.33 ± 0.39 16.64—18.28 (34)	21.69 ± 0.54 20.72—22.74 (34)	
P. l. lowii	15.58 ± 0.39 14.84—15.95 (6)	12.54 ± 0.34 12.15—13.11 (8)	21.81 ± 0.82 20.63—22.84 (7)	18.26 ± 0.49 17.63—19.16 (8)	17.29 ± 0.45 16.65—17.94 (8)	21.86 ± 0.86 20.70—22.85 (5)	

Mandible

Taxon	LTL	MCH	MCIL	MCW	MH
P. l. continentis	15.97 ± 0.33 15.38—16.81 (33)	6.42 ± 0.24 5.94—6.99 (37)	26.26 ± 0.58 25.32—27.76 (34)	2.62 ± 0.16 2.27—2.92 (37)	11.58 ± 0.33 10.97—12.27 (37)
P. l. lowii	16.01 ± 0.50 15.27—16.80 (8)	6.55 ± 0.26 6.18—6.92 (8)	26.18 ± 1.04 25.19—27.87 (8)	2.85 ± 0.07 2.74—2.94 (6)	12.03 ± 0.43 11.44—12.68 (8)

Innominate

Taxon	ILL	ILW	INL	ISL
P. l. continentis	12.62 ± 0.63 12.11—13.50 (4)	2.89 ± 0.08 2.82—3.00 (4)	21.24 ± 0.86 20.14—22.15 (4)	5.77 ± 0.13 5.57—5.85 (4)
P. l. lowii	12.49 ± 0.53 12.17—13.10 (3)	2.47 ± 0.17 2.28—2.58 (3)	20.42 ± 0.97 19.49—21.43 (3)	5.48 ± 0.28 5.19—5.74 (3)

$P = 0.632$) or the *P. l. continentis* sample ($t = 0.573$, $P = 0.571$). Females and males were therefore combined in all subsequent analyses.

Our skull PCA included six size-corrected craniomandibular variables. Principal component (PC) 1 accounts for over 41% of the variance and represents a contrast between braincase breadth and negatively weighted mandibular condyle height (Table 4). PC2 explains over 26% of the variance and is most influenced by negatively weighted least interorbital breadth (Table 4). A bivariate plot of these two components reveals some separation between the subspecies

Table 3 Discriminant function analysis (DFA) classification tables by sex for samples of *P. lowii* (above) and *P. l. continentis* (below) based on six skull variables: CNL, CPL, LIB, MTL, MCH, MH (abbreviations are defined in Table 1)

Actual group	Predicted group		
P. lowii			
Sex	Female	Male	Correct classification rate
Female	9	8	52.9%
Male	5	15	75.0%
Overall correct classification rate			64.9%
P. l. continentis			
Sex	Female	Male	Correct classification rate
Female	8	8	50.0%
Male	5	11	68.8%
Overall correct classification rate			59.4%

Table 4 Component loadings from principal component analysis of six craniomandibular variables (abbreviations are defined in Table 1). Loadings in bold are discussed in the text

Variable	Principal component	
	1	2
BB	**0.78**	-0.14
MTL	0.62	0.31
PPL	0.60	0.57
LIB	0.04	**-0.89**
MH	-0.62	0.59
MCH	**-0.86**	0.03
Eigenvalue	2.50	1.58
Percentage of total variance explained	41.60	26.29

along PC1, with *P. l. lowii* plotting mostly in negative morphospace and *P. l. continentis* spanning both positive and negative morphospace (Fig. 2), indicating that the former has a narrower cranium and taller mandible relative to the latter, on average. The single specimen of *P. l. continentis* from Pini plots within the area of overlap between mainland

P. l. continentis and *P. l. lowii* (Fig. 2). In contrast, the two Siberut specimens plot separately from the two subspecies in negative morphospace along PC2, suggesting that these island individuals have wider crania on average than either of the mainland populations (Fig. 2).

In a DFA of four skull variables by subspecies, over 88% of individuals were correctly classified (Table 5). All but two *P. l. continentis* specimens were correctly classified, including the two individuals from Siberut and the lone Pini specimen, and five of eight specimens of *P. l. lowii* were also correctly classified (Table 5). The Siberut and Pini individuals were still classified as *P. l. continentis* when excluded from the training dataset and treated as unknowns.

We further compared the two subspecies using a PCA including four innominate variables. PC1 is a size vector and accounts for almost 62% of the variance (Table 6). PC2 accounts for over 21% of the variance and represents a contrast between ilium length and negatively weighted ilium width (Table 6). A bivariate plot of these two components reveals separation along both axes (Fig. 3). *Ptilocercus l. lowii* plots mostly in negative morphospace along PC1 and positive morphospace along PC2, indicating that it generally

Fig. 2 Plot of principal component (PC) scores from a principal component analysis of *P. l. lowii* from Borneo, *P. l. continentis* from the Malay Peninsula, and *P. l. continentis* from offshore islands (Pini and Siberut) based on six craniomandibular variables. The percentages on the axes represent the percentage of total variance explained by each PC (Table 4)
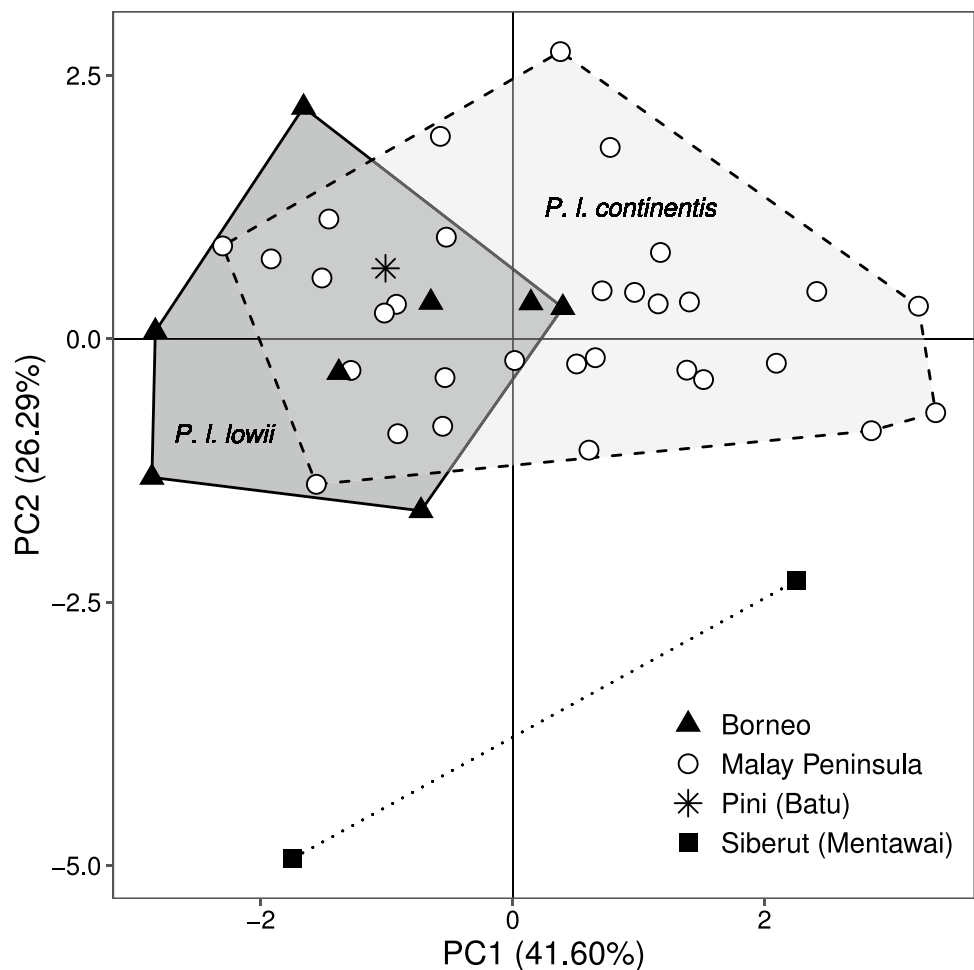
Table 5 Discriminant function analysis (DFA) classification table by subspecies based on four skull variables: LIB, MCH, MCIL, MH (abbreviations are defined in Table 1)

| Actual group | Predicted group | | |
Subspecies	*P. l. continentis*	*P. l. lowii*	Correct classification rate
P. l. continentis	32	2	94.1%
P. l. lowii	3	5	62.5%
Overall correct classification rate			88.1%

has a smaller (PC1) and longer and narrower (PC2) ilium compared to *P. l. continentis* from both Sumatra and the Malay Peninsula (Fig. 3).

In the cluster analysis of 50 postcranial variables, the two *Ptilocercus* subspecies are predictably more similar to one another than either is to the two *Dendrogale* species (Fig. 4). Most importantly, the phenetic distance between the two *Ptilocercus* subspecies is comparable to that between the two *Dendrogale* species.

Discussion

We found no evidence of sexual dimorphism in *Ptilocercus lowii* (Table 3). This is congruent with earlier conclusions about a lack of sexual dimorphism in *Ptilocercus* and other treeshrew species (Emmons 2000; Woodman et al. 2020; Juman et al. 2021).

Our morphometric analyses of *P. l. continentis* and *P. l. lowii* revealed some separation between these two subspecies in our skull PCA and complete separation in the innominate PCA (Figs. 2, 3). Over 88% of the individuals in our sample were correctly classified by subspecies in a DFA (Table 5), and the phenetic distance between the *Ptilocercus* subspecies in our cluster analysis was comparable to the distance between two well-accepted and similarly

Table 6 Component loadings from principal component analysis of four innominate variables (abbreviations are defined in Table 1). Loadings in bold are discussed in the text

| Variable | Principal component | |
	1	2
ISL	0.90	-0.06
INL	0.89	0.12
ILL	0.71	**0.55**
ILW	0.60	**-0.74**
Eigenvalue	2.48	0.86
Percentage of total variance explained	61.88	21.46

allopatric *Dendrogale* species (Fig. 4). This evidence indicates some morphological divergence between these subspecies, but further morphometric analyses with larger sample sizes are required to determine whether these taxa represent independent lineages worthy of species-level recognition. Analyses of additional postcranial data—such as those from the manus, which have been used in previous studies of treeshrew species limits (Sargis et al. 2013a, 2013b, 2014a, 2017; Juman et al. 2021)—would allow for a more robust test of the osteological differences between *P. l. lowii* and *P. l. continentis*. Our preliminary results should also be further investigated from a molecular perspective, which could explore the phylogeographic history of these two subspecies. Recent research has suggested that some small mammals spread through Sundaland in multiple waves of colonization, with Borneo colonized more recently than other islands (Camacho-Sanchez and Leonard 2020); this remains to be examined in *P. lowii*.

The colonization of offshore islands by *P. lowii* also warrants additional investigation. The single specimen of *P. l. continentis* from Pini plotted within the area of overlap between the Peninsular Malaysian *P. l. continentis* and Bornean *P. l. lowii* populations in our PCA (Fig. 2), indicating that its skull is very similar to that of mainland populations. Pini, which is one of the Batu Islands (Fig. 1), is separated from Sumatra by a shallow sea and was connected to the mainland as recently as 400 ka (Husson et al. 2020), enabling fairly recent gene flow between the populations on Pini and those on Sumatra and the Malay Peninsula. A comparable pattern of similarity is seen between *Tupaia ferruginea* on Sumatra and the Batu island of Tanahbala (Sargis et al. 2014a). In contrast, the nearby Mentawai Islands, including Siberut, have been separated from the Sunda shelf by a deep (1500 m) basin since the mid-Pleistocene (Wilting et al. 2012). The two specimens of *P. l. continentis* from Siberut are distinct from the two mainland populations in our PCA (Fig. 2). This result suggests some morphological differentiation of the more isolated Siberut population, which may represent preliminary evidence for a distinct taxon on this island. The Mentawai Islands are known for their high level of endemism (Wilting et al. 2012), including the Mentawai (or Golden-bellied) Treeshrew, *T. chrysogaster*, which ranges throughout the four major islands (Sargis et al. 2014a). However, the Mentawai *Ptilocercus* specimens still group with *P. l. continentis* rather than *P. l. lowii* in our DFA (Table 5). Because of the extremely small sample of this Siberut population (*n*=2), we require additional specimens and morphometric data, as well as molecular phylogeographic data, to fully assess its potential distinction from the rest of *P. l. continentis*.

Ptilocercus lowii is currently listed as a species of Least Concern on the *IUCN Red List of Threatened Species* (Cassola 2016). Regardless, the conservation
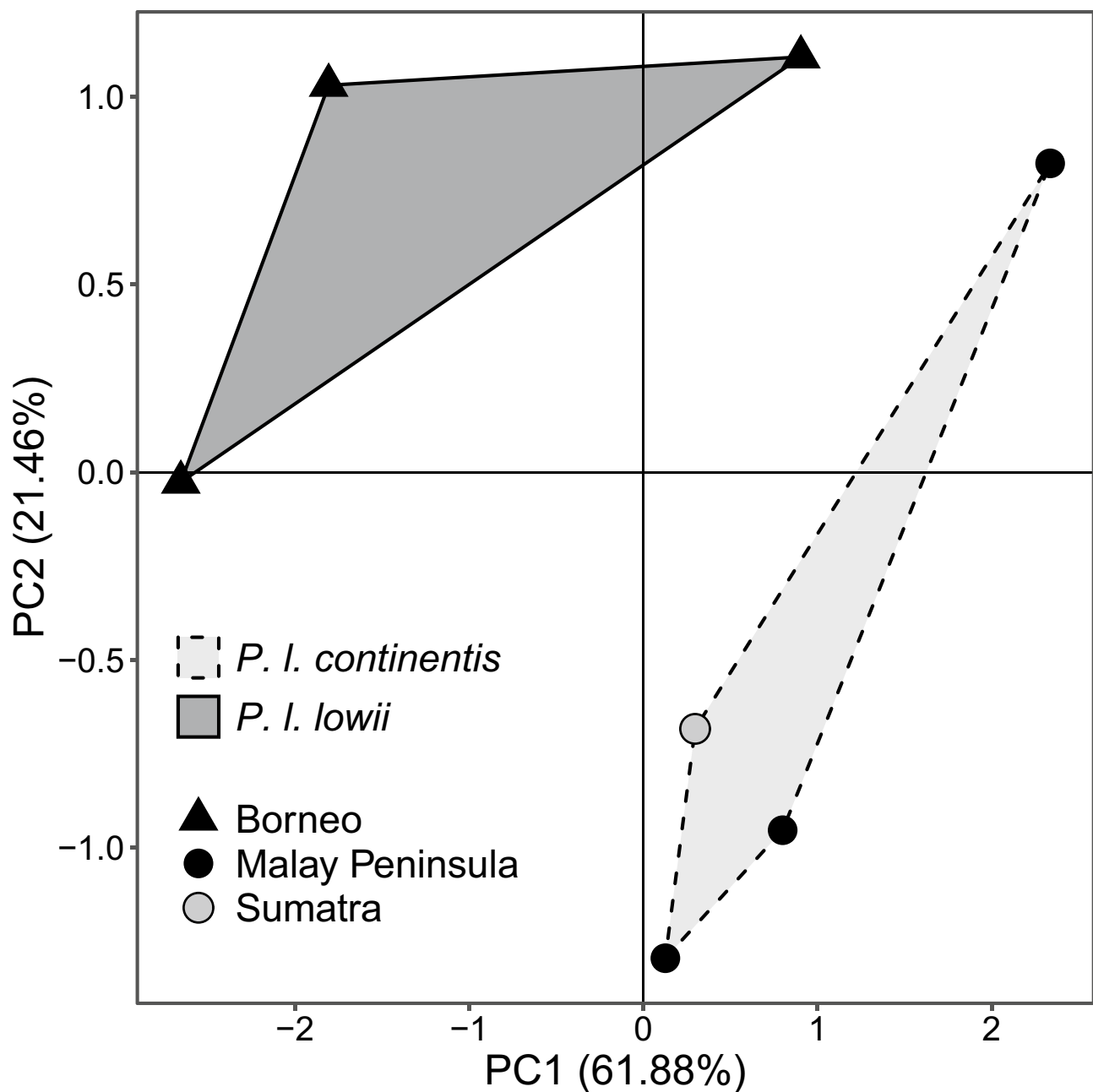
Fig. 3 Plot of principal component (PC) scores from a principal component analysis of the two subspecies of *Ptilocercus lowii* (*P. l. continentis* and *P. l. lowii*) based on four innominate variables. The percentages on the axes represent the percentage of total variance explained by each PC (Table 6)

priorities for *P. lowii* should be reevaluated considering the possibility of evolutionary divergence of the two subspecies, especially in light of the IUCN's determination that the *P. lowii* population is "decreasing." As exclusively arboreal treeshrews that apparently only nest in mature trees (Emmons 2000; Hawkins 2018), both *P. l. lowii* and *P. l. continentis* will be negatively impacted by ongoing deforestation occurring on Borneo, Sumatra, and the Malay Peninsula. However, deforestation and habitat fragmentation are driven by different forces on these landmasses, and each subspecies may require separate conservation interventions. Malaysian Borneo, home to *P. l. lowii*, is losing vast amounts of forest to oil palm and pulpwood plantations (Gaveau et al. 2016; Miettinen et al. 2016). These industries also contribute to vegetation loss in regions where *P. l. continentis* resides, but there are additional anthropogenic threats on the densely populated Malay Peninsula, including fragmentation due to large

Fig. 4 Phenogram, with Euclidean distances, derived from a cluster analysis of 50 postcranial variables (see Supplementary Information 1). The phenetic distance between the *Ptilocercus* subspecies is similar to that between the *Dendrogale* species
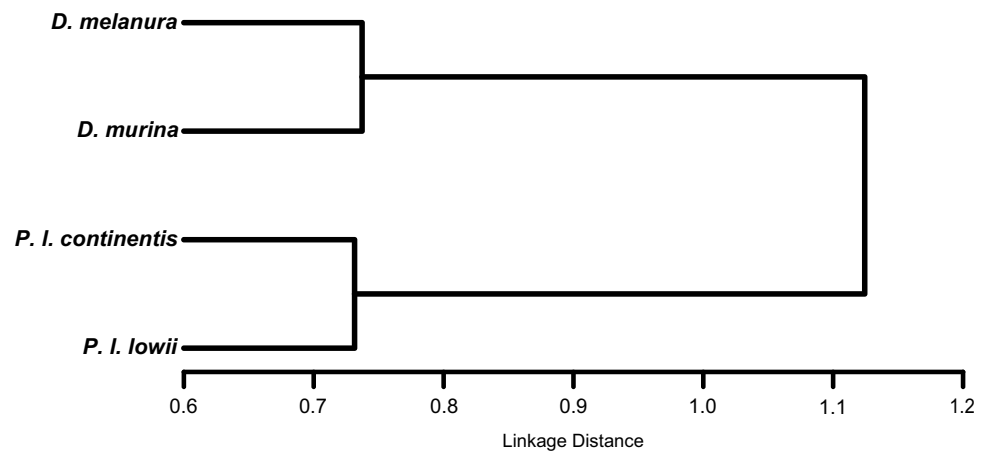
highways, human-wildlife conflict near urban centers, and pollution (Azlan 2006; Tee et al. 2018; Jambari et al. 2019). Thus, population trends and specific threats should be separately assessed for *P. l. lowii* and *P. l. continentis* to ensure that both subspecies are adequately protected, especially because these are the only extant members of this distinctive family of treeshrews.

Our study reaffirms the importance of quantitatively delineating Southeast Asian mammal species to better inform conservation decisions, particularly for remarkable and phylogenetically critical taxa like *P. lowii*. The ranges of both *P. l. lowii* and *P. l. continentis* are contained within the Sundaland biodiversity hotspot, which is increasingly threatened by anthropogenic impacts (Myers et al. 2000; Hawkins 2018; Tee et al. 2018; Han et al. 2020). Despite these concerns, this region is still poorly studied relative to other areas that are less biodiverse and less threatened (Sodhi et al. 2004). Further studies on *P. lowii* and other Sundaland mammals will be crucial for illuminating and protecting biodiversity in disappearing habitats. In order to obtain robust samples for future analyses, it is critical to conduct more biological surveys in underrepresented regions such as Bangka, Siberut, and Sumatra.

Appendix 1 Specimens Examined

Specimens from the following institutions were included in this study: Field Museum of Natural History (FMNH), Chicago, IL; Museum of Comparative Zoology at Harvard University (MCZ), Cambridge, MA; The Natural History Museum (NHMUK), London, UK; Oxford University Museum of Natural History (OUMNH), Oxford, UK; Natinaal Natuurhistorisch Museum (RMNH), Leiden, Netherlands; United States National Museum of Natural History (USNM), Washington, DC; and Yale Peabody Museum of Natural History (YPM), New Haven, CT. Specimens used in the innominate analysis are indicated with an asterisk.

Ptilocercus lowii lowii (*n* = 8).—Borneo: no locality (OUMNH ZC-08974); Sabah: Sapagaya Forest Reserve (FMNH 76855*); mainland opposite Labuan (NHMUK 76.5.2.8); Sarawak, no locality (YPM MAM 10179*, NHMUK 1934.5.6.1*); Balingian (NHMUK 55.662); Bintulu (FMNH 57450); Kuching (MCZ 35380).

Ptilocercus lowii continentis (*n* = 35).—Malay Peninsula: Bukit Cherakah Forest Reserve (USNM 488065); Bukit Lagong Forest Reserve (NHMUK 61.1154, 61.1155, 1960.8.4.6*; USNM 481104, 481105, 488062); Gunung Benom (NHMUK 67.1479*); Johore (USNM 112611, 612250); Kepong (USNM 291272); Kuala Langat Forest Reserve (USNM 481108, 488057, 488059, 488060, 488061, 488064, 488071, 488072); Kuala Lumpur (type locality; NHMUK 10.4.17.1—holotype); Singapore (MCZ 51736*); Subang Forest Reserve (USNM 481103, 488053, 488054, 488055, 488066, 488067, 488068, 488069, 488070); Sungei Buloh Forest Reserve (USNM 481102, 488052, 488063, 488073); Sumatra: Deli: Tandjong Morawa (RMNH a*).

Ptilocercus lowii continentis (*n* = 3).—Batu Islands, Pini (= Pinie) (USNM 121855); Mentawai Islands, Siberut: Daman River (NHMUK 78.2939); Paitan River (NHMUK 78.2938).

Declarations

Conflicts of interest The authors declare that they have no conflicts of interest.

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