

Taxonomic Boundaries and Craniometric Variation in the Treeshrews (Scandentia, Tupaiidae) from the Palawan Faunal Region

Eric J. Sargis · Kyle K. Campbell · Link E. Olson

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Abstract The taxonomy of treeshrews (Order Scandentia) has long been complicated by ambiguous morphological species boundaries, and the treeshrews of the Palawan faunal region of the Philippines are no exception. Four named forms in the genus *Tupaia* Raffles, 1821, have been described from four island groups based on subtle qualitative morphological characters, and as many as three distinct species have been recognized. A recent molecular phylogenetic study of relationships among *Tupaia* species suggests that the two currently-recognized treeshrew species from the Palawan faunal region diverged very recently relative to other sister-species divergences within the genus and may not represent species-level taxonomic entities. Here we review the taxonomic and biogeographic histories of the *Tupaia* taxa from this region. We also collected craniodental data from 133 skulls of all four named forms, representing five island populations, and conducted univariate and multivariate analyses on these data. Our morphometric results are consistent with molecular results, further suggesting that there is insufficient evidence to recognize *T. moellendorffi* Matschie, 1898, as a separate species from *T. palawanensis* Thomas, 1894. Our analyses also revealed a craniodentally divergent population from the island of Balabac, which has

never been considered a distinct subspecies (or species) from the population on Palawan. These results have conservation implications for the island populations in our analyses, but additional surveys and molecular evidence will be required to fully assess conservation priorities for the treeshrews of the Palawan faunal region.

Keywords Cranium · Morphology · Philippines · Skull · Taxonomy · *Tupaia*

Introduction

Background

Treeshrews (Scandentia) are an ordinal clade of Indomalayan small mammals whose interordinal relationships have been well studied and debated (reviewed by Sargis 2004, 2007; Sargis et al. 2013). Despite this, the species-level taxonomy of treeshrews has not been comprehensively reviewed since the first and only monographic account was published a century ago (Lyon 1913). Bouts of splitting and lumping as recently as the 1990s have served to further obscure the taxonomic boundaries and evolutionary history of treeshrews (e.g., Corbet and Hill 1992; Olson et al. 2005; Sargis et al. 2013). One group in particular, the species complex of *Tupaia palawanensis* Thomas, 1894 (Sanborn 1952), has experienced a dynamic taxonomic history of recurrent species elevations and synonymizations.

The *T. palawanensis* species complex is endemic to the Palawan faunal region of the Philippines (Fig. 1). As currently recognized (Helgen 2005), the monotypic Palawan treeshrew, *T. palawanensis*, is distributed throughout the island of Palawan and its associated minor islands (e.g., Balabac), while the Calamian treeshrew, *T. moellendorffi* Matschie, 1898, is represented by three subspecies on the

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E. J. Sargis (✉)
Department of Anthropology, Yale University, P.O. Box 208277,
New Haven, CT 06520, USA
e-mail: eric.sargis@yale.edu

E. J. Sargis
Division of Vertebrate Zoology, Yale Peabody Museum of Natural
History, New Haven, CT 06520, USA

K. K. Campbell · L. E. Olson
University of Alaska Museum, University of Alaska Fairbanks,
Fairbanks, AK 99775, USA

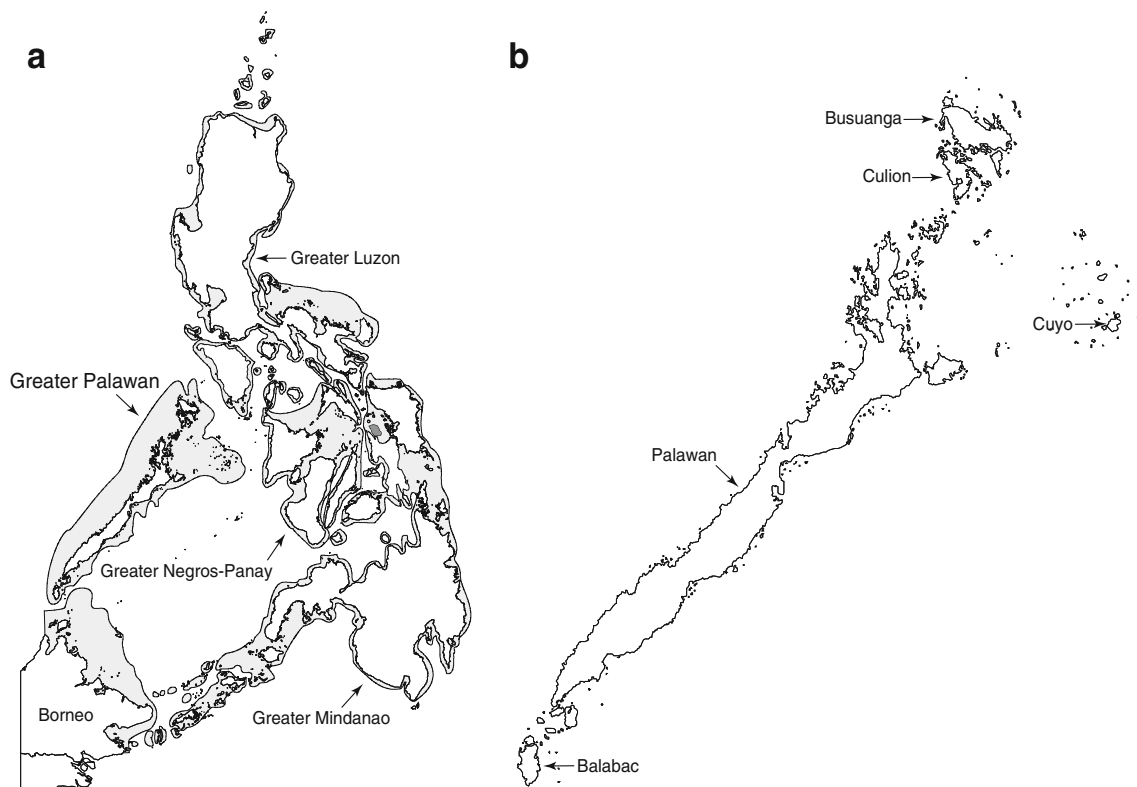


Fig. 1 **a** The Philippines, showing Pleistocene aggregate island complexes (indicated in grey) resulting from a 120 m drop in sea level. **b** Palawan faunal region showing Palawan, Balabac, Culion, Busuanga, and Cuyo. Maps modified from Roberts (2006a, b: fig. 1)

islands of Culion, Busuanga, and Cuyo and their smaller surrounding islands. Shallow seas and relatively short distances (Tables 1, 2 and 3) separate these five islands (see Heaney 1986: table 1), and treeshrews are believed to be very poor overwater dispersers (Olson et al. 2005). Collectively, this suggests the existence of connective landbridges during the Pleistocene glacial maxima that likely coincided with the overland dispersal and/or vicariant persistence of non-volant mammals in the Palawan faunal region (Holloway 1982; Heaney 1985, 1986; Hall and Holloway 1998; see Fig. 1). The current distribution of the Palawan and Calamian treeshrews is highly fragmented and is presumably susceptible to anthropogenic forces in the Philippines that include, but are not limited to, habitat loss due to logging, mining and rural farming, and the subsequent soil erosion in montane forests (Heaney and Regalado 1998). Although the conservation status of the Palawan treeshrew is ranked as “Least Concern” (Gonzalez et al. 2008) and that of the Calamian treeshrew is “Data Deficient” (Heaney 2008), this group represents a unique and irreplaceable component of the biodiversity of the Palawan faunal region. Preserving such biological distinctiveness is an essential component of the conservation priorities in the Philippines, which is described as a mega-diverse country and one of the “hottest” biodiversity hotspots. With less than 11 % of its original forests currently

intact, nearly half of its endemic species are threatened with extinction (Myers et al. 2000; Conservation International 2008; http://www.conservation.org/where/priority_areas/hotspots/asia-pacific/Philippines/Pages/default.aspx).

Taxonomic History

The first descriptions of treeshrews collected from Palawan identified them as the more widely-distributed common treeshrew, *T. glis* (Diard, 1820), without assigning subspecies status (Everett 1889). Thomas (1894) later deemed treeshrews from the island of Palawan to be distinct enough from the *typica* form of *T. ferruginea* Raffles, 1821, to be described as a subspecies, *T. f. palawanensis*, based on the presence of a black tail and a slightly narrower muzzle (Lyon 1913). Four years later, the Calamian treeshrew, *T. moellendorffi*, was described from Culion Island based on smaller overall size and buffier tail color compared to Palawan treeshrews (see Table 4). In 1910, treeshrews from the Cuyo Islands, the most isolated island group of the Palawan faunal region (Tables 1, 2 and 3, Fig. 1b), were described as *T. cyonis* Miller, 1910, based on subtle pelage variation on the venter and sides. In 1913, Lyon compiled the most comprehensive review of treeshrews to date, in which he elevated the Palawan treeshrew to full species status and continued to recognize *T. moellendorffi* and *T.*

cuyonis as distinct species. By 1952, the Palawan treeshrew had subsumed the Cuyo and Calamian treeshrews as subspecies of *T. palawanensis*, and a new form from Busuanga Island, *T. p. busuanga* Sanborn, 1952, was described based on a slightly longer and narrower skull and subtle pelage variation in the tail.

Although karyotypic data (Arrighi et al. 1969) and immunological distances (Dene et al. 1978, 1980) both supported the distinctiveness of *T. palawanensis* from *T. glis*, Corbet and Hill (1992) synonymized all four named forms with *T. glis* without assigning any infraspecific ranks, though they suggested a possible elevation of *T. palawanensis* to full species status. Wilson (1993) and Heaney et al. (1998) followed Honacki et al. (1982) in recognizing *T. palawanensis* without assigning any infraspecific ranks. In 2000, over a century after the Palawan treeshrew was first identified and described within *Tupaia* [*glis*], *T. palawanensis* was empirically separated from the common treeshrew, being placed in a different subgenus (*Lyonogale* Conisbee, 1953) based on morphometrics of craniodental and external measurements (Han et al. 2000). In the most recent (third) edition of *Mammal Species of the World* (Wilson and Reeder 2005), the Calamian treeshrew was once again provisionally elevated to full species status, including three subspecies: *T. m. moellendorffi*, *T. m. cuyonis*, and *T. m. busuanga* (Helgen 2005; Table 4). Furthermore, the synonymization of the *T. palawanensis* group with *T. glis* by Corbet and Hill (1992), based on the perceived lack of discrete characters differentiating many of the described *Tupaia* species and subspecies, has since been regarded as an example of over-lumping that ignored much cryptic diversity (Wilson 1993; Helgen 2005).

Relying on subtle quantitative or qualitative morphological characters alone to define infraspecific taxonomic boundaries involves varying degrees of subjectivity. In a family as phenotypically conservative as Tupaiidae (see Sargis 2001, 2002a, b, c, 2004), morphology-based phylogenies can undoubtedly be obscured by plesiomorphic and convergent characters (Olson et al. 2004a). Cryptic diversity may be one of the factors contributing to the confusing taxonomic history of Tupaiidae, with early collectors and taxonomists placing a great deal of emphasis on qualitative pelage variations as subtle as “underparts a grizzled buffy-brown scarcely different from color of sides” (Miller 1910:

393). In recognition that external morphology alone cannot always clearly delineate species and subspecies boundaries in poorly characterized species complexes such as the *T. palawanensis* group, it is necessary to draw on other lines of evidence, such as DNA sequence variation and morphometric analyses, to infer phylogenetic relationships and species limits that may better reflect their true evolutionary histories.

Subsequent species-level phylogenies of Scandentia, based on mitochondrial and nuclear DNA sequences, have supported the separation of the *T. palawanensis* group from *T. glis*, though not the monophyly of *Lyonogale* (Olson et al. 2005; Roberts et al. 2009, 2011). Given that Borneo is the closest landmass to the Palawan faunal region that is inhabited by treeshrews (Table 2), it is not surprising that the closest relative of the *T. palawanensis* complex is a clade of treeshrews from Borneo, including *T. minor* Günther, 1876, *T. splendidula* Gray, 1865, and *T. tana* Raffles, 1821 (Roberts et al. 2009), as well as *T. picta* Thomas, 1892, and *T. montana* Thomas, 1892 (Roberts et al. 2011). In some places current sea level depth between Palawan and Borneo is less than 140 m (Table 3) and sea level may have dropped as much as 165 m during a glacial period around 165,000 years ago (Heaney 1985, 1986; Esselstyn et al. 2004). This would have resulted in a landbridge between Borneo and the Palawan island group during the Pleistocene (Heaney 1985, 1986; Esselstyn et al. 2004). However, sea level may have only dropped 115–135 m (Voris 2000; Esselstyn et al. 2004), which could have narrowed the gap between Borneo and Palawan without forming a continuous landbridge. Furthermore, Roberts et al. (2011) suggested a much earlier divergence between the Bornean and Palawan clades during the Miocene (10–15 Mya), so treeshrew colonization of Palawan from Borneo may not have been related to Pleistocene geography (see also Jones and Kennedy 2008; Blackburn et al. 2010; Oliveros and Moyle 2010). In contrast, the split between *T. palawanensis* (from Palawan) and *T. moellendorffi* (from Culion) is much more recent, having probably occurred during the Pleistocene (0.68 Mya), and there is very little mitochondrial DNA differentiation between these two taxa (Roberts et al. 2011).

In the case of treeshrews of the *T. palawanensis* complex, current phylogenies confirm many of the observations made by the taxonomists who originally described tupaiid

Table 1 Area, elevation, depth, and distance to largest island, Palawan (from Heaney 1986)

Island	Palawan	Busuanga	Culion	Cuyo	Balabac
Area (km ²)	11785	938	400	57	306
Elevation (m)	2084	695	495	34	605
Depth to Palawan (m)		73	73	138	91
Distance to Palawan (km)		86	55	91	31

Table 2 Pair-wise minimum distances among islands generated using Google Earth version 6.1.0.5001

Minimum distance (km)	Palawan	Busuanga	Culion	Cuyo	Balabac	Borneo
Palawan		83	55	145	31	145
Busuanga	83		6	140	542	636
Culion	55	6		138	508	601
Cuyo	145	140	138		529	598
Balabac	31	542	508	529		89
Borneo	145	636	601	598	89	

diversity in the Philippines. Lyon (1913: 79) observed that although previous authors (Everett 1889; Nehring 1894) had described tupaiids from both Palawan and Culion as *T. ferruginea*, “*Tupaia palawanensis* is a very distinct form, and quite different from its geographic neighbor, *T. longipes* [formerly *T. ferruginea longipes*], of Borneo” based on its unique pelage color and pattern and the absence of the elongated feet diagnostic of *T. longipes* (Thomas, 1893). As early as 1898, Matschie referred to the Palawan treeshrew as *T. palawanensis* when describing the type specimen of *T. moellendorffi*. Indeed, phylogenies derived from DNA sequence data consistently recover treeshrews of the *T. palawanensis* group as being very distinct from both *T. glis* and *T. longipes* (Olson et al. 2005; Roberts et al. 2009, 2011). Lyon (1913: 81–82) added that “*Tupaia moellendorffi* is quite different and apparently very distinct from its geographic neighbor, *T. palawanensis*” (p. 81) and that “*T. moellendorffi* and *T. cuyonis* are closely related forms” (p. 82) based on measurements of the skull and body length and subtle pelage variation. Although the relationships among *T. palawanensis* and all subspecies of *T. moellendorffi* have yet to be assessed in molecular analyses, Lyon’s acknowledgement of the close relationship between the Calamian treeshrews is reflected in current taxonomy (Helgen 2005). Sanborn (1952: 110) also recognized *T. p. busuanga* to be more similar to *T. p. moellendorffi* and *T. p. cuyonis* than to *T. p. palawanensis* on the basis that the “three races [*T. p. moellendorffi*, *T. p. cuyonis*, and *T. p. busuanga*] are lighter than [*T. p. palawanensis* and have the same body color, but differ in the color of the tail.” A similar observation constitutes the basis of Helgen’s (2005) provisional recognition of *T. moellendorffi*.

In addition to the four described forms, further sampling and comparisons could potentially reveal one or more

additional forms on islands included in the range of *T. palawanensis*, such as Balabac, that have been separated from Palawan for equal amounts of time as those in the *T. moellendorffi* complex. Here we analyze the craniodental morphology of *T. palawanensis* from Palawan and Balabac and *T. moellendorffi* from Culion, Busuanga, and Cuyo to assess morphometric variation in these taxa. We use univariate and multivariate statistics to compare the two currently recognized species, three *T. moellendorffi* subspecies, and five island populations. We then evaluate the provisional recognition of *T. moellendorffi* by Helgen (2005) in light of our morphometric results.

Materials and Methods

We recorded 22 craniodental measurements (Table 5) from the skulls of 133 adult (those with fully erupted permanent dentition) specimens (Table 6) to the nearest 0.01 mm using digital calipers. Summary statistics, including means and standard deviations, are presented in Table 7. The specimens we analyzed are housed in the following museums: American Museum of Natural History (AMNH), New York; The Natural History Museum (BMNH), London; Field Museum of Natural History (FMNH), Chicago; Museum of Comparative Zoology at Harvard University (MCZ), Cambridge, MA; Senckenberg Naturmuseum (SMF), Frankfurt; United States National Museum of Natural History (USNM), Washington, D.C.; and the Museum für Naturkunde (ZMB), Berlin.

We conducted univariate and multivariate analyses in STATISTICA (Version 6.0, StatSoft, Tulsa, OK). Each measurement was compared between the two species using

Table 3 Pair-wise minimum sea depths among islands generated using GeoMapApp 3.3.0. (<http://www.geomapapp.org>; Ryan et al. 2009)

Minimum sea depth (m)	Palawan	Busuanga	Culion	Cuyo	Balabac	Borneo
Palawan		58	58	82	55	136
Busuanga	58		23	82	58	136
Culion	58	23		82	58	136
Cuyo	82	82	82		82	136
Balabac	55	58	58	82		136
Borneo	136	136	136	136	136	

Table 4 Taxonomy, holotypes, and descriptions of the *T. palawanensis* group (Lyon 1913; Sanborn 1952; Helgen 2005)

Species and authority	Current taxonomy	Type specimen	Island	Original descriptions of distinguishing characters
<i>Tupaia ferruginea palawanensis</i> Thomas, 1894	<i>T. palawanensis</i>	BMNH 94.2.1.3	Palawan	black tail and narrower muzzle than <i>T. ferruginea</i>
<i>Tupaia moellendorffi</i> Matschie, 1898	<i>T. moellendorffi moellendorffi</i>	ZMB 9858	Culion	smaller size and buffier tail than <i>T. palawanensis</i>
<i>Tupaia cuyonis</i> Miller, 1910	<i>T. m. cuyonis</i>	USNM 239182	Cuyo	grizzled buffy brown undersides that differed from sides more so than in <i>T. moellendorffi</i>
<i>Tupaia palawanensis busuangae</i> Sanborn, 1952	<i>T. m. busuangae</i>	FMNH 62969	Busuanga	differentiated from <i>T. m. moellendorffi</i> and <i>T. m. cuyonis</i> by blackish tail much darker than back

Student's *t*-test. They were also compared among the five island populations (Palawan, Balabac, Culion, Busuanga, and Cuyo) using one-way ANOVA, with the Tukey honest significant difference (HSD) post-hoc test ($P < 0.05$).

In addition to the univariate analyses, we also performed cluster and principal components analyses. The cluster analysis (unweighted pair-group average; UPGMA) of population means included all 22 measurements. The principal components analyses (PCA) were conducted on correlation matrices (generalized inverse) of both population means and individuals. The PCA of population means maximized the

number of variables (all 22) that could be included in the analysis, as several variables are missing in individual specimens. Because of missing data due to broken specimens, ten variables were eliminated from the PCA of individuals (see Table 5); this allowed several specimens, particularly from taxa with small sample sizes (e.g., *T. moellendorffi moellendorffi* and *T. m. cuyonis*), to be included in the analysis. Given that the PCA of means and individuals include different numbers of variables (22 vs. 12, respectively), they produce different results in morphospace (see Sargis et al. 2013).

Table 5 Measurement descriptions (and abbreviations) following Olson et al. (2004b, 2009). The 12 measurements included in the PCA of individuals are indicated with an asterisk. Upper-case

abbreviations for teeth (i.e., I, C, P, M) refer to maxillary and premaxillary teeth; lower-case abbreviations (i, c, p, m) refer to mandibular teeth

- 1.) Condyl-premaxillary length (CPL): greatest distance between rostral surface of premaxilla and caudal surface of occipital condyle.
- 2.) Condyl-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.) Condyl-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 condyl-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.*

Table 6 Specimens examined. Museum abbreviations: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; FMNH, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology at Harvard

University, Cambridge, MA; SMF, Senckenberg Naturmuseum, Frankfurt; USNM, United States National Museum of Natural History, Washington, DC; ZMB, Museum für Naturkunde, Berlin

Tupaia moellendorffi busuanga ($n=13$).—Busuanga: Dimaniang (type locality) (FMNH 62969—holotype); Boco Boco Coron (AMNH 207598–207599); Papaya Coron (AMNH 207596–207597); San Nicolas, 6 km NE (USNM 477830–477837).

Tupaia moellendorffi cuyonis ($n=7$).—Cuyo: no locality (AMNH 242088; FMNH 63007, 63008; USNM 239182—holotype); Balaguen (FMNH 63006); Centro (FMNH 63004); San Carlos (FMNH 63005).

Tupaia moellendorffi moellendorffi ($n=6$).—Culion: no locality (SMF 4946; ZMB 9858—holotype); Siuk (FMNH 62974, 62975); 6.5 km SW (USNM 477838, 477839).

Tupaia palawanensis ($n=9$).—Balabac: no locality (AMNH 175465); Dalawan Bay, Minagas Point (USNM 477755, 477758–477762, 477764, 477765).

Tupaia palawanensis ($n=98$).—Palawan: no locality (BMNH 94.2.1.3—holotype, 94.2.1.4, 97.9.12.1, 2010.217^a); Aborlan, Kabigaan (AMNH 207594, 207595); Brooke's Point (AMNH 175466, 175467, 242089, 242090), Kabelnekan (FMNH 63009), Macagua (USNM 477738–477740, 477742, 477743, 477745, 477746, 477748–477751), Pinigisan (USNM 477753); Iwahig (AMNH 29724, 29725); Maojan (SMF 25977, 25979); Puerto Princesa (FMNH 62937, 62939–62942, 62946–62950, 62952–62956, 62960, 62961, 62963–62968, 62976, 62985, 62986, 62988, 62998, 63000, 63016, 63018–63020; MCZ 35244), Canigaran (FMNH 62978, 62979, 62980, 62983, 62984), Concepcion, Tarabanan River (USNM 477768, 477773–477775, 477778, 477779, 477790, 477792, 477794–477796, 477801, 477803, 477805, 477806, 477808, 477810, 477811–477815, 477817, 477818); Roxas, Malabusog, Tinitian (USNM 477820–477823, 477825–477828).

^a Palawan or Basilan, but unlikely from Basilan near Mindanao (Lyon 1913)

Results

Univariate

In the *t*-tests comparing *T. palawanensis* to *T. moellendorffi*, the two taxa were significantly different from one another in 17 of the 22 variables (see Online Resource 1). However, the results of the ANOVA show that most of the significant differences are between *T. palawanensis* from Balabac and the other four island populations (Table 8). The Balabac population is significantly different from the three *T. moellendorffi* populations in 20 or 21 out of the 22 variables, but it also differs in 21 variables from its conspecific on the island of Palawan. Two *T. moellendorffi* populations, those from Culion and Cuyo, differ from Palawan *T. palawanensis* in seven and eight variables, respectively (Table 8), whereas the *T. moellendorffi* from Busuanga only differs from the Palawan population in one variable, lacrimal breadth.

Multivariate

Means

In the cluster analysis of all 22 variables, *T. moellendorffi moellendorffi* is most similar to *T. m. cuyonis*, but *T. m. busuanga* is most similar to *T. palawanensis* from Palawan (Fig. 2). *Tupaia palawanensis* from Balabac is the least similar to the other four populations.

The PCA of population means included all 22 variables. The bivariate plot of factors 1 and 2 shows the separation of *T. moellendorffi* in positive morphospace from *T. palawanensis* in negative morphospace along factor 1 (Fig. 3). The first factor, which represents size (inverted so larger populations

are toward the left), accounts for more than 91 % of the total variance and factor 2 accounts for more than 6 % (Table 9a; factor loadings in Online Resource 1).

Individuals

In the PCA of individuals, 12 of the 22 variables were included in the analysis. Bivariate plots of the first 2 factors are shown in Fig. 4. Factor 1, a size vector (inverted so larger individuals are toward the left), accounts for more than 74 % of the total variance and factor 2 accounts for nearly 8 % (Table 9b; factor loadings in Online Resource 1). In the comparison of two species, *T. moellendorffi* plots towards the right and *T. palawanensis* on the left, but there is considerable overlap in morphospace between the two taxa (Fig. 4a). When the two taxa are divided into the five island populations, *T. moellendorffi moellendorffi* and *T. m. cuyonis* do not overlap with *T. palawanensis*, but *T. m. busuanga* overlaps substantially with *T. palawanensis* from Palawan (Fig. 4b); *T. palawanensis* from Balabac and Palawan mostly do not overlap, with only one individual of the former occupying the morphospace of the latter.

Discussion

Tupaia moellendorffi was “provisionally” recognized by Helgen (2005: 107), and we found some support for its distinction from *T. palawanensis* in the results of our *t*-tests. Further support for the separation of these two taxa comes from the PCA of means, in which *T. moellendorffi* and *T. palawanensis* plot in positive and negative morphospace, respectively, along factor 1 (Fig. 3). This is indicative of the

Table 7 Craniodental measurements (mm), including means±SD, range of measurements, and sample sizes in parentheses. See Table 5 for measurement abbreviations and descriptions

Genus	Species	Subspecies	Island	1) CPL	2) CIL	3) UTL	4) MTL	5) EPL	6) PPL
<i>Tupaia</i>	<i>moellendorffi</i>	<i>busuanga</i>	Busuanga	44.13±0.98	43.64±1.11	24.79±0.65	16.65±0.39	32.05±0.99	26.12±0.64
				42.93–46.43	42.38–46.04	24.12–26.26	16.02–17.28	30.93–34.00	25.39–27.48
				(9)	(8)	(11)	(11)	(9)	(11)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>cuyonis</i>	Cuyo	43.30±0.59	42.70±0.44	23.82±0.14	16.19±0.22	31.91±0.48	25.28±0.40
				42.76–44.12	42.31–43.32	23.69–24.03	15.81–16.46	31.50–32.51	24.90–25.79
				(4)	(4)	(5)	(6)	(4)	(5)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>moellendorffi</i>	Culion	43.47±0.53	42.79±0.58	24.01±0.24	16.13±0.22	31.15±0.50	25.44±0.21
				43.11–44.08	42.36–43.45	23.74–24.27	15.82–16.41	30.75–31.87	25.17–25.71
				(3)	(3)	(4)	(5)	(4)	(5)
<i>Tupaia</i>	<i>palawanensis</i>		Palawan	44.84±1.24	44.24±1.19	25.11±0.76	17.03±0.59	32.45±1.06	26.49±0.76
				42.20–49.79	41.66–48.83	23.76–27.69	15.91–19.32	27.65–34.08	24.76–28.36
				(73)	(66)	(72)	(77)	(50)	(57)
<i>Tupaia</i>	<i>palawanensis</i>		Balabac	47.19±1.24	46.62±1.17	26.77±0.63	18.11±0.41	34.52±1.27	28.16±0.96
				45.16–49.41	44.84–48.75	25.67–27.70	17.28–18.79	32.06–35.98	26.64–29.44
				(9)	(9)	(9)	(9)	(9)	(7)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>busuanga</i>	Busuanga	10.57±0.63	17.51±0.32	16.87±0.54	13.51±0.50	23.85±0.55	18.43±0.41
				9.87–11.23	16.93–17.91	16.12–17.86	12.74–14.59	22.98–24.83	17.63–19.03
				(4)	(9)	(13)	(13)	(10)	(10)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>cuyonis</i>	Cuyo	11.00±0.05	17.08±0.12	16.71±0.42	13.17±0.57	24.23±0.43	18.05±0.27
				10.96–11.03	17.00–17.25	16.17–17.27	12.46–14.01	23.70–24.72	17.73–18.40
				(2)	(4)	(5)	(7)	(4)	(4)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>moellendorffi</i>	Culion	10.66±0.06	17.50±0.49	16.30±0.50	12.93±0.49	24.09±0.53	18.77±0.49
				10.61–10.70	16.98–17.96	15.81–16.99	12.53–13.78	23.56–24.81	18.39–19.32
				(2)	(3)	(4)	(5)	(4)	(3)
<i>Tupaia</i>	<i>palawanensis</i>		Palawan	10.72±0.48	17.50±0.50	17.36±0.60	13.69±0.63	24.30±0.71	18.61±0.40
				9.66–11.72	16.59–19.16	16.02–18.73	12.45–15.04	22.60–26.16	17.95–20.27
				(24)	(61)	(75)	(90)	(66)	(73)
<i>Tupaia</i>	<i>palawanensis</i>		Balabac	11.60±0.57	18.64±0.38	18.22±0.48	14.65±0.62	26.12±0.55	18.61±0.42
				10.90–12.20	17.98–19.39	17.66–19.28	13.80–15.96	25.40–27.33	18.15–19.46
				(4)	(9)	(8)	(9)	(9)	(9)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>busuanga</i>	Busuanga	47.80±0.94	42.52±0.81	31.50±0.79	21.23±0.65	11.94±0.31	12.86±0.59
				46.66–49.56	41.76–44.47	30.44–33.17	20.36–22.59	11.54–12.55	12.14–14.19
				(12)	(9)	(13)	(13)	(9)	(11)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>cuyonis</i>	Cuyo	46.48±0.69	41.97±0.57	30.97±0.32	20.55±0.18	11.72±0.27	12.29±0.31
				45.78–47.36	41.25–42.63	30.59–31.37	20.31–20.73	11.34–11.97	11.79–12.71
				(4)	(4)	(5)	(4)	(4)	(6)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>moellendorffi</i>	Culion	46.94±0.32	41.36±0.26	30.88±0.50	20.46±0.46	11.76±0.17	12.47±0.45
				46.64–47.28	41.17–41.66	30.06–31.28	19.84–21.00	11.58–11.91	11.92–12.95
				(3)	(3)	(5)	(6)	(3)	(6)
<i>Tupaia</i>	<i>palawanensis</i>		Palawan	48.32±1.32	43.14±1.09	32.04±0.97	21.85±0.84	11.93±0.36	13.18±0.62
				45.90–52.83	40.88–45.66	30.03–35.09	20.50–24.32	11.27–13.05	11.94–15.03
				(72)	(65)	(85)	(87)	(67)	(89)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>busuanga</i>	Busuanga	47.80±0.94	42.52±0.81	31.50±0.79	21.23±0.65	11.94±0.31	12.86±0.59
				46.66–49.56	41.76–44.47	30.44–33.17	20.36–22.59	11.54–12.55	12.14–14.19
				(12)	(9)	(13)	(13)	(9)	(11)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>cuyonis</i>	Cuyo	46.48±0.69	41.97±0.57	30.97±0.32	20.55±0.18	11.72±0.27	12.29±0.31
				45.78–47.36	41.25–42.63	30.59–31.37	20.31–20.73	11.34–11.97	11.79–12.71
				(4)	(4)	(5)	(4)	(4)	(6)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>moellendorffi</i>	Culion	46.94±0.32	41.36±0.26	30.88±0.50	20.46±0.46	11.76±0.17	12.47±0.45
				46.64–47.28	41.17–41.66	30.06–31.28	19.84–21.00	11.58–11.91	11.92–12.95
				(3)	(3)	(5)	(6)	(3)	(6)
<i>Tupaia</i>	<i>palawanensis</i>		Palawan	48.32±1.32	43.14±1.09	32.04±0.97	21.85±0.84	11.93±0.36	13.18±0.62
				45.90–52.83	40.88–45.66	30.03–35.09	20.50–24.32	11.27–13.05	11.94–15.03
				(72)	(65)	(85)	(87)	(67)	(89)

Table 7 (continued)

Genus	Species	Subspecies	Island						
<i>Tupaia</i>	<i>palawanensis</i>		Balabac	13) LPL	14) CNL	15) PBPL	16) LTPL	17) LCH	18) MH
				50.99±1.22	45.42±1.23	33.61±0.96	23.19±0.92	12.68±0.36	14.32±0.52
				48.74–52.64	43.32–47.56	31.70–34.62	21.50–24.24	12.13–13.43	13.49–15.20
				(9)	(9)	(9)	(8)	(9)	(8)
<i>Tupaia</i>	<i>moellendorffi</i>	<i>busuanga</i>	Busuanga	19) MCH	20) MCW	21) MCIL	22) LTL		
				8.57±0.37	3.15±0.20	34.65±0.89	23.08±0.55		
				8.07–9.31	2.78–3.53	33.51–36.56	22.53–24.57		
				(12)	(12)	(11)	(11)		
<i>Tupaia</i>	<i>moellendorffi</i>	<i>cuyonis</i>	Cuyo	8.09±0.25	3.14±0.25	34.09±0.26	22.33±0.28		
				7.76–8.27	2.67–3.35	33.68–34.46	21.90–22.61		
				(6)	(6)	(6)	(6)		
<i>Tupaia</i>	<i>moellendorffi</i>	<i>moellendorffi</i>	Culion	8.26±0.26	2.88±0.18	33.80±0.54	22.51±0.30		
				7.98–8.57	2.53–3.07	33.03–34.28	22.24–22.84		
				(6)	(6)	(4)	(4)		
<i>Tupaia</i>	<i>palawanensis</i>		Palawan	8.77±0.46	3.14±0.25	35.02±1.09	23.32±0.72		
				7.72–9.86	2.55–3.78	31.45–38.09	21.90–25.94		
				(91)	(93)	(75)	(70)		
<i>Tupaia</i>	<i>palawanensis</i>		Balabac	9.43±0.47	3.92±0.20	37.51±0.91	25.05±0.61		
				8.62–10.05	3.67–4.29	36.13–39.03	24.07–25.83		
				(8)	(9)	(9)	(7)		

larger size of *T. palawanensis*, particularly the population from Balabac (see Table 7).

Despite this limited support for recognition of two species, the results of most of our analyses indicate a more complicated pattern of morphometric variation among the five treeshrew populations of the Palawan faunal region. The results of the ANOVA indicate that the differences between *T. moellendorffi* and *T. palawanensis* found in the *t*-tests are driven by the distinct *T. palawanensis* population from Balabac, which is equally different from the *T. palawanensis* population from Palawan as it is from the three *T. moellendorffi* populations (Table 8). The unique craniodental morphology of Balabac *T. palawanensis* is also

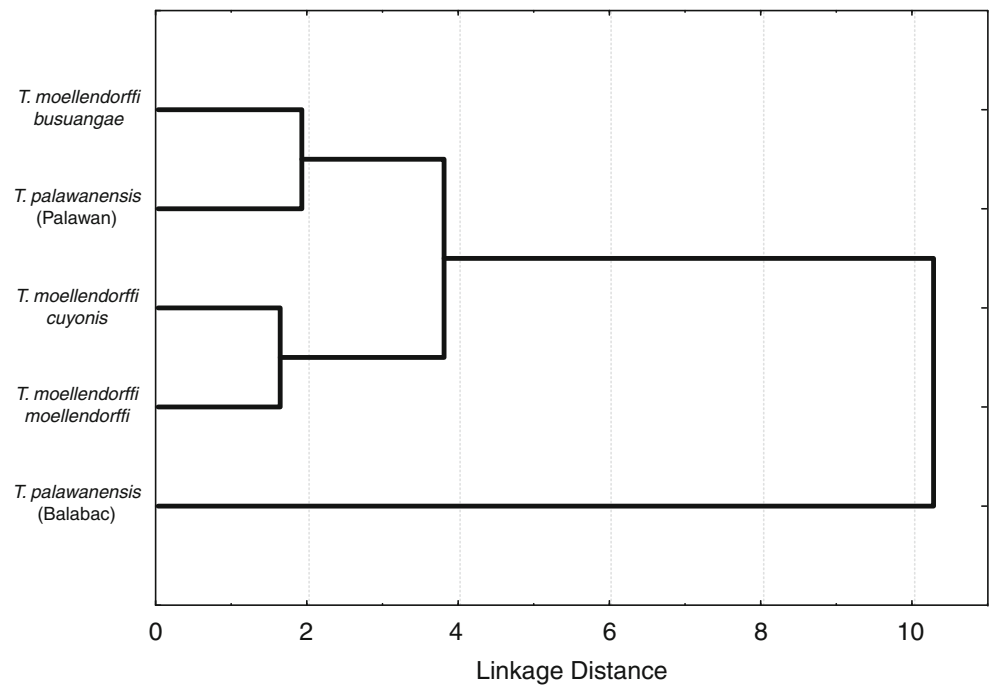
evident in the cluster analysis, as it is by far the most phenetically distinct population in the study (Fig. 2). The cluster analysis fails to separate *T. moellendorffi* from *T. palawanensis*, with *T. m. busuanga* being most similar to *T. palawanensis* from Palawan. These two populations also plot close to one another (in negative morphospace) in the PCA of means along factor 2 (Fig. 3). The PCA of individuals also fails to distinguish *T. moellendorffi* from *T. palawanensis*, as there is significant overlap between these two taxa (Fig. 4a), particularly between *T. m. busuanga* and *T. palawanensis* from Palawan (Fig. 4b).

However, underestimating diversity among treeshrews may obscure not only their evolutionary history but also

Table 8 Number of statistically significant ($P < 0.05$) univariate differences among island populations. Each of the 22 variables were compared in the ANOVA

	<i>T. moellendorffi</i> <i>busuanga</i> (Busuanga)	<i>T. m. cuyonis</i> (Cuyo)	<i>T. m. moellendorffi</i> (Culion)	<i>T. palawanensis</i> (Balabac)	<i>T. palawanensis</i> (Palawan)
<i>T. m. busuanga</i> (Busuanga)	X	0	0	21	1
<i>T. m. cuyonis</i> (Cuyo)	0	X	0	20	8
<i>T. m. moellendorffi</i> (Culion)	0	0	X	20	7
<i>T. palawanensis</i> (Balabac)	21	20	20	X	21
<i>T. palawanensis</i> (Palawan)	1	8	7	21	X

Fig. 2 Phenogram from cluster analysis of 22 variables (presented with Euclidean distances). *Tupaia palawanensis* from Palawan is more similar to *T. moellendorffi busuanga* than to *T. palawanensis* from Balabac



the biogeographical events responsible for tupaiid diversification in Southeast Asia. Treeshrews are known to be relatively poor overwater dispersers, even over short distances, making overwater colonization unlikely (Olson et al. 2005). This is supported by the presence of tupaiid treeshrews on Philippine islands that may have once been connected to the

Asian mainland by Pleistocene landbridges (Heaney 1985; Heaney et al. 1998), though the presence of *T. everetti* Thomas, 1892, on Mindanao suggests that overwater dispersal has played at least some role in the treeshrew colonization of the Philippines (Roberts et al. 2009). The current distribution of treeshrews in the Palawan faunal region may

Fig. 3 Plot of factor coordinates on first 2 axes from PCA of 22 variables (generalized inverse) for population means (Table 9a); PB: *T. palawanensis* from Balabac, PP: *T. palawanensis* from Palawan, MC: *T. moellendorffi cuyonis*, MB: *T. m. busuanga*, MM: *T. m. moellendorffi*. *T. moellendorffi* plots in the right quadrants and *T. palawanensis* on the left

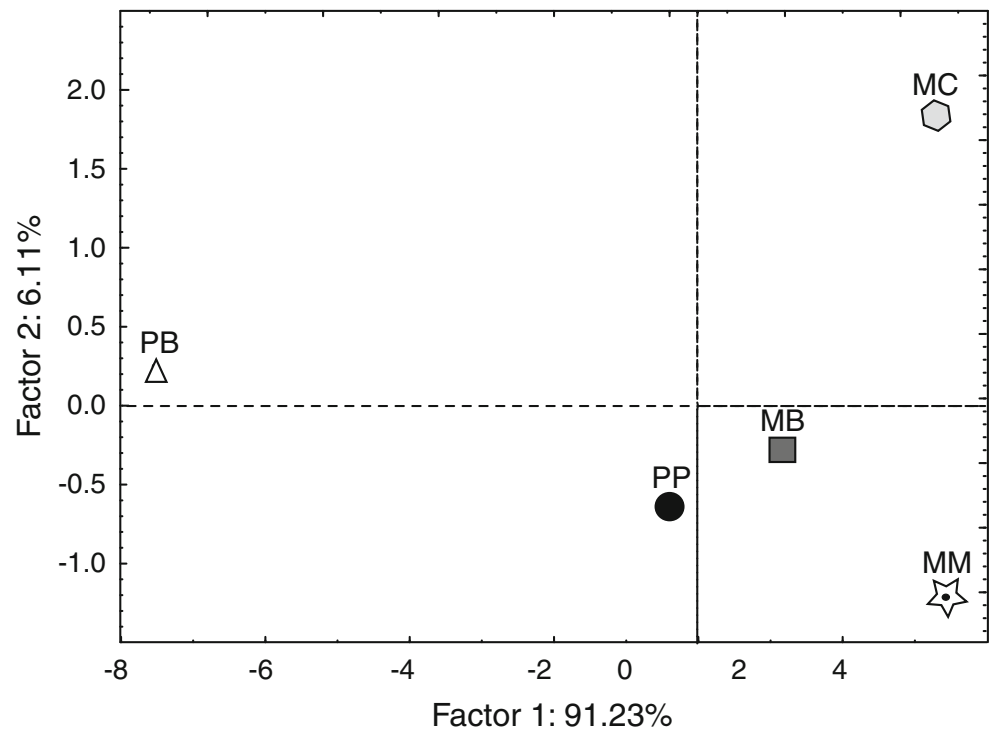


Table 9 Eigenvalues and percent of total variance from PCA of **a** means and **b** individuals

Factor	Eigenvalue	% Total variance	Cumulative eigenvalue	Cumulative %
A				
1	20.07	91.23	20.07	91.23
2	1.34	6.11	21.41	97.33
B				
1	8.91	74.26	8.91	74.26
2	0.95	7.95	9.87	82.21

be explained by two principle episodes of vicariance: (1) a landbridge connecting Palawan to Borneo may have existed during glacial maxima in the late middle Pleistocene, some 165,000 years ago, that would have facilitated the initial dispersal of treeshrews (as well as many other taxa) into Palawan from Borneo (Heaney 1985, 1986; but see Esselstyn et al. 2004), and (2) during the last glacial maximum (LGM: 26.5 to 19–20 ka, Clark et al. 2009), sea levels may have dropped sufficiently to connect most islands of the Palawan faunal region (forming the Pleistocene aggregate island complex Greater Palawan; Fig. 1a), but not enough to reconnect Palawan to Borneo and mainland Asia (Heaney 1986; Fig. 1a). This would suggest that gene flow between the treeshrews of the *T. palawanensis* group and all other treeshrews has been restricted for at least the last 165,000 years, and that the four populations have been diverging from each other for at least 19,000 years. However, molecular divergence estimates between Palawan and Bornean treeshrews support a much earlier split in the Miocene, and those for the Palawan and Culion taxa support divergence between these two populations in the middle Pleistocene around 680,000 years ago (see above; Roberts et al. 2011). Based on these divergence dates, colonization of Palawan from Borneo as late as the Pleistocene may not be likely. Treeshrews may have colonized Palawan, possibly via overwater dispersal, when it first emerged, but the divergence between the Palawan and Culion populations in the middle Pleistocene may still be related to sea level fluctuations (Roberts et al. 2011). From this perspective, it seems more likely that recent fluctuations in sea level may have led to periods of high gene flow between established populations rather than to colonization events.

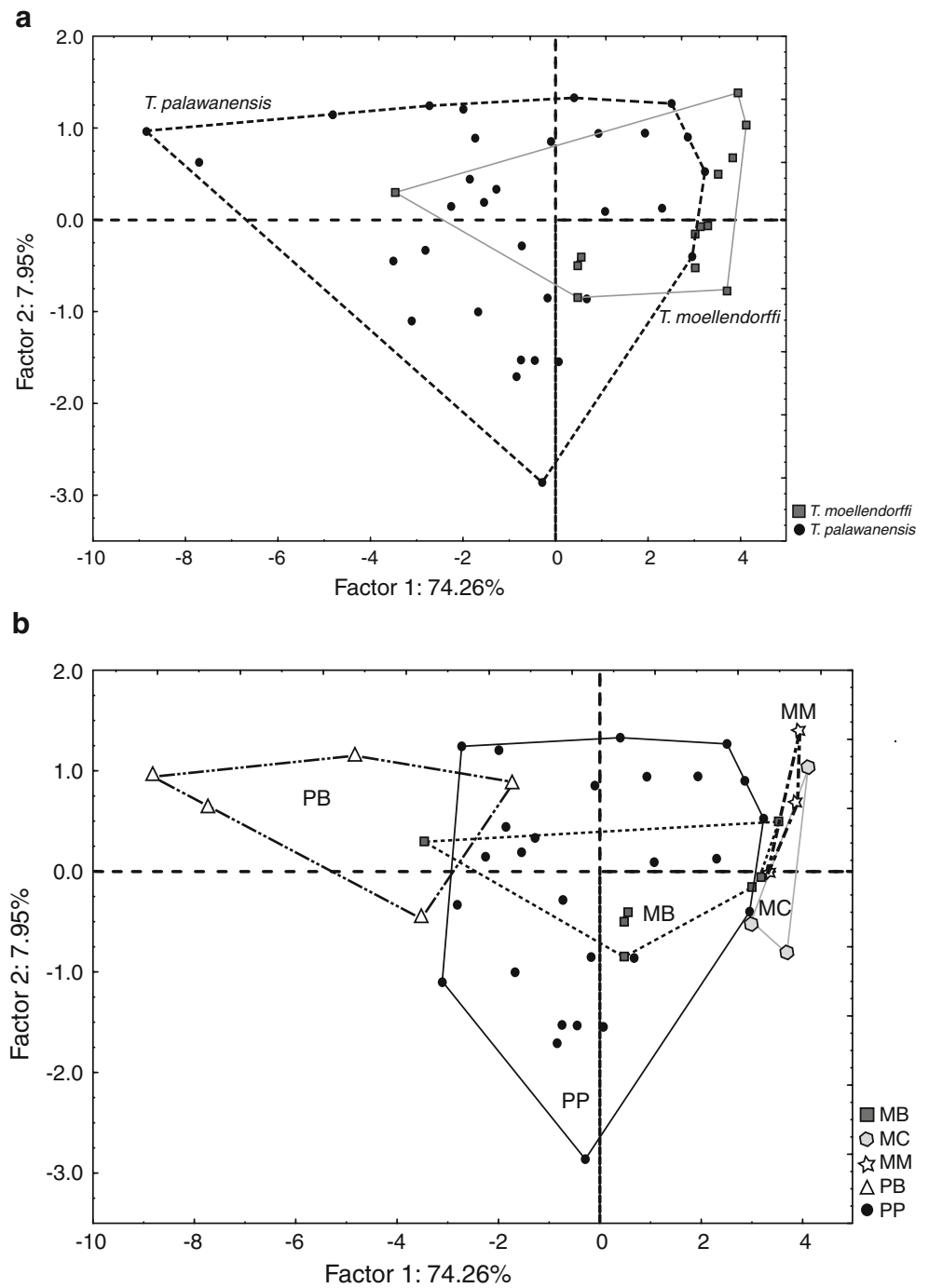
In summary, the bulk of our morphometric evidence does not support the recognition of *T. moellendorffi* as a separate species from *T. palawanensis*. This is consistent with the results of the molecular analysis conducted by Roberts et al. (2011), which indicated that these two taxa diverged recently and that there is insufficient genetic difference between them to recognize two species. To represent these two taxa, they

sampled *T. palawanensis* from Palawan and *T. moellendorffi moellendorffi*, which are clearly morphologically distinct in our analyses (Figs. 2, 3 and 4b; Table 8), thereby making the minor genetic differences between the two even more striking; based on our morphometric analyses, genetic similarities would be expected between *T. palawanensis* from Palawan and *T. moellendorffi busuanga*, but not necessarily between the two populations sampled by Roberts et al. (2011). However, low levels of genetic differentiation are not unique to the treeshrews of this region, as indicated by similarly negligible genetic distances among four species of tree squirrels (*Sundasciurus*) from Greater Palawan (den Tex et al. 2010).

Regarding subspecies, a case could be made to continue recognizing the populations from Culion and Cuyo as morphologically distinct subspecies, but the same is not true for the population from Busuanga, which is morphometrically similar to the Palawan population. This is surprising given that Culion is located between Busuanga and Palawan (Fig. 1), as gene flow between the Palawan and Busuanga populations would be expected to involve the Culion population as well. If the Culion and Cuyo populations are recognized as distinct subspecies, then the same should be done for the Balabac population because it exhibits the most distinct craniodental morphology (Figs. 2, 3 and 4b; Table 8).

Taxonomic uncertainty continues to complicate attempts to assess conservation priorities in treeshrews (Sargis et al. 2013), so taxonomic revisions based on synthesizing morphological and molecular results are crucial for conservation efforts (Olson et al. 2004b; Schlick-Steiner et al. 2007). The Palawan faunal region is part of the Philippines hotspot (Myers et al. 2000), and it has complicated biogeographic connections to the Sunda Shelf and oceanic Philippines (Esselstyn et al. 2010). Hence, revising the taxonomy of the treeshrews from this critical region could have significant conservation implications for these taxa. In fact, Heaney (2008) considered such studies to be a conservation priority for *T. moellendorffi*, which is currently classified as “Data Deficient” on the IUCN Red List of Threatened Species (www.iucnredlist.org). *Tupaia palawanensis*, on the other hand, is ranked as “Least Concern” (Gonzalez et al. 2008), so the evaluation of one vs. two species is clearly important from a conservation perspective. Though our morphometric analysis did not support the recognition of *T. moellendorffi*, it did reveal morphologically divergent populations from Culion, Cuyo, and Balabac, and these small island populations may be more threatened than the one from Palawan, which is approximately 30 to 200 times larger in area than Culion and Cuyo, respectively (Table 1, Fig. 1; Heaney 1986). In addition to taxonomic studies, Heaney (2008) listed surveys of the *T. moellendorffi* range as a conservation priority. Such

Fig. 4 Plot of factor coordinates on first 2 axes from PCA of 12 variables (generalized inverse) for individuals (Table 9b); PB: *T. palawanensis* from Balabac, PP: *T. palawanensis* from Palawan, MC: *T. moellendorffi cuyonis*, MB: *T. m. busuanga*, MM: *T. m. moellendorffi*. **a** Comparison of 2 species shows significant overlap between *T. moellendorffi* and *T. palawanensis*. **b** Comparison of five populations shows significant overlap between *T. m. busuanga* and *T. palawanensis* from Palawan



surveys of Culion, Cuyo, and Busuanga will be the key to understanding the abundance of these populations and the immediate threats to them, but we would add Balabac to this list of islands that require further survey. Finally, additional molecular evidence from the Cuyo, Busuanga, and Balabac populations is required to assess genetic differences among these populations and those from Culion and Palawan, and to further test the validity of *T. moellendorffi* relative to *T. palawanensis*.

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