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Craniometric variation and taxonomic boundaries in the Madras Treeshrew (Scandentia, Tupaiidae: *Anathana ellioti* [Waterhouse, 1850]) from India

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Abstract

The Madras Treeshrew, *Anathana ellioti* (Waterhouse, 1850), is a small, poorly studied mammal from South Asia. It is the only treeshrew found across the southern half of the Indian subcontinent and is the westernmost member of its order (Scandentia). The phylogenetic relationship between *Anathana* and its putative sister genus, *Tupaia*, remains unresolved, and the morphological differences between these two genera have yet to be analyzed with craniometric data. Here we describe some features that distinguish *Anathana* from other treeshrews. However, our comparative morphometric analyses reveal that *Anathana* overlaps with *Tupaia* in morphospace; it is smaller than most species (including the only other species found on the Indian mainland, *T. belangeri*) but larger than *T. minor*, *Dendrogale melanura*, and *Ptilocercus lowii*. At the infraspecific level, there is some separation between eastern and western populations, but this requires further investigation with larger sample sizes. Unfortunately, *Anathana* is disproportionately scarce in museum collections relative to other scandentians, and additional biological surveys across South India will be critical for future research on the taxonomy, distribution, and conservation of this elusive taxon.

Keywords Cranium · Morphology · Morphometrics · Skull · South Asia · Taxonomy

Introduction

Treeshrews are small mammals endemic to South and Southeast Asia comprising the order Scandentia, which includes the families Tupaiidae and Ptilocercidae (Hawkins 2018a, b; Sargis 2020). Tupaiidae contains three genera: *Tupaia*, *Dendrogale*, and the monospecific *Anathana*. The Madras Treeshew, *Anathana ellioti* (Waterhouse 1850), also known as the Indian Treeshrew, has the westernmost geographic distribution of any treeshrew species, ranging across the southern half of the Indian subcontinent (Molur 2016; Hawkins 2018a). A large portion of the treeshrew fossil record has been found in South Asia (Sargis 2004; Sehgal et al. 2022), and it is possible that *A. ellioti* is the sole remaining representative of a group of extinct western lineages. Consequently, unraveling the relationship between *Anathana* and other treeshrews has important implications for our broader understanding of scandentian biogeography and diversification.

Molecular studies have suggested that *Anathana* is the sister taxon to the genus *Tupaia*, which includes 19 of the 23 recognized treeshrew species; however, this proposed relationship still lacks strong genetic support (Olson et al. 2005; Roberts et al. 2011). Some have suggested that *Anathana* should not be recognized as a distinct genus from *Tupaia* (Fiedler 1956) or that, at the very least, the two genera are quite closely related (Helgen 2005). In fact, the

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Madras Treeshrew was originally described as *Tupaia ellioti* Waterhouse 1850 before being described as a separate genus by Lyon (1913) on the basis of smaller canines, a shortened rostrum and premaxilla (but see Verma 1965), and small fenestrae in the zygoma (but see Verma 1965). Lyon (1913: p. 120) also mentioned some differences in the cheek teeth ("unusually well-developed hypocones") as well as external soft-tissue features such as pelage ("coarser and harsher" relative to *Tupaia*) and toe pads (distinct rather than fused).

Lyon (1913) also delineated three species within the genus—*A. ellioti* from southeastern India, *A. pallida* from northeastern India, and *A. wroughtoni* from western India—entirely on the basis of pelage color, a plastic feature that has repeatedly proven unreliable for delimiting treeshrew taxa (see Juman et al. 2021b for a review of this issue). He noted that "[t]here are apparently no characters by which the skull and teeth of *Anathana ellioti* may be distinguished from those of other species in the genus" (Lyon 1913: p.

123). These taxa were later synonymized and are not currently recognized as subspecies (Corbet and Hill 1992; Helgen 2005).

The anatomical features that distinguish *Anathana* and *Tupaia* have never been assessed in modern statistical analyses. Moreover, very few specimens exist in museum collections (Helgen 2005). Here we evaluated the cranial distinctiveness of *Anathana* relative to other treeshrews. To do so, we conducted morphometric analyses on the largest existing dataset of *Anathana* specimens and an assembled dataset of other treeshrew species to quantitatively compare: 1) *Anathana* with the geographically closest *T. belangeri* specimens; 2) *Anathana* with seven other treeshrew species (*T. belangeri*, *T. glis*, *T. minor*, *T. palawanensis*, *T. tana*, *Dendrogale melanura*, and *Ptilocercus lowii*) for which craniometric data are available; and 3) the three taxa within *Anathana* formerly recognized by Lyon (1913) to test his hypothesis about their distinctiveness using modern

Fig. 1 Map of India showing localities of *Anathana* museum specimens. Adult individuals that were measured and included in this study are indicated with circles, whereas subadults and juveniles that were not included in analyses are indicated with triangles
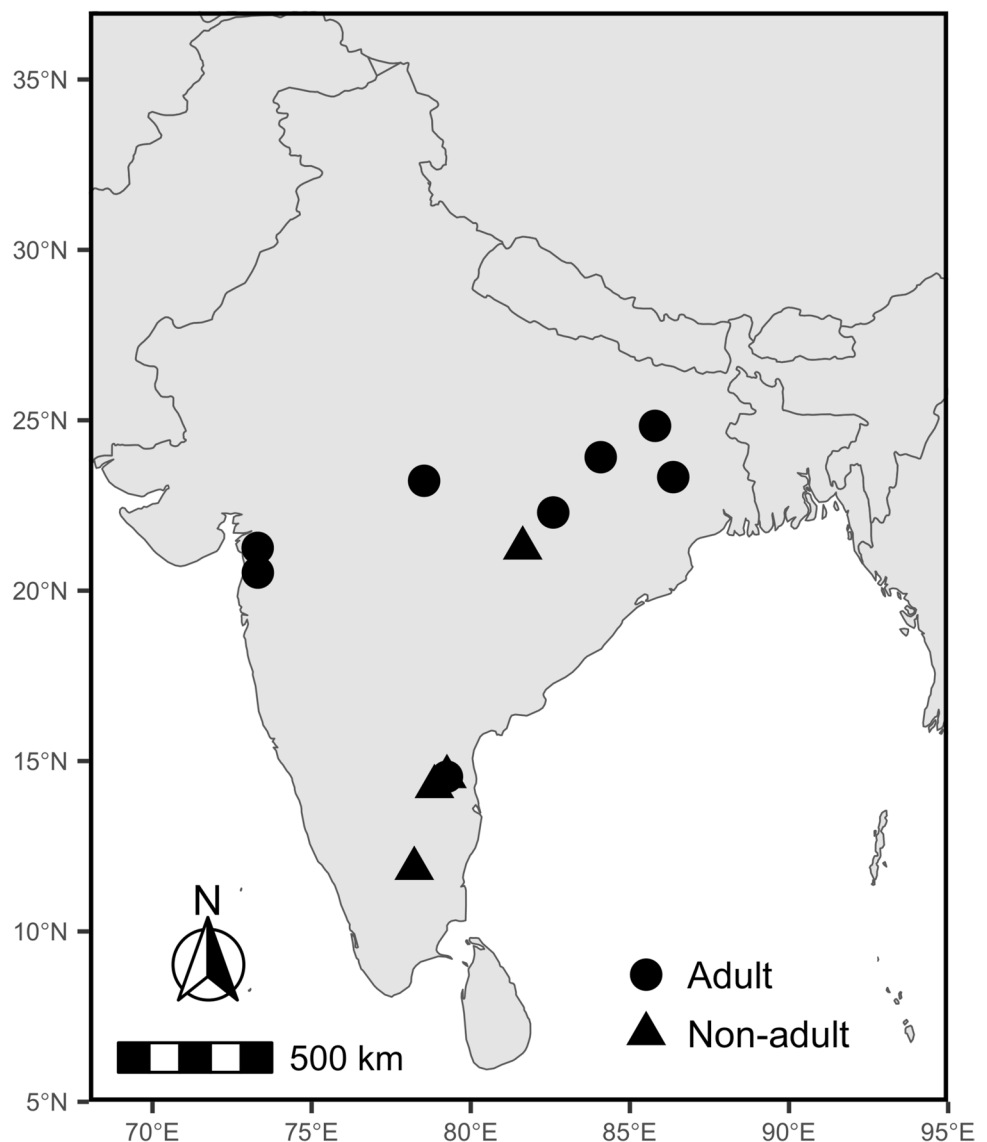
statistical analyses, which have the potential to reveal subtle osteological differences among populations. Finally, we mapped the localities of *Anathana* specimens to visualize geographic sampling gaps.

Materials and methods

Our *Anathana* sample included four specimens of *A. e. ellioti*, six specimens of *A. e.* "*pallida*", and two specimens of *A. e.* "*wroughtoni*" (Appendix 1; Online Resource 1). All three are represented by holotypes or paratypes in our sample (Appendix 1). Of these 12 specimens, only the eight adults (those with fully erupted permanent dentition; see Woodman et al. 2020) were included in our analyses. However, we georeferenced all specimen localities and generated a map using the ggplot2, rnaturalearth, and ggspatial packages in R (R Core Team 2022; Wickham 2016; South 2017; Dunnington 2020) (Fig. 1). Examined specimens are housed in the following museums: American Museum of Natural History (AMNH), New York, NY; Field Museum of Natural History (FMNH), Chicago, IL; and The Natural History Museum (NHMUK), London, UK (Appendix 1; Online Resource 1).

We recorded 19 craniomandibular measurements (Online Resource 1; Sargis et al. 2013, 2014a, b, 2017, 2018; Juman et al. 2021a, b, 2022a, b) from the eight adult specimens using Mitutoyo digital calipers that read to 0.01 mm, with a foot pedal for inputting data. Because some skulls were broken or damaged, we were unable to record all measurements for all individuals. Original measurements (in mm) are provided in Online Resource 1. We conducted all subsequent analyses with the following seven complete variables to maximize sample size: upper toothrow length (UTL), braincase breadth (BB), lambdoid-premaxillary length (LPL), postorbital bar-premaxillary length (PBPL), mandibular height (MH), mandibular condyle width (MCW), and mandibular condyle height (MCH).

Additional data for the same variables from the following seven treeshrew species were assembled from existing datasets: *T. belangeri* (*n* = 530; Juman et al. 2022a); *T. glis* (*n* = 152; Sargis et al. 2018); *T. minor* (*n* = 55; Juman et al. 2022b); *T. palawanensis* (*n* = 76; Online Resource 1; Sargis et al. 2014a); *T. tana* (*n* = 142; Juman et al. 2021b); *Ptilocercus lowii* (*n* = 36; Juman et al. 2021a); and *Dendrogale melanura* (n = 8; previously unpublished; Online Resource 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 ggplot2 (Wickham 2016).

We first investigated morphometric variation between *Anathana* (*n* = 8) and a subset of neighboring *T. belangeri* (defined as west of the Arakan Mountains, longitude < 92.5° E in the south and < 97° E in the north; *n* = 30) using a PCA of the seven variables listed above. We then performed a DFA of these same two groups and cross-validated our model with a jackknifing procedure. We also investigated shape differences in this subset using a PCA of the same seven variables standardized with a size proxy (calculated as the geometric mean of these measurements for each individual). Next, we conducted a PCA on the overall combined dataset with all eight species included (*n* = 1,007). Finally, we performed a PCA grouped by population (species or subspecies) within the *Anathana* sample: *A. e. ellioti* (*n* = 1), *A. e.* "*pallida*" (*n* = 5), and *A. e.* "*wroughtoni*" (*n* = 2). We were unable to assess sexual dimorphism within the *Anathana* sample due to an uneven composition of two females, five males, and one unknown. However, most other treeshrews do not exhibit sexual size dimorphism (Emmons 2000; Woodman et al. 2020; Juman et al. 2021a, b), so we therefore combined males and females in all analyses.

Results

In our PCA of seven skull variables from *Anathana* and neighboring *Tupaia belangeri*, principal component (PC) 1 accounts for almost 83% of the variance and has high loadings across all variables (Table 1), suggesting that it represents size. PC2 explains over 7% of the variance and is most influenced by negatively weighted mandibular height variables (Table 1). A bivariate plot of these two components reveals complete separation between the two taxa along PC1, with *Anathana*

Table 1 Component loadings from principal component analyses (PCA) of raw and size-corrected skull variables from *Anathana ellioti* and neighboring *Tupaia belangeri*. Abbreviations for skull variables are defined in "Materials and methods" section. Loadings in boldface type are discussed in the text. Variables are arranged in decreasing order of PC1 score in raw PCA

	Raw		Size-corrected	
	Principal component		Principal component	
	1	2	1	2
PBPL	0.97	0.20	**0.95**	0.25
LPL	0.96	0.19	**0.98**	0.16
UTL	0.94	0.16	**0.96**	0.11
BB	0.90	0.14	**0.96**	0.11
MCH	0.89	**-0.39**	0.00	**-0.96**
MH	0.85	**-0.49**	0.69	**-0.59**
MCW	0.85	0.12	**-0.98**	0.19
Eigenvalue	5.80	0.53	5.13	1.41
Percentage of total variance explained	82.92	7.52	73.30	20.11

Fig. 2 Plots of principal component (PC) scores from principal ▶ component analyses of seven craniomandibular variables: **a**. Plot of *Anathana ellioti* and neighboring *Tupaia belangeri* (Table 1); **b**. Size-corrected plot of *A. ellioti* and neighboring *T. belangeri* (Table 1); **c**. Plot of *A. ellioti*, *T. belangeri* (complete dataset), *T. glis*, *T. minor*, *T. palawanensis*, *T. tana*, *Dendrogale melanura*, and *Ptilocercus lowii* with polygons for each genus (Table 2)

plotting in negative morphospace and *T. belangeri* plotting mostly in positive morphospace (Fig. 2a), suggesting that *Anathana* has a smaller skull than *T. belangeri*. A DFA of this sample using the same variables produced a 100% correct classification rate. In our size-corrected version of this PCA, PC1 accounts for over 73% of the variance and represents a contrast between skull length/breadth and mandibular condyle width, while PC2 represents over 20% of the variance and tracks negatively weighted mandibular height variables (Table 1). A plot of these PC scores revealed almost complete separation along PC1 in the reverse order as the original PCA (Fig. 2b), suggesting that *Anathana* has a longer skull relative to its mandibular condyle width when compared to *T. belangeri*.

We further examined the morphometric distinctiveness of *Anathana* in another PCA of the same seven skull variables from *Anathana*, *T. belangeri*, *T. glis*, *T. minor*, *T. palawanensis*, *T. tana*, *Dendrogale melanura*, and *Ptilocercus lowii*. PC1 is once again a size vector, accounting for over 86% of the variance, while PC2 accounts for almost 8% of the variance and represents negatively weighted mandibular height and condylar width variables (Table 2). A resulting bivariate plot shows *Anathana* to be completely separated from all other taxa along PC1, with varying degrees of overlap among the other seven taxa (Fig. 2c). This suggests that the *Anathana* skull is larger than those of *T. minor*, *D. melanura*, and *P. lowii* but smaller than those of *T. belangeri*, *T. glis*, *T. palawanensis*, and *T. tana*. However, *Anathana* still falls entirely within the range of variation of *Tupaia* as a whole (Fig. 2c), even in a size-corrected version of this PCA (not shown).

Finally, we examined possible intraspecific variation within the *Anathana* sample with a PCA of seven skull variables. PC1 represents over 47% of the variance and has high loadings for cranial variables, suggesting that it tracks cranial size more than mandibular size (Table 3). PC2 accounts for almost 33% of the variance and represents negatively weighted mandibular variables, suggesting that it is inversely correlated with mandibular size (Table 3). A bivariate plot of these two components reveals separation between *A. e.* "*pallida*" ($n=5$) and *A. e.* "*wroughtoni*" ($n=2$) along PC1, while the single specimen of *A. e. ellioti* falls within the polygon of *A. e.* "*pallida*" (Fig. 3a). This suggests that *A. e.* "*pallida*" and *A. e. ellioti* have smaller crania than *A. e.* "*wroughtoni*", though our sample sizes for all populations are small.
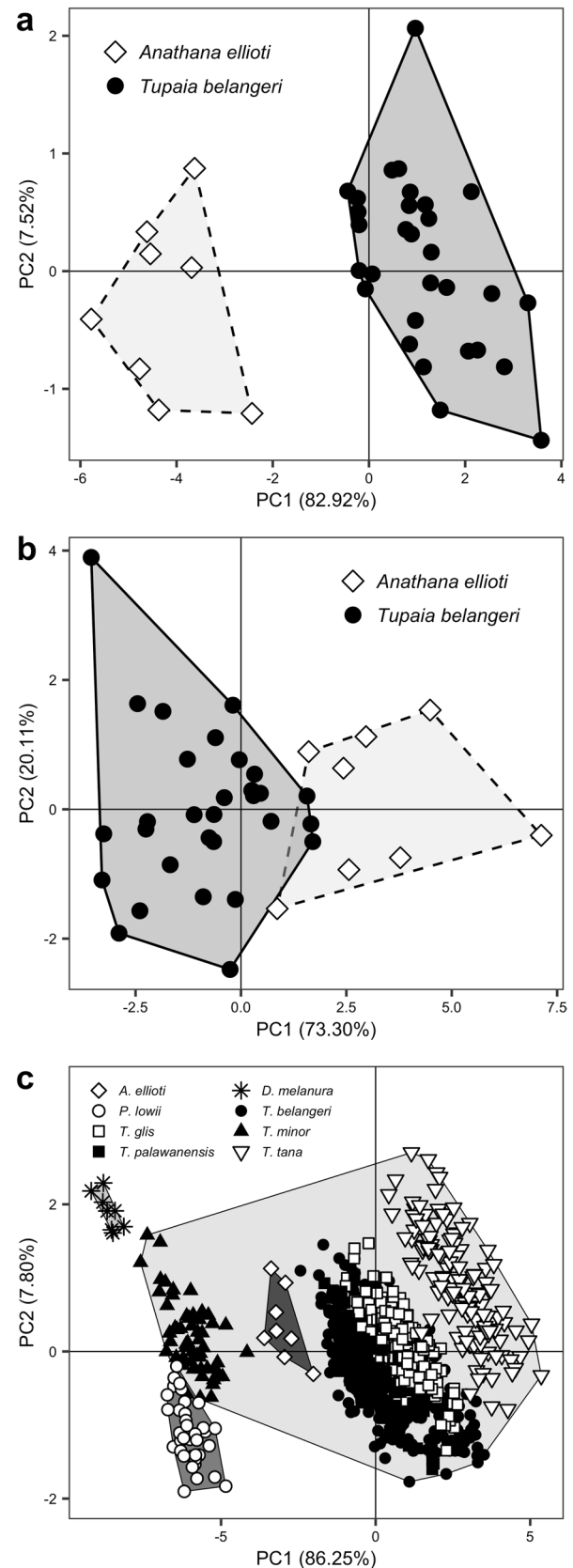
Table 2 Component loadings from a principal component analysis (PCA) of skull variables from *Anathana ellioti*, *Tupaia belangeri*, *T. glis*, *T. minor*, *T. palawanensis*, *T. tana*, *Dendrogale melanura*, and *Ptilocercus lowii*. Abbreviations for skull variables are defined in "Materials and methods" section. Loadings in boldface type are discussed in the text. Variables are arranged in decreasing order of PC1 score
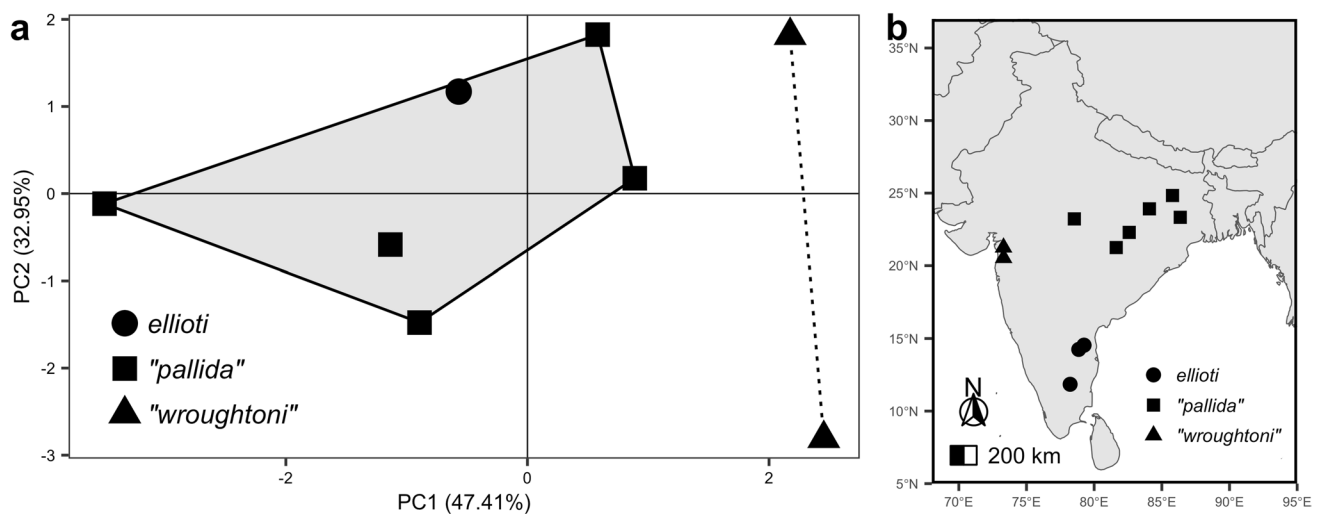
	Principal component	
	1	2
LPL	0.97	0.20
UTL	0.97	0.22
PBPL	0.94	0.30
MCH	0.94	-0.19
BB	0.93	0.19
MH	0.88	**-0.41**
MCW	0.86	**-0.37**
Eigenvalue	6.04	0.55
Percentage of total variance explained	86.25	7.80

Discussion

Our morphometric analyses suggest that the skull of *Anathana* is morphometrically distinct from the most proximate *T. belangeri* specimens on the Indian mainland in both size and shape (Fig. 2a, b). However, in a broader analysis with seven other treeshrew taxa included, *Anathana* fell within the range of size variation across *Tupaia* species (Fig. 2c; Table 2). Our results indicate that *Anathana* is larger than the three smallest species in our analyses (*T. minor*, *D. melanura*, and *P. lowii*) but is smaller than all other members of *Tupaia* that were

Table 3 Component loadings from a principal component analysis (PCA) of skull variables from three *Anathana* populations previously proposed to represent distinct species by Lyon (1913). Abbreviations for skull variables are defined in "Materials and methods" section. Loadings in boldface type are discussed in the text. Variables are arranged in decreasing order of PC1 score

	Principal component	
	1	2
PBPL	**0.92**	0.28
LPL	**0.90**	0.33
UTL	**0.84**	0.37
BB	**0.81**	-0.18
MH	0.40	**-0.87**
MCH	0.38	**-0.90**
MCW	0.06	**-0.62**
Eigenvalue	3.32	2.31
Percentage of total variance explained	47.41	32.95

included in the study. This is congruent with the original description of the genus, which cited a "shortened rostrum" and "correspondingly short" premaxilla (Lyon 1913: p. 121). The overlap between *Anathana* and *Tupaia* in skull size and shape casts doubt on the validity of the former's generic status, especially given the morphometric distinctiveness of *Ptilocercus* and *Dendrogale* (Fig. 2c). Previous molecular research has supported *Anathana* as the sister taxon to *Tupaia* (Olson et al. 2005; Roberts et al. 2011). Although the relevant node lacked strong support, it nonetheless remains the best-supported hypothesis adduced to date using modern phylogenetic methods. An updated molecular analysis with more data is needed to help clarify the phylogeny of tupaiids and shed light on ancient patterns of diversification among scandentians.

We also conducted a qualitative examination to identify possible diagnostic features that distinguish *Anathana* from *Tupaia*. As outlined above, Lyon (1913) described several such differences, including a "relatively short and heavy rostrum" (p. 120) in *Anathana* (Fig. 4a). One distinguishing feature not noted by Lyon (1913) involves the size and shape of the nuchal crest (Fig. 4). The nuchal crest of *Anathana* overhangs the supraoccipital (Fig. 4c), whereas this is not the case in *Tupaia* (Fig. 4d; see also Wible 2011). Furthermore, the shape of this crest differs in the two genera. In *Anathana*, it is characterized by two lateral convexities, resulting in a bilobate appearance in dorsal view (Fig. 4a), whereas *Tupaia* exhibits a single rounded convexity (Fig. 4b).

Within our small *Anathana* sample ($n = 8$), the single adult individual of *A. ellioti* from southeastern India (Fig. 3b) falls inside the range of morphometric variation among ("*pallida*") individuals from northeastern India (Fig. 3a). This result is expected based on the fact that the three taxa (formerly species) were originally differentiated from each other based on pelage, with no diagnostic cranial characteristics (Lyon 1913). Lyon (1913: p. 124) specifically noted that "[t]here are no tangible characters by which the skull and teeth of *Anathana wroughtoni* may be distinguished from those of *A. ellioti*." However, the two ("*wroughtoni*") specimens from western India (Fig. 3b) are morphometrically distinct from the other six individuals due to their larger crania (Fig. 3a). This might be related to their geographic separation on the opposite side of India from the more eastern populations (Fig. 3b); perhaps a barrier to east-west dispersal, such as the Western Ghats mountain range, could explain the potential distinction of this population. Similarly, east-west rainfall patterns may produce ecophenotypic size variation, as has been observed in other small mammals (Teta et al. 2022). Although we cannot rule out that this western ("*wroughtoni*") population may be craniometrically distinct from other *Anathana* populations, we still follow

Fig. 3 **a**. Plot of principal component (PC) scores from a principal component analysis of *Anathana ellioti* populations, based on seven craniomandibular variables (Table 3); **b.** Map of India showing localities of museum specimens with species designations recognized by Lyon (1913), including subadults and juveniles not used in analyses

Helgen (2005) in not recognizing any subspecies due to the small available sample sizes.

The geographic range of *A. ellioti* spans most of the Indian subcontinent, yet there are fewer *Anathana* specimens in museum collections than those of *T. palawanensis* or *T. nicobarica*, both of which are restricted to small archipelagos. Its rarity in museum collections relative to other scandentians could be a result of elusiveness and apparent sensitivity to anthropogenic disturbance (Hawkins 2018a; Patel et al. 2020).

Anathana is currently listed as "Least Concern" on the IUCN Red List of Threatened Species, but populations are thought to be undergoing localized declines and the overall trend is "decreasing" (Molur 2016).

Another possible explanation is the British East India Company's heavier focus on collecting natural history specimens from northern and eastern colonial territories—rather than South India—by the mid-19th century (Ratcliff 2016). Many of these specimens were added to The Natural History Museum collection in London (Leviton and Aldrich
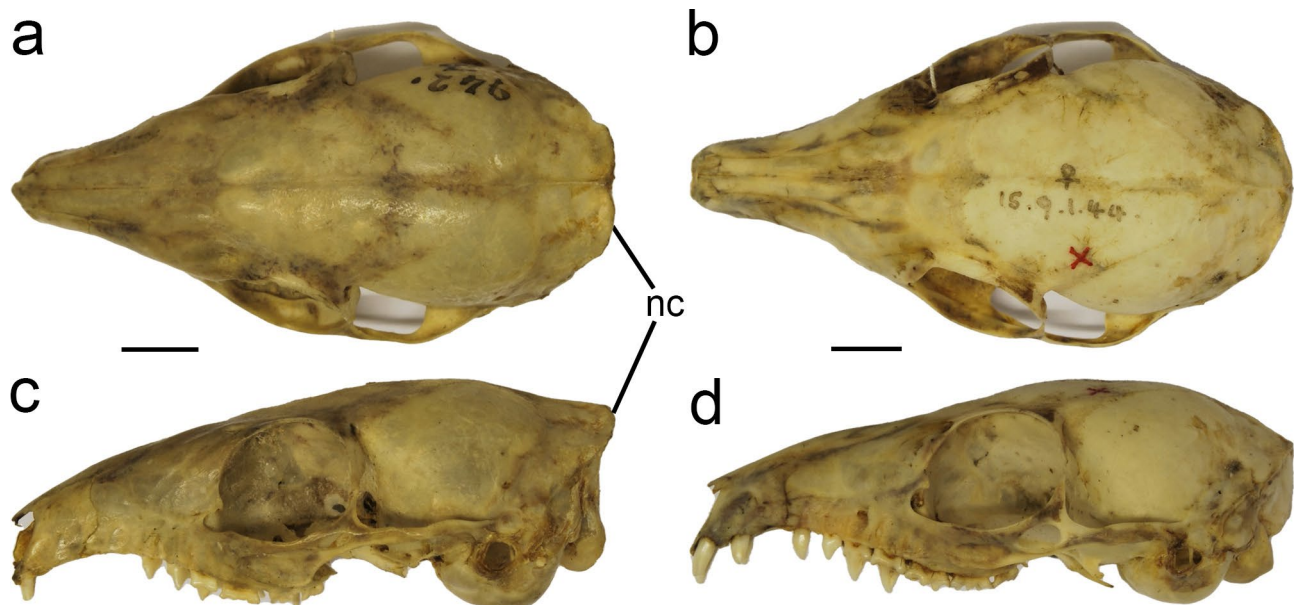
Fig. 4 Crania of *Anathana ellioti* (left column, NHMUK 1850.8.21.17, paratype) and *Tupaia belangeri* "*lepcha*" (right column, NHMUK 15.9.1.44, subspecies holotype) in dorsal (**a, b**) and lateral (**c, d**) views (from the collections of the Natural History Museum, London). Abbreviation: nc, nuchal crest. Specimens scaled to cranium length. Scale bars equal 5 mm

2000), which today reflects uneven collecting of different treeshrew taxa across former British colonies. The scarcity of *Anathana* specimens is likely exacerbated by ongoing logistical difficulties associated with collecting specimens—and, more generally, performing wildlife research—in India (Madhusudhan et al. 2006). This species in particular is severely lacking a sufficiently large and evenly distributed sample of museum specimens (Fig. 1), hindering future efforts to study South India's only treeshrew—a potentially threatened monotypic genus. A larger sample size is necessary to thoroughly investigate the morphological and molecular distinctiveness of *Anathana* and determine whether it warrants generic status. Our study highlights the critical need for continued specimen collection to examine, delineate, and ultimately conserve Indian mammal species.

Appendix 1 Specimens examined

Specimens from the following institutions were included in this study: American Museum of Natural History (AMNH), New York, NY; Field Museum of Natural History (FMNH), Chicago, IL; and The Natural History Museum (NHMUK), London, UK. Non-adult specimens omitted from analyses but included in maps are indicated with an asterisk.

Anathana ellioti ellioti ($n = 4$)—India: Andhra Pradesh: hills between Cuddapah [Kadapa] and Nellore, near Madras [Chennai] (NHMUK 1850.8.21.17—paratype; NHMUK 1850.1.21.7*—paratype); Palkonda Hills (FMNH 82603*); Shevaroy Hills (NHMUK 91.10.7.49*).

Anathana ellioti "*pallida*" ($n = 6$)—India: Manbhum [Purulia] (NHMUK 66.12.28.2—holotype); Bengal, Palamai [Palamu] (NHMUK 78.2527); Madhya Pradesh (FMNH 91265); Bihar, Nawadeh [Nawadih] (AMNH M-150086); Central Provinces [Chhattisgarh]: Nawpara [Nawapara] (AMNH M-171125); Rajpur [Raipur] (NHMUK 85.8.1.97*).

Anathana ellioti "*wroughtoni*" ($n = 2$)—India: Gujarat: Surat, Mandvi (NHMUK 96.11.7.1—holotype); Dangs, Maheskatri (NHMUK 96.11.7.2).

Declarations

Competing interests The authors declare no competing interests.

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