

Using three-dimensional geometric morphometric and dental topographic analyses to infer the systematics and paleoecology of fossil treeshrews (Mammalia, Scandentia)

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Abstract.—Treeshrews are small, Indomalayan mammals closely related to primates. Previously, three-dimensional geometric morphometric analyses were used to assess patterns of treeshrew lower second molar morphology, which showed that the positions of molar landmarks covary with intraordinal systematics. Another analysis used dental topographic metrics to test patterns of functional dental morphology and found that molar curvature, complexity, and relief were an effective means for examining patterns of variation in treeshrew dietary ecology. Here, we build on these analyses by adding two fossil taxa, *Prodendrogale yunnanica* Qiu, 1986 from the Miocene of China and *Ptilocercus kylin* Li and Ni, 2016 from the Oligocene of China. Our results show that *Pr. yunnanica* had a dental bauplan more like that of a tupaiid than that of a ptilocercid, but that the extant tupaiids, including *Tupaia* and *Dendrogale*, are more similar to one another in this regard than any are to *Prodendrogale*. This is contrary to our expectations as *Prodendrogale* is hypothesized to be most closely related to *Dendrogale*. *Ptilocercus kylin*, which has been proposed to be the sister taxon of *Pt. lowii* Gray, 1848, is characterized by dental morphology like that of *Pt. lowii* in crest and cuspal position but is interpreted to have been more frugivorous. It has been claimed that *Ptilocercus* has undergone little morphological change through time. Our results suggest that *Pt. kylin* was more ecologically distinct from *Pt. lowii* than previously proposed, providing a glimpse into a more complex evolutionary history of the group than had been inferred.

Introduction

Scandentia (treeshrews) is an order of small-bodied, Indomalayan mammals composed of two families. Tupaiidae is the more speciose of the two, comprising the genera *Tupaia*, *Dendrogale*, and the monospecific *Anathana*. By contrast, Ptilocercidae includes only a single extant species, *Ptilocercus lowii* Gray, 1848. Among living treeshrews, *Pt. lowii* is the most plesiomorphic; as such, this taxon is often considered a good living model for extinct euarchontans and, particularly, early primates (Sargis, 2001, 2002, 2004; Bloch et al., 2007). During the period in which treeshrews were considered primates, they were the focus of study from a number of perspectives (e.g., Carlsson, 1922; Le Gros Clark, 1924, 1925; Saban, 1963; Napier and Napier, 1967). As this view became less broadly accepted (e.g., Van Valen, 1965; McKenna, 1966; Butler, 1972; Luckett, 1980), study of treeshrews decreased. However, interest in the order Scandentia has experienced a revival within the past two decades. For example, several recent studies have examined the relationship of treeshrews with regard to primates and colugos in Euarchonta (e.g., Sargis, 2002, 2004, 2007; Bloch et al., 2007; Ni et al., 2013; O’Leary et al., 2013; Chester et al., 2015; Li and Ni, 2016). The complex taxonomy within the order has

also received a lot of attention recently. For example, several analyses have used morphometrics (e.g., Sargis et al., 2013a, b, 2014a, b, 2017) to assess species boundaries among extant treeshrew taxa. Furthermore, Roberts et al. (2009, 2011) analyzed molecular data to assess the phylogenetic relationships of treeshrews and found that *Urogale* is not a distinct genus from *Tupaia*. They also used molecular evidence to show that *T. moellendorffi* Matschie, 1898 is not a distinct species from *T. palawanensis* Thomas, 1894, a conclusion that is supported by morphological evidence as well (Sargis et al., 2014a).

A handful of studies have also sought to understand the ecology of living treeshrews. Emmons (2000) wrote the most comprehensive analysis of treeshrew ecology currently available, addressing topics such as habitat use and activity patterns, diet and foraging, social behavior, and life history. There are also some studies that took a more general approach to examining the ecology of various species (e.g., Langham, 1982, 1983; Timmins et al., 2003; Kvartalnov, 2009). Although the diet of treeshrews has not been as extensively studied as the diet of primates, Emmons (1991, 2000), Langham (1982, 1983), Wiens et al. (2008), and Clarke et al. (2010) have examined the dietary patterns of extant treeshrews and found that they consume mainly a variable mix of fruit and insects.

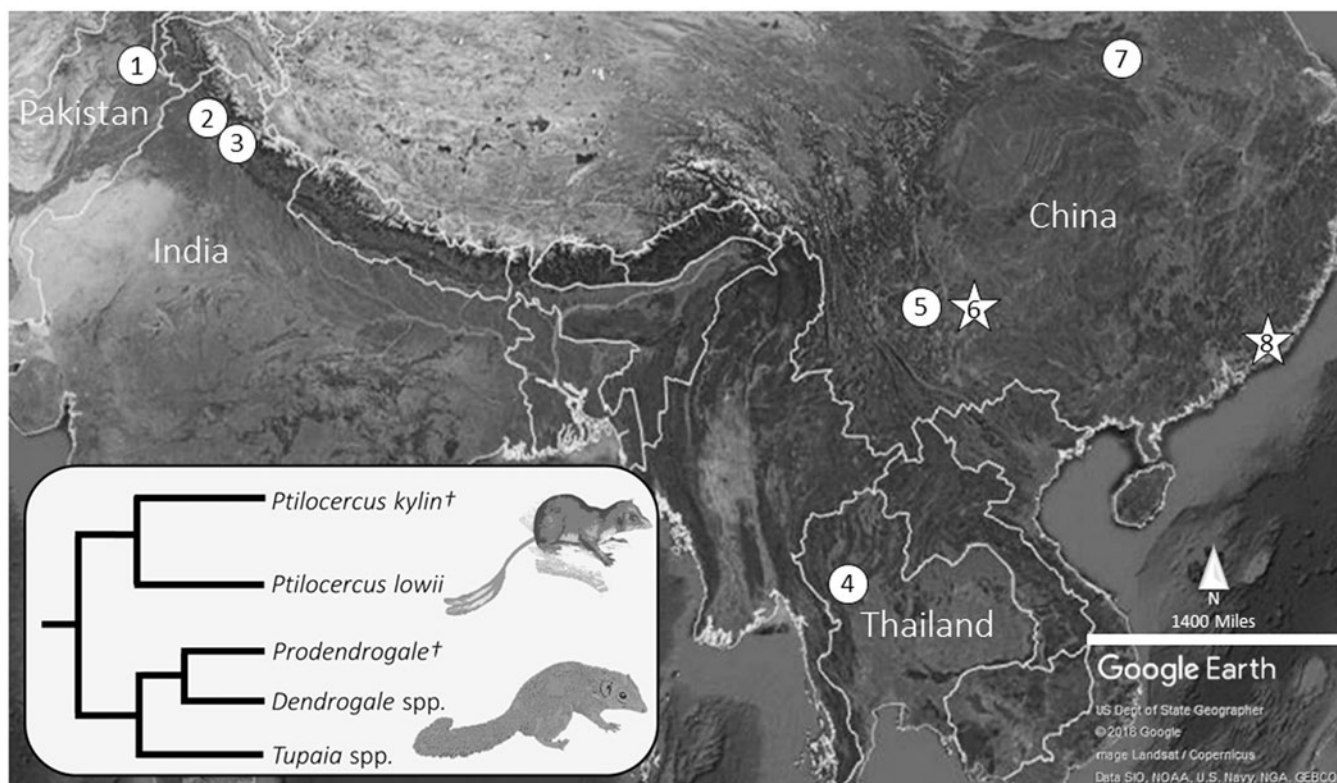


Figure 1. Approximate positions of the localities of the currently known fossil treeshrew taxa. See Table S1 for more details. 1, Tupaiidae (Jacobs, 1980); 2, *Tupaia sivalicus* (Chopra and Vasishat, 1979; Chopra et al., 1979; Luckett and Jacobs, 1980); 3, *Tupaia* sp. (Dutta, 1975); 4, *Tupaia miocena* (Mein and Ginsburg, 1997); 5, *Prodendrogale engesseri*, *Tupaia storchi* (Ni and Qiu, 2012), and Ptilocercidae (an unnamed specimen) (Ni and Qiu, 2002, 2012); 6, *Ptilocercus kyllin* (Li and Ni, 2016); 7, *Eodendrogale parvum* (Tong, 1988); 8, *Prodendrogale yunnanica* (Qiu, 1986). Stars represent taxa included in the current analysis. Inlaid are the hypothesized evolutionary relationships of the included taxa based on previous, character-based analyses (Qiu, 1986; Li and Ni, 2016). †Indicates extinct taxon. *Pt. lowii* and *T. belangeri* illustrations adapted from those of Joseph Wolf and Joel Sartore, respectively.

What currently remains very poorly understood is the handful of fossil treeshrew taxa that have been described in the literature. To date, some seven fossil species have been named (Table S1, Fig. 1; see Sargis, 2004; Li and Ni, 2016), whereas other specimens remain unassigned to a particular taxon within Scandentia. This is the case for the Miocene ptilocercid noted by Ni and Qiu (2002, 2012) from Yuanmou, China, which may represent a new genus; the Pliocene rib cage of a possible species of *Tupaia* from the Upper Siwaliks of India (Dutta, 1975); and the Miocene tupaiid skull fragment and teeth from the Siwaliks of Pakistan (Jacobs, 1980). Aside from a recent phylogenetic analysis (Li and Ni, 2016) that included two fossil treeshrew species (*Ptilocercus kyllin* Li and Ni, 2016 and *Prodendrogale engesseri* Ni and Qiu, 2012), and the suggestion that the Miocene and Oligocene ptilocercids are likely similar to living *Ptilocercus* (Ni and Qiu, 2002; Li and Ni, 2016) in their habits, there is very little known about extinct treeshrew systematics or ecology, in part due to the paucity of fossils.

Dental morphology has contributed little in terms of clarifying treeshrew systematics in the past (see Steele, 1973; Butler, 1980; Olson et al., 2004), which is problematic as most treeshrew fossils are dentognathic (Table S1). Selig et al. (2019a) used three-dimensional (3D) geometric morphometric analysis (GMA) to study the lower second molar (m2) morphology of extant treeshrew species as a means for exploring patterns of variation and systematics within the order. They found that the

two treeshrew families, Ptilocercidae and Tupaiidae, were well separated in morphospace. Moreover, they noted that many individual species plotted within morphospace in a pattern consistent with clades identified in a molecular study (Roberts et al., 2011), which implies that the morphology of the m2 tracks aspects of phylogeny among treeshrews.

In a subsequent analysis, Selig et al. (2019b) used dental topographic analysis (DTA) to examine patterns of functional dental morphology and diet in a sample of extant treeshrews. They found that treeshrews do not vary greatly in overall patterns of functional dental morphology, with much lower levels of variation than seen in primates. They did find evidence, however, for some important differences in the dietary patterns among extant scandentians. For example, they found that taxa such as *T. dorsalis* Schlegel, 1857, *T. belangeri* (Wagner, 1841), *D. melanura* (Thomas, 1892), and *Pt. lowii* are the best adapted to an insectivorous diet, whereas *T. salatan* (Lyon, 1913), *T. gracilis* Thomas, 1893, *T. minor* Günther, 1876, and *T. palawanensis* are better adapted for the consumption of fruit, judging from the varying levels of molar curvature, complexity, and relief. Overall, they found that dental topography is useful for examining patterns of variation within the dietary morphospace of Scandentia. Although the GMA (Selig et al., 2019a) and DTA (Selig et al., 2019b) examined the morphology of the m2 in extensively overlapping samples of treeshrews, the differences in the methodology used in each analysis provided

complementary and nonredundant results. Evans (2013) and Winchester (2016a) proposed that GMA is a ‘shape specifier’ approach to analyzing morphology as it captures the specific geometries of form, relating the position of landmarks to one another within morphospace. As such, GMA picks up on morphology more strongly related to genetics rather than to the physical properties of foods that are consumed. Alternatively, DTA provides a landmark-free method for analyzing form, and as such this method is a ‘shape descriptor,’ providing a means for measuring more functional aspects of dental morphology rather than strictly comparing the positions of cusps and other landmarks. Therefore, when both methods are used to examine the morphology of the same structures, they capture somewhat different types of information.

In the following, we have built on the analyses of Selig et al. (2019a, b) by expanding the sample to include the two casts of extinct treeshrew species that were available for study: *Proden-drogale yunnanica* Qiu, 1986 (IVPP V8282.13) (Fig. S1) from the latest Miocene of China (Qiu, 1986) and *Ptilocercus kylin* (IVPP V20696) (Fig. S1) from the early Oligocene of China (~34 Ma) (Li and Ni, 2016). A previous study suggested that *Pr. yunnanica* is closely related to the extant genus *Dendrogale* on the basis of the overall pattern of resemblance between these two taxa (Qiu, 1986) (Fig. 1). *Ptilocercus kylin* is the oldest definitive evidence of a crown scandentian (Li and Ni, 2016). It has been hypothesized that *Pt. kylin* is an extinct sister taxon to the extant *Pt. lowii* on the basis of a phylogenetic analysis of 1,857 dental, cranial, postcranial, soft-tissue, and molecular characters (Li and Ni, 2016) (Fig. 1). Li and Ni (2016) proposed that the morphology of *Ptilocercus* is highly conserved given the general resemblance of *Pt. kylin* to *Pt. lowii* and suggested that this may be a result of a relatively stable ecological niche in ptilocercids throughout the Cenozoic. Others have made similar arguments based on the apparently conservative morphology of *Pt. lowii*, suggesting that certain dietary habits of ptilocercids, such as the intensive intake of alcoholic nectar, may have remained unchanged over the past >55 million years (Wiens et al., 2008; Li and Ni, 2016). We used both GMA and DTA to examine the morphological distinctiveness and dietary adaptations of these two fossil treeshrew species.

Materials and methods

The samples included in our analyses are listed in Tables 1 and S2. Mandibles from a mixed sample of extant males and females were downloaded from MorphoSource (Boyer et al., 2016) or were scanned on a Nikon XT H 225 ST High Resolution X-ray CT Scanner at the Shared Materials Instrumentation Facility at Duke University. Voxel sizes range from 10 to 29 μm . Treeshrews lack sexual dimorphism (Emmons, 2000, table 2.2), so mixing males and females should not add additional variation into our analyses. Mandibles were scanned so that the m2s could be analyzed. In total, the sample includes specimens representing 15 extant species and 2 extinct species (Table 1). The GMA comprises 47 specimens in total, including single specimens of both *Pr. yunnanica* and *Pt. kylin*. The specimen of *Pr. yunnanica* was scanned in a Scanco Medical μCT 35 machine housed in the Department of Internal Medicine at Yale University, whereas the cast of *Pt. kylin* was scanned in a

Table 1. Species and number of specimens (n) included in the GMA and DTA. †Indicates extinct taxon.

Species	n (GMA)	n (DTA)
<i>Ptilocercus lowii</i>	4	6
<i>Ptilocercus kylin</i> †	1	1
<i>Dendrogale melanura</i>	1	2
<i>Dendrogale murina</i>	2	3
<i>Tupaia chrysogaster</i>	5	5
<i>Tupaia salatana</i>	3	5
<i>Tupaia glis</i>	2	4
<i>Tupaia belangeri</i>	5	5
<i>Tupaia gracilis</i>	4	4
<i>Tupaia dorsalis</i>	4	5
<i>Tupaia javanica</i>	4	5
<i>Tupaia palawanensis</i>	1	6
<i>Tupaia minor</i>	4	5
<i>Tupaia picta</i>	1	-
<i>Tupaia montana</i>	1	-
<i>Tupaia tana</i>	4	5
<i>Proden-drogale yunnanica</i> †	1	-
Total	47	61

General Electric phoenix vltomelx s240 housed at the American Museum of Natural History Microscopy and Imaging Facility Computed Tomography Laboratory. The molars included in the GMA are relatively unworn, with little to no wear on the cusp tips, so that landmarks can be placed accurately. The sample for the DTA comprises 61 specimens in total, including the cast of the holotype of *Pt. kylin*. The hypoconid on the specimen of *Pr. yunnanica* is broken, so it could not be included in the DTA. The molars of these specimens are relatively unworn; however, some specimens may be characterized by slightly greater wear than those used in the GMA analysis because worn teeth can be included in analyses using dental topographic metrics (e.g., Ungar and M’Kirera, 2003; Dennis et al., 2004; Pampush et al., 2016b). As a result, the sample for the DTA is larger than that used for the GMA. For both analyses, no specimens exhibiting exposed dentine in the occlusal basin were included, a phenomenon that happens relatively quickly as the teeth are worn in thin-enameled taxa such as treeshrews (see Selig et al., 2019c), indicating that the specimens are at most lightly worn.

Using Avizo 9.01 (Visualization Sciences Group, 2009), micro-CT scans were opened and the m2s were segmented to remove adjacent teeth. Once segmented, the meshes were cropped along the cervix to isolate the crown following standard conventions for dental topographic analyses (e.g., Boyer, 2008; Bunn et al., 2011; Prufrock et al., 2016b). The cropped surfaces were simplified to 10,000 faces and smoothed 100 iterations with the lambda set at 0.6 to remove noise irrelevant to the morphology of the meshes (Bunn et al., 2011; Pampush et al., 2016a; Prufrock et al., 2016a, b; Winchester, 2016a; Spradley et al., 2017; López-Torres et al., 2018). These protocols have been adapted for the analysis of dental topography; however, geometric morphometric landmarks can still be successfully and accurately placed on the resulting meshes (see Selig et al., 2019a).

For the GMA, we collected 18 landmarks representing tips of cusps, regions where anatomical features meet, widest points along curves, and low points along crests (Fig. 2). These landmarks are the same as those collected by Selig et al. (2019a);

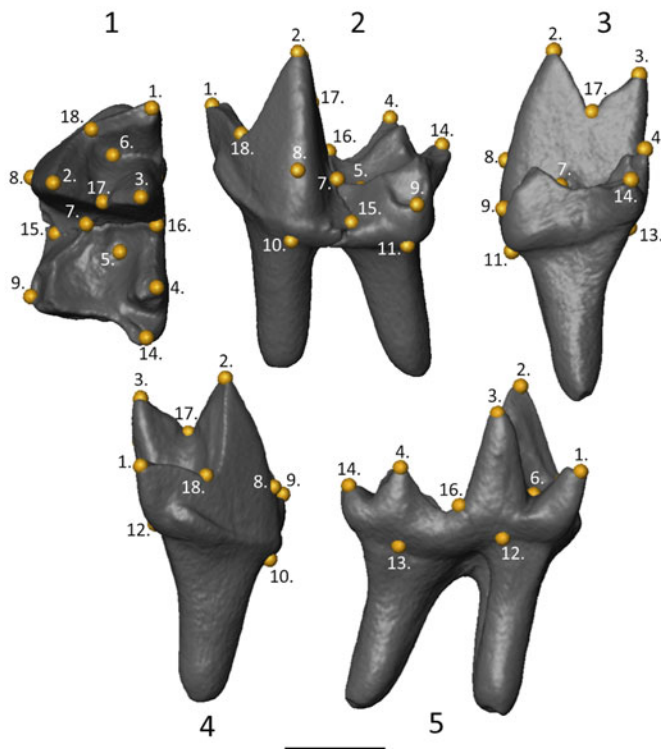


Figure 2. Landmarks included in the analysis placed on *Prodendrogale yunnanica* left m2 (IVPP V8282.13). (1) Occlusal; (2) buccal; (3) distal; (4) mesial; (5) lingual views. 1, Paraconid tip; 2, protoconid tip; 3, metaconid tip; 4, entoconid tip; 5, lowest point in talonid basin; 6, lowest point in trigonid basin; 7, where cristid obliqua meets trigonid; 8, widest point on protoconid (in occlusal view); 9, widest point on hypoconid (in occlusal view); 10, cervical point on protoconid; 11, cervical point on hypoconid; 12, cervical point below metaconid; 13, cervical point below entoconid; 14, distalmost point on postcristid (or hypoconulid); 15, lowest point on hypoflexid; 16, talonid notch; 17, proto-cristid notch; 18, lowest point on paracristid. Scale bar = 1 mm.

a closely related set of landmarks was assessed in an error study by Cooke (2011) and found to be highly repeatable. As the hypoconid of *Pr. yunnanica* is broken, the landmark at the tip of the cusp was omitted from this analysis. Landmark 9 (widest point on hypoconid) in the present analysis was not omitted, however, as the specimen of *Pr. yunnanica* still exhibits this landmark. This landmark was placed with the tooth mesh in occlusal orientation, but the mesh was rotated from all angles to ensure that it was placed correctly. Given that the buccal margin of the hypoconid shifts lingually toward the cusp tip, we are confident in the placement of this landmark at the widest point of the hypoconid on this specimen, even though the cusp tip is missing. We used the same landmark coordinates for the extant taxa as those collected by Selig et al. (2019a) with the addition of single specimens of *P. lowii* (YPM MAM 10179) and *D. murina* (Schlegel and Müller, 1843) (UAM:Mamm:103000). Landmark coordinates were analyzed in PAST 3.14 (Hammer et al., 2001), which was used for all statistical analyses. We applied generalized Procrustes superimposition, which eliminates variation in the landmark data caused by orientation, size, and translation so only variation in shape is represented. We then used principal components analysis (PCA) on the variance–covariance matrix to visualize how taxa plot in morphospace. Using the resulting PC scores of the first four PCs (which each explain at least

10% of the total variation, see below), we calculated mean PC scores for each genus of extant treeshrew and included those of each fossil taxon in an unweighted pair group method with arithmetic mean (UPGMA) cluster analysis to examine overall similarity among groups.

Once the meshes were prepared in Avizo, they were opened in MorphoTester (Winchester, 2016b) to conduct the DTA. Although several topographic metrics exist (e.g., Ungar and M’Kirera, 2003; Dennis et al., 2004; Guy et al., 2013, 2015; Ungar et al., 2016; Berthaume et al., 2019), three of the most commonly used are Dirichlet normal energy (DNE; Bunn et al., 2011), 3D orientation patch count rotated (3D-OPCR; Evans et al., 2007; Winchester, 2016b), and relief index (RFI; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Boyer, 2008). DNE is a measure of how much a surface deviates from being planar and measures the degree of curvature of a tooth, which relates to its ability to effectively shear foodstuffs (Bunn et al., 2011). Taxa with mechanically challenging diets, such as insectivores or folivores, tend to have teeth with higher DNE values, as their teeth have sharper crests and taller cusps. By contrast, frugivorous taxa tend to have significantly lower DNE values, as frugivores tend not to have teeth with well-developed shearing crests. The 3D-OPCR measures surface complexity on the basis of the number of discrete patches on a surface that face the same cardinal direction. As such, 3D-OPCR acts as a measurement of the number of ‘tools’ present on a tooth (Bunn et al., 2011) wherein higher 3D-OPCR values, and therefore more complex teeth, are found in taxa with more mechanically challenging diets such as insectivores or folivores, whereas frugivores tend to have simpler teeth. Finally, RFI measures crown height calculated as a natural log of the square root of the crown’s 3D area divided by its 2D planimetric footprint (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Boyer, 2008). Higher values are found for teeth that possess tall, sharp cusps and crests and tend to correlate with the consumption of insects or leaves, whereas low values indicate low, flat teeth, which relate to the consumption of fruit. As such, this method serves as a relative measure of hypsodonty. Although all three metrics tend to contrast among dietary guilds that differ in terms of mechanical complexity of their key food items, they operate on different scales, with DNE being very sensitive to subtle differences in the crown surface, 3D-OPCR being best suited to comparing quite different dental morphologies, and RFI falling somewhere in between (Prufrock et al., 2016b). Note that these trends were established primarily in the study of primates. Although treeshrews were included in earlier studies of topographic trends (see Boyer, 2008; Bunn et al., 2011), contrasts noted by Selig et al. (2019b) and in the following are based on those established largely among other mammalian groups in light of the lack of ecological data for treeshrews (see Langham, 1982; Emmons, 1991, 2000; see Selig et al., 2019b for a summary of available dietary information).

The RFI values produced by MorphoTester are simply the ratio of the 3D surface area of the mesh over the 2D area of the crown. To make our results consistent with those of Selig et al. (2019b) and others (e.g., Boyer, 2008; Bunn et al., 2011; López-Torres et al., 2018), we recalculated RFI as the natural log of the square root of the crown’s 3D area divided by its 2D area. Although species-level differences in topographic values were

examined previously (see Selig et al. 2019b), we used Bonferroni-corrected Mann-Whitney U tests to examine differences among genera. To examine how *Pt. kylin* plots with regard to the morphospace of the sampled extant treeshrew taxa, we performed a PCA of the topographic variables on the covariance matrix by including *Pt. kylin* in the analysis of Selig et al. (2019b) with the addition of the single specimens of *Pt. lowii* (YPM MAM 10179) and *D. murina* (UAM:Mamm:103000). We used the species means of the extant taxa in the PCA.

Finally, we used reduced major axis (RMA) regression to determine whether dental topography has any effect on the GMA and the plotting of taxa within the GMA morphospace. To do so, we calculated average PC scores for PC 1 for each species from both the GMA and DTA. We included only specimens that were used in both analyses.

Repositories and institutional abbreviations.—American Museum of Natural History, New York, NY (AMNH); Field Museum of Natural History, Chicago, IL (FMNH); Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); University of Alaska Museum of the North, Fairbanks, AK (UAM); University Museum of Zoology, Cambridge, England (UMZC), United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Yale Peabody Museum of Natural History, Yale University, New Haven, CT (YPM).

Results

GMA.—The GMA identified four PCs that each explain at least 10% of the total variation and 59.69% of the cumulative variation in the sample (Table S3). Along PC1, which explains 22.56% of the total variation, there is little separation among the included genera (Fig. 3.1). *Pr. yunnanica* overlaps with both *Dendrogale* and *Tupaia*, whereas *Pt. kylin* overlaps with the tupaiids and plots near, though not among, the specimens of extant *Ptilocercus lowii*. Selig et al. (2019a) found that PC1 mainly distinguished among various species of *Tupaia* and does not distinguish among the treeshrew genera or families. They found that taxa with lower values on PC1 plot in negative morphospace and are largely characterized by a narrower crown, a mesially shifted paraconid, and a protoconid that is taller and wider toward the cervix relative to taxa that plot in positive morphospace. With the exception of the taller protoconid, these differences are evident in the comparison between *Pt. kylin* (Fig. 4.3) and *Pt. lowii* (Fig. 4.4), which plot separately along this axis (Fig. 3.1).

PC2 (15.68% of the total variation) represents a lower crown and a mesially shifted paraconid and hypoconulid/post-cristid relative to the rest of the tooth in taxa that plot in negative morphospace; variation along this axis separates *Ptilocercus* from the tupaiids (Fig. 3.1; Selig et al., 2019a). In this analysis, along PC2 *Dendrogale* and *Prodendrogale* plot separately (Fig. 3.1), which reflects subtle differences in these features (Fig. 4.1, 4.2). When PC1 and PC2 are plotted together, the specimen of *Pr. yunnanica* plots among extant tupaiids, but it falls more closely to specimens of *Tupaia* than it does to those of

Dendrogale (Fig. 3.1). *Ptilocercus kylin* is distinct from *Pt. lowii*, but it does plot closer to the *Pt. lowii* polygon than to that of the tupaiids.

PC3 explains 11.14% of the total variation and is characterized by taxa with a wider talonid basin, with a shallower talonid notch, and in which the widest point on the hypoconid shifts toward the cusp tip and away from the cervix, moving from positive to negative morphospace (Selig et al., 2019a). The separation between *Pt. kylin* and *Pt. lowii* on this axis (Fig. 3.2) reflects the previously observed differences in talonid morphology discussed by Li and Ni (2016). As in the case of PC1, PC3 does not distinguish among the extant genera, but it does distinguish *Pt. kylin* from the other taxa. When plotted with PC2, *Pt. kylin* plots in distinctive morphospace, whereas *Pr. yunnanica* plots among tupaiids, falling closer to specimens of *Tupaia* than to those of *Dendrogale* (Fig. 3.2).

Although PC4 explains over 10% of the total variation and is included in a subsequent analysis (see below), it is difficult to interpret when plotted because it does not distinguish among any extant treeshrew genera, with the *Ptilocercus* and *Tupaia* specimens overlapping completely. It only distinguishes between *Pt. kylin* and all other specimens. Therefore, it will not be discussed further.

The average PC scores for the first four PCs (Table S3) of each genus and the fossil taxa were included in the UPGMA cluster analysis (Fig. 3.3). The cophenetic correlation is high ($cc = 0.982$), which indicates that the dendrogram is accurately representing the pairwise distances among taxa. According to the UPGMA, *Pt. kylin* is most similar to *Pt. lowii*, whereas *Pr. yunnanica* is more similar to the extant tupaiids; however, the extant tupaiids, including *Dendrogale*, cluster to the exclusion of *Pr. yunnanica*. Although *Pt. kylin* and *Pt. lowii* cluster with one another, the high distance value calculated from the PC scores implies that they are more dissimilar from one another than any of the tupaiids are from each other (including *Pr. yunnanica*) on the basis of the specific geometries of the m2.

DTA.—Results of the DTA are summarized in Table 2 and Figures 5 and 6. Results of the Mann-Whitney U test suggest that there are significant differences between *Ptilocercus* and *Tupaia* ($p = 0.034$) but not between *Ptilocercus* and *Dendrogale* ($p = 0.060$) or *Dendrogale* and *Tupaia* ($p = 1$) on the basis of the measurement of DNE. According to the measurement of 3D-OPCR, only *Ptilocercus* and *Tupaia* differ significantly ($p = 0.037$; *Dendrogale* versus *Ptilocercus* $p = 1$; *Dendrogale* versus *Tupaia* $p = 0.965$). There are no significant differences between *Ptilocercus* and *Dendrogale* ($p = 0.060$), *Ptilocercus* and *Tupaia* ($p = 0.144$), or *Dendrogale* and *Tupaia* ($p = 0.160$) on the basis of the measurement of RFI. For statistical analyses and discussion of differences among extant taxa at the species level, see Selig et al. (2019b).

Ptilocercus kylin is characterized by a DNE value of 343.99 and a 3D-OPCR value of 66.25, which are both considerably lower than the mean values reported for extant *Ptilocercus* (372.17 and 78.48, respectively), falling at the lower end of the range of *Ptilocercus* variation for DNE and outside the range of *Ptilocercus* variation for 3D-OPCR (Fig. 5).

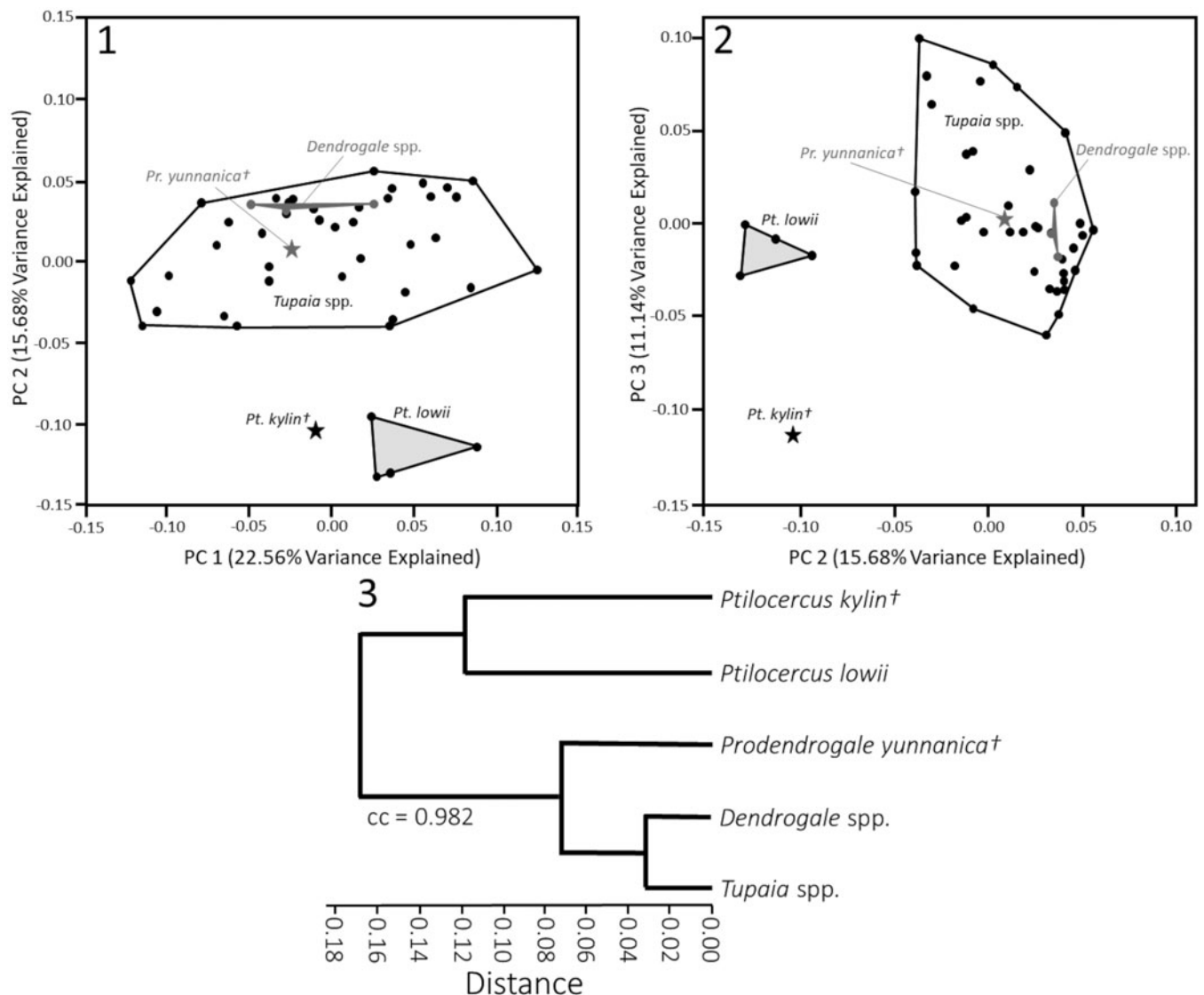


Figure 3. (1) Bivariate plot of principal components 1 and 2 and (2) bivariate plot of principal components 2 and 3 from the geometric morphometric analysis of the Procrustes transformed landmark data. (3) Dendrogram of the UPGMA cluster analysis based on the generic-level average PC scores from the first four PCs. The cophenetic correlation (cc) is high, indicating that the dendrogram is an accurate representation of the pairwise distances among taxa. †Indicates extinct taxon.

Ptilocercus lowii is characterized by a distinctive pattern of dental topography relative to other treeshrews included in the analysis of Selig et al. (2019b) by having high DNE and 3D-OPCR but low RFI. The absence of an ectoloph in *Pt. kylin* (Li and Ni, 2016) is likely why that taxon has a relatively low RFI (see below), within the range of *Pt. lowii* (Fig. 5). However, it more closely resembles the tupaiids in having lower DNE and 3D-OPCR values (Fig. 5). As such, this taxon has a more typical combination of dental topographic values than *Pt. lowii*, with low scores for all three metrics.

The PCA identified three PCs, of which the first two explain nearly 84% of the cumulative variation in the analysis (Table S3). The addition of two extant and one fossil specimen in the analysis does not change the results very much from those reported by Selig et al. (2019b). The first PC (49.18% of the total variation) should separate taxa based primarily on higher levels of insectivory in positive morphospace and more frugivory in

negative morphospace on the basis of the fact that all three variables are loaded positively along PC1 (Table S4). According to Selig et al. (2019b), PC2 (34.76% of the total variation in the present analysis) may separate taxa on the basis of the physical properties of the food rather than strict differences between levels of insectivory and frugivory. It has previously been shown, for example, that taxa that consume the same plant species but differ in terms of which part of the plant they consume differ in terms of their molar complexity (Godfrey et al., 2012). Similarly, treeshrews might differ in molar complexity due to differences in the mechanical properties of the insect and plant species they consume. In the plot of PCs 1 and 2 in the present analysis (Fig. 6), *Pt. kylin* plots in more frugivorous morphospace along PC1, near the mean values for *T. tana* Raffles, 1821 and *T. palawanensis*, taxa that are considered more frugivorous compared with taxa such as *T. belangeri*, *T. dorsalis*, *D. melanura*, and *Pt. lowii* (see Selig et al., 2019b and references therein).

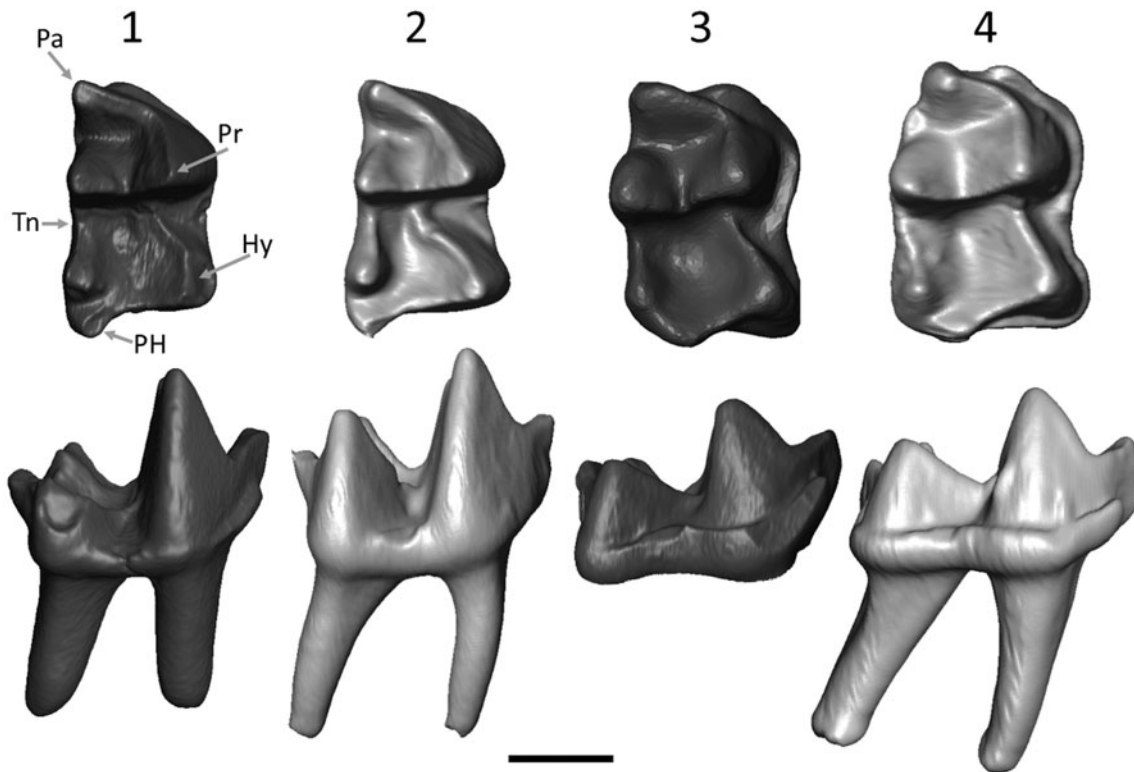


Figure 4. Micro-CT renderings of the occlusal (top) and buccal (bottom) aspects of m2 of (1) *Prodendrogale yunnanica* (IVPP V8282.13; mirrored), (2) *Dendrogale murina* (UAM:Mamm:103000), (3) *Ptilocercus kylin* cast (IVPP V20696), and (4) *Ptilocercus lowii* (USNM 488052) illustrating similarities between putative closely related species and differences between the two families. Arrows denote select features that distinguish taxa in the PCA, including the hypoconid (Hy), paraconid (Pa), protoconid (Pr), postcrisid/hypoconulid (PH), and talonid notch (Tn). Scale bar = 1 mm.

The RMA regression of species-average PC scores from the GMA and DTA suggests that dental topography does not have a significant effect on the plotting of taxa within the GMA morphospace (slope = -2.614 , intercept = 6.366 , $R^2 = 0.077$, $p = 0.338$).

Discussion

A previous assessment of the dental morphology of *Pr. yunnanica* suggested that this taxon is closely related to and potentially the ancestor of *Dendrogale* (Qiu, 1986). A phylogenetic

analysis that included another species of *Prodendrogale*, *Pr. engesseri* (Li and Ni, 2016), found that *Prodendrogale* and *Dendrogale* were likely sister taxa, although only one species of *Dendrogale*, *D. melanura*, was included in the study. The results of our analyses indicate that *Pr. yunnanica* is very similar in dental morphology to modern tupaiids, although it is not more similar to *Dendrogale* than it is to other tupaiids. In fact, our UPGMA cluster analysis groups modern tupaiids to the exclusion of *Pr. yunnanica*. Our PCA shows that *Pr. yunnanica* consistently plots closer to specimens of *Tupaia* than it does to those of *Dendrogale*. This could be a product of the smaller sample

Table 2. Results of the dental topographic analysis listing the means, coefficients of variation (CV), and standard deviations (SD) for each taxon included in the analysis. The specimen of *Prodendrogale yunnanica* was not included in this analysis. †Indicates extinct taxon.

Species	DNE			3D-OPCR			RFI		
	Mean	CV	SD	Mean	CV	SD	Mean	CV	SD
<i>Ptilocercus lowii</i>	372.17	7.63	28.40	78.48	9.44	7.41	0.562	4.26	0.024
<i>Dendrogale melanura</i>	352.56	7.73	13.17	83.86	8.43	7.07	0.647	3.59	0.023
<i>Dendrogale murina</i>	325.89	9.26	30.18	66.54	6.25	4.16	0.660	2.33	0.015
<i>Tupaia chrysogaster</i>	337.13	5.32	17.95	67.35	3.75	2.53	0.644	2.68	0.017
<i>Tupaia salatana</i>	309.06	6.20	19.16	68.33	4.83	3.30	0.604	4.58	0.028
<i>Tupaia glis</i>	323.95	8.80	28.49	73.06	3.64	2.66	0.636	5.16	0.033
<i>Tupaia belangeri</i>	380.46	6.85	20.42	74.28	4.37	2.89	0.686	5.24	0.040
<i>Tupaia gracilis</i>	316.31	6.43	20.35	65.66	6.36	4.17	0.611	2.81	0.017
<i>Tupaia dorsalis</i>	381.88	7.61	29.07	69.80	7.48	5.22	0.646	5.22	0.034
<i>Tupaia javanica</i>	332.86	9.52	31.70	72.30	7.42	5.36	0.553	8.21	0.045
<i>Tupaia palawanensis</i>	308.21	11.63	35.86	76.17	9.42	7.18	0.543	11.85	0.064
<i>Tupaia minor</i>	328.21	6.94	22.77	71.13	6.38	4.54	0.560	6.39	0.036
<i>Tupaia tana</i>	315.87	11.02	34.81	66.53	12.84	8.54	0.621	4.73	0.029
<i>Ptilocercus kylin</i> †	343.99	-	-	66.25	-	-	0.552	-	-

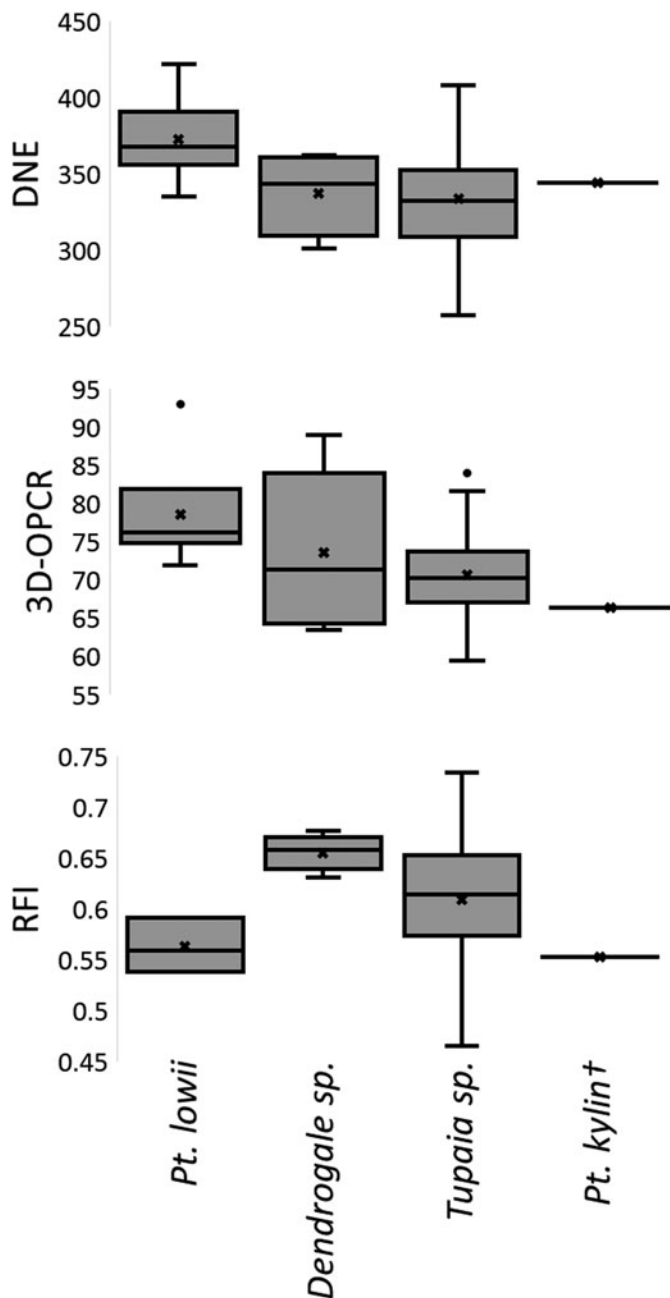


Figure 5. Box plots of the DTA results for DNE, 3D-OPCR, and RFI for each genus (and fossil species) included in the analysis. The X represents the mean, the horizontal lines represent the median, the boxes represent the upper and lower quartiles, and whiskers denote the highest and lowest values for each taxon. Note that *Pt. lowii* differs from the tupaids in having low RFI values and relatively high DNE and 3D-OPCR values. Although *Pt. kylin* is similar to *Pt. lowii* in its RFI value, it is actually more tupaoid-like in having lower values for DNE and 3D-OPCR.

size representing *Dendrogale*, as it is likely that the true morphospace occupied by this genus is greater than that represented in our analysis. Alternatively, it could suggest that the phylogenetic position of *Prodendrogale* with respect to *Tupaia* and *Dendrogale* may warrant further consideration. In particular, *Pr. yunnanica* has never been included in a cladistic analysis; our results suggest that a closer relationship of this species to *Dendrogale* than to *Tupaia* is a hypothesis that should be tested further in

a future phylogenetic analysis. Unfortunately, the hypoconid of the *Pr. yunnanica* specimen is broken, so its dental topography could not be measured, and its diet could not be assessed.

It has previously been suggested that *Ptilocercus lowii* is an example of a ‘living fossil,’ having gone relatively unchanged since at least the early Oligocene (Li and Ni, 2016). The results of our GMA do suggest that the early Oligocene *Pt. kylin* is more similar in dental morphology to extant *Ptilocercus* than it is to other members of Scandentia. Although the UPGMA cluster analysis does group *Pt. kylin* with *Pt. lowii*, it is notable that the distance between them is greater than that among all the tupaids. Moreover, certain aspects of dental morphology, particularly functional aspects as inferred by DTA, suggest that *Pt. kylin* differs from *Pt. lowii*. The results of our topographic analysis suggest that *Pt. kylin* and *Pt. lowii* likely differed ecologically, with *Pt. kylin* showing a pattern of m2 morphology consistent with higher levels of frugivory than in extant *Ptilocercus* and more like that of *Tupaia*. Relief does not differ greatly between *Pt. kylin* and *Pt. lowii*, which potentially relates to the lack of an ectoloph on the upper molars in both taxa (see Selig et al., 2019b), as having an ectoloph requires that lower molars be characterized by tall cusps to allow for proper occlusion during mastication. Therefore, the relatively brachydont upper molars of *Ptilocercus* may relate to their brachydont upper molars that lack ectolophs. However, *Pt. kylin* has lower curvature and complexity than *Pt. lowii*, suggesting that *Pt. kylin* may have been more reliant on fruit. Whereas the ptilocercids are similar in m2 morphology in that they both possess a buccal cingulum (Li and Ni, 2016) and low molar relief, the shearing ability and dental complexity of *Pt. kylin* is more comparable to that of extant tupaids such as *T. minor* and *T. javanica* Horsfield, 1824, which are hypothesized to be more frugivorous than *Pt. lowii* (Emmons, 2000; Selig et al., 2019b). This suggests that *Ptilocercus* has not gone unchanged since the Oligocene, and it is likely that this taxon has varied in ecology through time. Although it is possible that certain dietary behaviors of extant *Ptilocercus*, such as feeding on alcoholic floral nectar (Wiens et al., 2008), were present in extinct species of *Ptilocercus*, our results suggest that the ecology of modern *Ptilocercus* cannot be assumed to mirror precisely the ecology of extinct species of *Ptilocercus*. These differences could reflect the geological age of this specimen, as it is likely that many of the prey and fruit species this animal would have consumed in the Oligocene would have been different from those available to treeshrews today. These differences could also reflect the fact that the specimen of *Pt. kylin* was recovered from an area much farther north than the current distribution of extant *Ptilocercus*, which could suggest that access to different prey species or plant resources may help explain the difference in inferred ecology between these two species.

Ptilocercus lowii is commonly regarded as a good modern analogue for the ancestral euarchontan and primate (Sargis, 2001, 2002, 2004; Bloch et al., 2007). Selig et al. (2019b) found that the dental morphology of *Pt. lowii* is suggestive of high levels of insectivory relative to plesiomorphic stem primate taxa such as *Purgatorius*, which is the oldest known euarchontan to begin to rely partly on fruits (Chester et al., 2015; Silcox et al., 2017). This contrast may have been less marked with more plesiomorphic ptilocercids. Our findings highlight the fact that

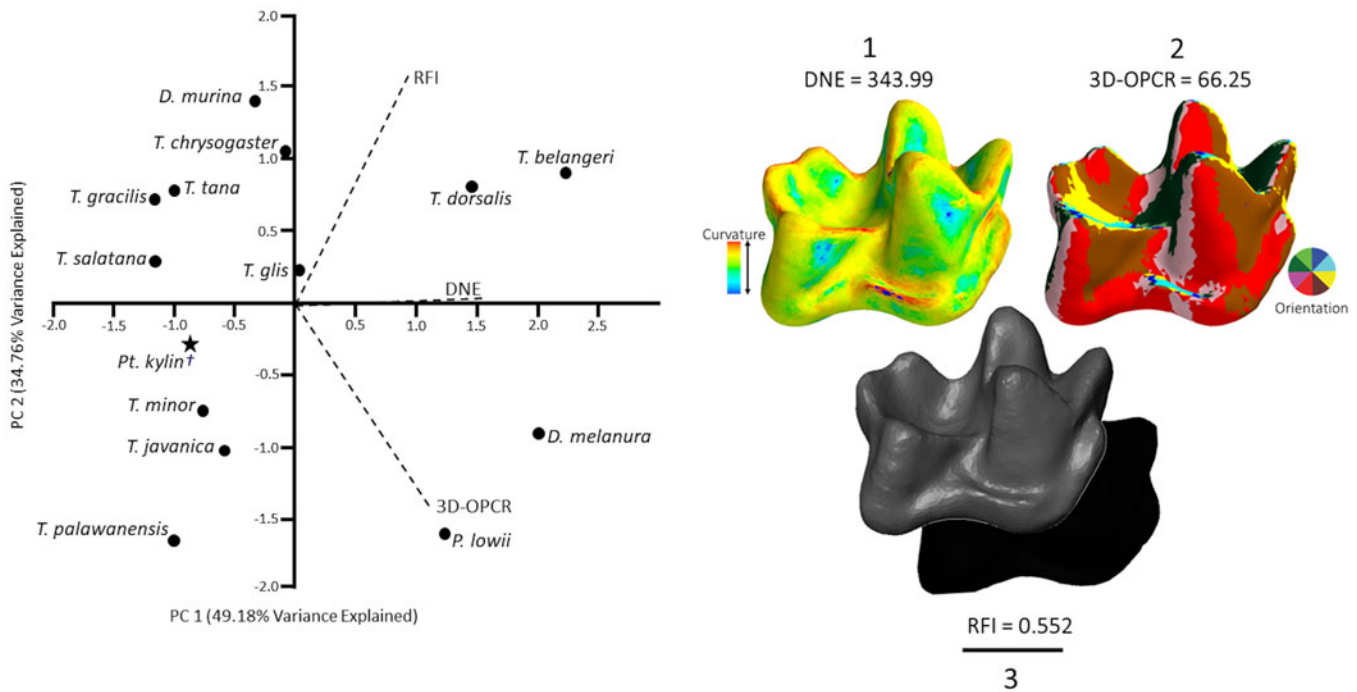


Figure 6. Left: plot depicting PC 1 and 2 of species means for all three topographic variables. The biplot indicates how curvature (DNE), complexity (3D-OPCR), and relief (RFI) load along the axes. Taxa inferred to be more insectivorous sit on the right side of the plot, whereas taxa inferred to be more frugivorous sit on the left. Right: reconstructed meshes showing the topographic maps of (1) DNE, (2) 3D-OPCR, and (3) RFI for the *Ptilocercus kylin* m2 cast (IVPP V20696). Scale bar = 1 mm.

very little is known about extinct ptilocercids or extinct scandentians in general. Although *Ptilocercus* is monospecific today, it is possible that the ptilocercid evolutionary tree was bushier and more ecologically diverse in the past, especially given the potential adaptive differences in dental morphology between *Pt. lowii* and *Pt. kylin*.

Overall, our study demonstrates the value of using both 3D GMA and DTA in the study of fossil taxa. Our results provide further evidence that these methods offer complementary, non-redundant information on dental morphology, and both provide insight into important paleobiological questions. As in the case of Selig et al. (2019b), who found that the patterns of dental topography did not necessarily reflect those of the GMA (Selig et al., 2019a), our results show that the functional morphology of the m2 of *Pt. kylin* is not necessarily well reflected by the specific geometry of occlusal features such as the position of cusps and other landmarks. If this were the case, we would expect *Pt. kylin* to plot closer to *Pt. lowii* in the topographic morphospace, as it does in the GMA. Therefore, both methods should be used in future analyses of fossil taxa.

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Accessibility of Supplemental Data

Data available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.kwh70rz1f>.

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