

## Phylogenetic Relationships among Treeshrews (Scandentia): A Review and Critique of the Morphological Evidence

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Although the supraordinal relationships of Scandentia (treeshrews) have been studied in great detail from both morphological and molecular perspectives, the phylogenetic relationships among treeshrews have been largely ignored. Here we review several published studies of qualitative morphological variation among living treeshrews and their contribution to our understanding of intraordinal phylogenetic relationships. Reanalysis of the data from each of these studies demonstrates that none of the trees in the original publications represents the most parsimonious interpretation. In addition to performing new analyses, we argue that all such studies to date suffer from one or more fundamental shortcomings, notably the failure to include reference to nonscandentian outgroups and the a priori assumption of generic monophyly of the relatively speciose genus *Tupaia*. Parsimony analyses of these data sets fail to resolve either intergeneric or interspecific relationships. Finally, several inconsistencies and conflicts with respect to character coding both within and between published studies are discussed. We conclude that a more rigorous investigation of morphological character state variation is sorely needed, one that explicitly identifies voucher specimens and does not make any assumptions of generic monophyly. This is necessary not only for the purpose of resolving phylogenetic relationships, but also for inference of ancestral states in a group that continues to figure prominently in studies of placental mammal diversification.

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**KEY WORDS:** morphology, Scandentia, systematics, treeshrews, Tupaiidae.

### INTRODUCTION

The phylogenetic position of the mammalian order Scandentia (treeshrews) among eutherian mammals has been explored in numerous morphological and molecular studies (e.g., Martin, 1990; MacPhee, 1993; Murphy *et al.*, 2001; Silcox, 2001; Bloch and Boyer, 2002; Sargis, in press) and remains a contentious issue. Relatively little attention, however, has been focused on relationships within the order. This is surprising given the role treeshrews have played in traditional studies of higher-level mammalian systematics, particularly in light of our growing knowledge of morphological variation within the order (e.g., Zeller,

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1986a,b; Wible and Zeller, 1994; Sargis, 2000, 2001, 2002a,b,c,d). Previous comparative studies have often included a single species of treeshrew as an ordinal representative, yet the taxa most often employed for these purposes (e.g., *Tupaia glis*, *T. tana*) frequently exhibit different character states than other, presumably more basal, treeshrews (e.g., *Ptilocercus*; Le Gros Clark, 1926; Campbell, 1974; Gould, 1978; Butler, 1980; Szalay and Drawhorn, 1980; Martin, 1990; Szalay and Lucas, 1993, 1996; Emmons, 2000; Sargis, 2000, 2001, 2002a,b,c,d, 2004, in press). While resolution of the interordinal position of Scandentia remains an important goal in understanding treeshrew origins, the lack of a well-supported phylogenetic framework at the intraordinal level represents a serious impediment to inferring the ancestral morphotype and interpreting evolutionary and biogeographic diversification of the group. Here we review the phylogenetic hypotheses proposed for treeshrews at the subordinal level. Because no molecular study to date has included more than a few of the taxa critical for assessing intergeneric relationships, we limit our scope to more inclusive studies based on morphological data.

The complicated taxonomic history of treeshrews, particularly at the generic level, is a potential hindrance to comparisons of published studies. While an exhaustive taxonomic review is beyond our scope here, we present a brief review of treeshrew taxonomy to avoid any nomenclatural confusion. Traditionally, six genera (*Anathana*, *Dendrogale*, *Lyonogale*, *Ptilocercus*, *Tupaia*, and *Urogale*) have been recognized in the single scandentian family Tupaiidae (but see below), but it is now generally agreed that *Lyonogale* should be included in *Tupaia*. Fiedler (1956) also proposed the inclusion of *Anathana* in *Tupaia*, and Han *et al.* (2000) suggested the return of the monotypic genus *Urogale* to *Tupaia* as well. This would leave only *Tupaia*, *Dendrogale*, and *Ptilocercus* as valid scandentian genera, but the rationale for bestowing or revoking generic status in treeshrews has so far been inconsistent and vague.

Because it has figured prominently in treeshrew taxonomy, the confusing history of the name *Lyonogale* Conisbee, 1953 warrants clarification here. Lyon (1913) erected the genus *Tana* to include all taxa currently referred to the species *Tupaia tana* and *Tupaia dorsalis*. Chasen (1940) later reallocated *Tana* to the genus *Tupaia*, but Ellerman and Morrison-Scott (1951) subsequently recognized *Tana* as a valid subgenus. Conisbee (1953) proposed *Lyonogale* as an alternative to *Tana*, noting that the name *Tana* was preoccupied (by a fly); this was subsequently adopted by Martin (1968, 1990, 2001), Butler (1980), and Luckett (1980), among others. Napier and Napier (1967) considered *Lyonogale* to be a subgenus composed of *T. tana* and *T. dorsalis*, whereas Dene *et al.* (1978, 1980) included *T. montana*, *T. minor*, *T. tana*, and *T. palawanensis* in the subgenus *Lyonogale*. However, the analysis on which the latter classification was proposed did not include *T. dorsalis*, and few authors have followed that classification. Throughout this paper, we use the name *Lyonogale* only as necessary when referring to the works of Butler (1980) and Luckett (1980), and in that context it can be equated with the species *Tupaia tana* and *T. dorsalis*.

Compared to disagreements about treeshrew generic distinction, the division of the family Tupaiidae into two subfamilies, Tupaiinae and Ptilocercinae (both of which have recently been elevated to familial rank; see below), has been far less contentious. Only Davis (1938) has opposed this separation, arguing that *Dendrogale* is morphologically intermediate between *Ptilocercus* and tupaiines, but the separation of *Ptilocercus* has been reaffirmed in numerous studies (e.g., Le Gros Clark, 1926; Steele, 1973; Butler, 1980;

Luckett, 1980; Zeller, 1986a,b; Sargis, 2000, 2001, 2002b,d, 2004, in press). Furthermore, most authors agree that *Ptilocercus* is the living treeshrew that most closely resembles the ancestral scandentian in both its ecology and its morphological attributes (e.g., Le Gros Clark, 1926; Campbell, 1974; Gould, 1978; Butler, 1980; Szalay and Drawhorn, 1980; Martin, 1990; Szalay and Lucas, 1993, 1996; Emmons, 2000; Sargis, 2000, 2001, 2002b,d, 2004, in press).

Throughout this paper, we attempt to reconcile previous studies with the classification proposed by Helgen (in press; Table I). Whereas most authors have followed Lyon (1913), who placed *Ptilocercus* in the monotypic subfamily Ptilocercinae, Helgen (in press) follows Shoshani and McKenna (1998) in according familial rank (Ptilocercidae) to this taxon, a decision we endorse in light of the numerous morphological and behavioral features unique to *Ptilocercus* (see above). Thus, whereas the names Scandentia and Tupaiidae have often been used interchangeably in the past, we use the former when referring to all living treeshrews and the latter in reference to all nonptilocercid taxa (equivalent to Tupaiinae of most previous authors).

To date, only three published studies have employed morphological character data to generate a phylogenetic hypothesis relating the living genera or species of treeshrews, each of which is briefly reviewed below.

**Table I.** Current Taxonomy of Treeshrews, following Helgen (in press)

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Order Scandentia Wagner, 1855
Family Tupaiidae Gray, 1825
<i>Anathana</i> Lyon, 1913
<i>A. ellioti</i> (Waterhouse, 1850)
<i>Dendrogale</i> Gray, 1848
<i>D. melanura</i> (Thomas, 1892)
<i>D. murina</i> (Schlegel and Müller, 1843)
<i>Tupaia</i> Raffles, 1821
<i>T. belangeri</i> (Wagner, 1841)
<i>T. chrysogaster</i> Miller, 1903
<i>T. dorsalis</i> Schlegel, 1857 <sup>a</sup>
<i>T. glis</i> (Diard, 1820)
<i>T. gracilis</i> Thomas, 1893a
<i>T. javanica</i> Horsfield, 1824
<i>T. longipes</i> (Thomas, 1893b)
<i>T. minor</i> Günther, 1876 <sup>b</sup>
<i>T. moellendorffi</i> Matschie, 1898
<i>T. montana</i> (Thomas, 1892) <sup>b</sup>
<i>T. nicobarica</i> (Zelevor, 1869)
<i>T. palawanensis</i> Thomas, 1894 <sup>b</sup>
<i>T. picta</i> Thomas, 1892
<i>T. splendidula</i> Gray, 1865
<i>T. tana</i> Raffles, 1821 <sup>a,b</sup>
<i>Urogale</i> Mearns, 1905
<i>U. everetti</i> (Thomas, 1892)
Family Ptilocercidae Lyon, 1913
<i>Ptilocercus</i> Gray, 1848
<i>Ptilocercus lowii</i> Gray, 1848

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<sup>a</sup>Formerly included in the genus *Tana* Lyon, 1913 by Lyon (1913) and subsequently *Lyonogale* Conisbee, 1953 by Martin (1984) and others.

<sup>b</sup>Included in the subgenus *Lyonogale* Conisbee, 1953 by Dene *et al.* (1978).

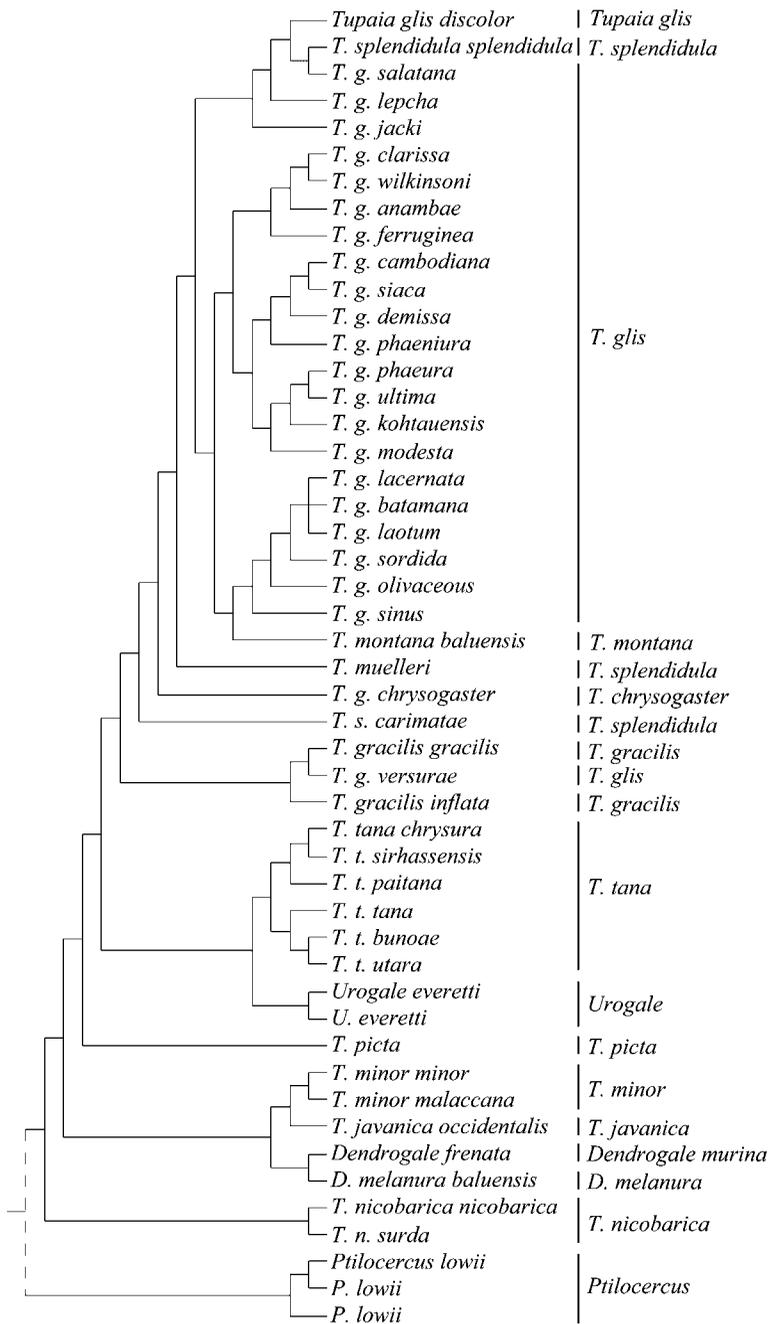
### Steele, 1973

Steele (1973) described dental variation in treeshrews on the basis of a sample of 301 museum specimens, mostly from the U.S. National Museum (the remainder being from the American Museum of Natural History). From these, he selected 49 specimens, for which he coded 43 discrete characters representing 91 character states. A dendrogram resulting from a distance-based (UPGMA) analysis, reproduced in Fig. 1, represents the first published tree relating multiple species and genera of treeshrews. Noting the study's exclusive reliance on dental variation, Steele (1973, p. 170) observed that the cluster analysis was "not expected to demonstrate exact taxonomic relationships." Nonetheless, he noted several interesting suggested relationships, including the "dissimilarity between the *T. tana* cluster and the *T. glis* (*et al.*) cluster" (Steele, 1973, p. 170) and the clustering of *Urogale* with *T. tana*. Lyon (1913) had earlier remarked on the numerous perceived similarities between the latter two taxa, believing them to be the result of descent from a common ancestor (thereby implicitly suggesting nonmonophyly of the genus *Tupaia* [as currently recognized]), with *Urogale*'s distinctiveness stemming from its isolation and small population size. Lockett (1980), however, countered that none of the dental features examined by Steele was unique to either *Lyonogale* or *Urogale*, and that all of their shared similarities could be found in several other tupaiines. Interestingly, no mention was made by Steele of the rampant paraphyly of several taxa suggested by his dendrogram, including the species *T. glis* and *T. splendidula*, as well as the genus *Tupaia*.

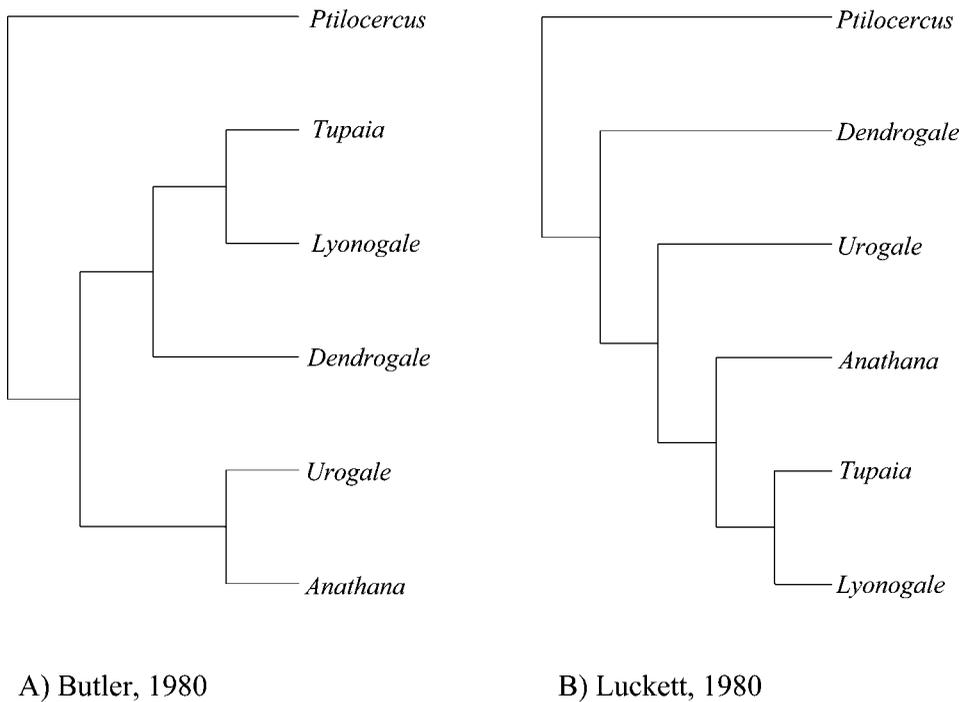
While Steele's (1973) paper remains a seminal review of both qualitative and quantitative variation in treeshrew dentition, several taxa were missing from his sample (e.g., *Anathana*, *Tupaia dorsalis*, and *T. palawanensis*). Furthermore, no list of specimens examined was provided, making comparisons to additional specimens difficult (particularly in light of taxonomic revisions in the intervening three decades). In addition, and certainly through no fault of the author, nearly half (20) of the 43 described characters are fixed for alternative states in *Ptilocercus* and the remaining treeshrews, leaving only 23 characters to sort out relationships among the 46 tupaiid specimens in his sample. Finally, no nonscandentian outgroup taxa were included to assess this basal split.

### Butler, 1980

Butler's chapter in a 1980 volume devoted to the evolutionary affinities of Scandentia included a cladogram relating the six genera of treeshrews (including *Lyonogale*), with apomorphic dental characters mapped according to the author's extensive knowledge of mammalian dental variation (see Fig. 2a). Like Steele (1973), Butler utilized only dental features and assumed a basal separation of *Ptilocercus* from the remaining tupaiine genera (Tupaiinae). Although no character matrix was provided, the apomorphies detailed in his fig. 12 can be reduced to 21 individual characters comprising 36 character states. Unlike Steele, Butler included the genus *Anathana* but assumed monophyly of the genera *Lyonogale* (which Steele regarded as a subgenus of *Tupaia*) and *Tupaia*. His recovery of a sister relationship between *Urogale* and *Anathana* is in contrast to both Steele (1973), who argued for a close relationship between *Urogale* and *Lyonogale*, and other authors who have discounted *Anathana*'s generic distinctiveness from *Tupaia* (e.g., Fiedler, 1956). Helgen (in press) has also suggested a close relationship between *Tupaia* and *Anathana*. A *Urogale* + *Anathana* clade is difficult to reconcile biogeographically given the distributions of these two genera



**Fig. 1.** Topology recovered by Steele's (1973) UPGMA analysis of 43 dental characters (modified from his fig. 4; branch lengths here do not represent distances). Labels on tips represent the individual specimens and their taxonomy as followed by Steele. The corresponding classification of Helgen (in press; Table I) is shown to the right of the grouping lines. The dashed line connecting *Ptilocercus* to the base of the tree was implied but not figured by Steele (1973).



**Fig. 2.** Topologies proposed by (A) Butler (1980; modified from his fig. 12) and (B) Lockett (1980; modified from his fig. 7) relating the six genera of tree shrews. Both authors recognized the genus *Lyonogale* as distinct from *Tupaia*.

(the island of Mindanao and associated smaller islands to the north in the Philippines as opposed to India south of the Ganges).

Butler (1980) readily acknowledged that his tree represented one of several possible interpretations, depending on how homoplasious characters were optimized, particularly with respect to the position of *Dendrogale*, which he chose to depict as nested within Tupaiinae rather than as its basal-most member (which he recognized as an equally parsimonious hypothesis).

### Lockett, 1980

Lockett's chapter in the same 1980 volume likewise included two "character phylogenies" relating the six scandentian genera (like Butler [1980], Lockett recognized *Lyonogale* as a distinct genus). In the first, he used 15 binary, polarized characters (his table 4) to construct a phylogeny establishing *Ptilocercus* as the basal member of the order. Of these 15 characters, eight were fixed for the putatively derived condition in *Ptilocercus* and each of the rest was fixed for the apomorphic state in the remaining genera (resulting in a pentachotomous sister group to *Ptilocercus*). The second phylogeny relating the six tree shrew genera was based on nine polarized characters (his table 5), with *Ptilocercus* possessing the plesiomorphic condition in each. The topology of Lockett's resulting tree is shown in Figure 2b. Unlike Steele (1973) or Butler (1980), Lockett's nine characters (with 20 character

states) included nondental cranial, postcranial, and soft anatomical features. However, like Butler, he assumed monophyly of the genus *Tupaia* with respect to the genera *Lyonogale* and *Anathana*. His proposed phylogeny and discussion of character polarity support a sister relationship between *Dendrogale* and the remaining tupaiine genera, something Butler (1980) considered plausible but seemingly discounted in his decision to publish the alternative arrangement shown in Figure 2a.

### Current Objectives

The data from these three studies have never been subjected to formal phylogenetic analysis using standardized procedures. The aims of this study are therefore to: (1) determine whether phylogenetic analysis of these published data sets recovers hypotheses of treeshrew interrelationships concordant with those inferred by the original authors, (2) test for agreement among authors in character conceptualization and coding, and (3) critically examine the nature of the morphological evidence adduced in the inference of phylogenetic relationships among treeshrew genera, and assess whether taxonomic assumptions underlying these inferences are valid. Given the total number of characters in all three studies (79), we have not consulted museum specimens in an attempt to confirm character codings; this will be addressed in a forthcoming study on morphological systematics of treeshrews (Sargis *et al.*, unpublished).

## MATERIALS AND METHODS

We reviewed and reanalyzed the above data sets under the criterion of maximum parsimony. Converting the data of Steele (1973) and Lockett (1980; his table 5) into matrix format (Appendices 1, 2 and 5, 6, respectively) was straightforward and involved no subjective decisions on our part. In the case of Butler's (1980) characters, states for each taxon were inferred based on the distribution of putative apomorphies shown in his fig. 12 and corresponding discussion in the text (see Appendices 3 and 4). Given the aforementioned objectives of this paper, we did *not* attempt to verify codings using voucher specimens (which would not have been possible anyway for those studies that did not include information on specimens examined), nor did we code additional ingroup or outgroup taxa.

Parsimony analyses were conducted using PAUP\* 4.0b (Swofford, 2003). All characters were treated as unordered and equally weighted in initial analyses. Additional analyses were conducted with select characters treated as ordered (see Appendices 1, 3, and 5). Tree searches employing the branch-and-bound search algorithm were possible for the Butler and Lockett matrices, but not for the Steele matrix. For the latter, the heuristic search algorithm was employed with the following options: starting trees obtained via stepwise addition, 100 random addition sequence replicates, and tree-bisection and reconnection (TBR) branch-swapping. Clade stability was explored using the nonparametric bootstrap (Felsenstein, 1985) and decay indices (Bremer, 1988). Bootstrapping of the Lockett and Butler data sets was performed by PAUP\*, with 1,000 heuristic search replicates using TBR branch-swapping and one random addition sequence per search replicate. For the Steele data set, nearest-neighbor interchange branch-swapping was performed and the maximum number of trees saved (maxtrees) was set to 100,000. Decay indices for select nodes were calculated using reverse constraint searches in PAUP\* (with otherwise identical search parameters). Because no outgroup taxon was scored by any of the authors whose data we reanalyzed,

**Table II.** Data Sets Analyzed

Data set	OTUs	Ord./unord.	Characters, states	No. of informative characters	Characters/OTU
Butler, 1980	6	U	21, 45	5	3.5
		O		6	
Luckett, 1980	6	U	9, 20	6	1.5
		O		6	
Steele, 1973	49	U	43, 85	43	0.88
		O		43	

*Ptilocercus* was used to root all resulting trees (i.e., monophyly of Tupaiidae was assumed but not tested).

Dental nomenclature follows each respective author with the exception of our use of upper case and lower case letters to refer to upper and lower teeth, respectively.

## RESULTS

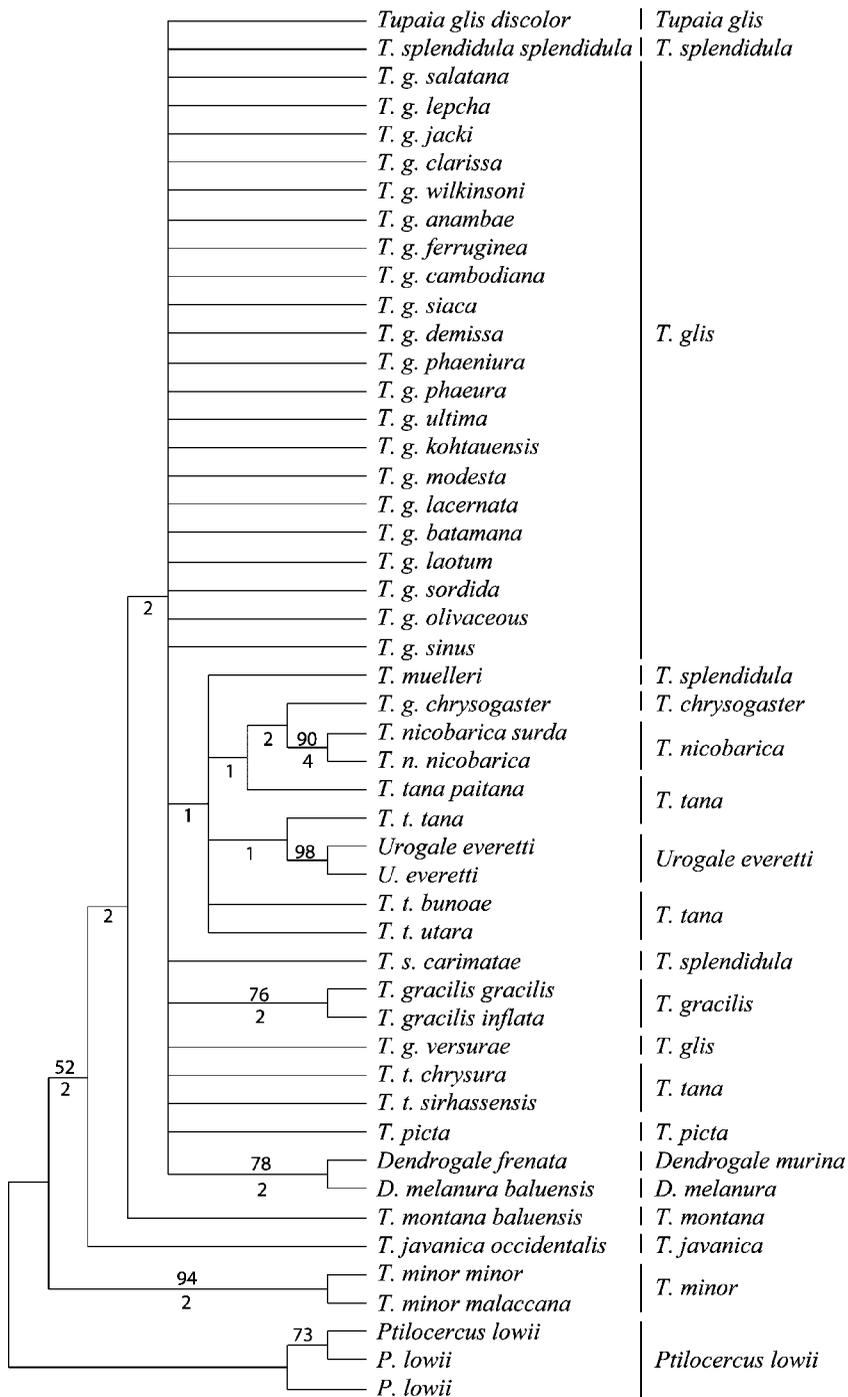
A summary of each data set analyzed is provided in Table II. Relative phylogenetic informativeness in a given data set varied widely, with only five out of 21 characters phylogenetically informative in the Butler (1980) data set, compared to all 43 of Steele's (1973) characters. Parsimony analysis of the three published data sets resulted in some marked differences from the trees originally accompanying each publication, as is summarized below.

### Steele (1973) Data

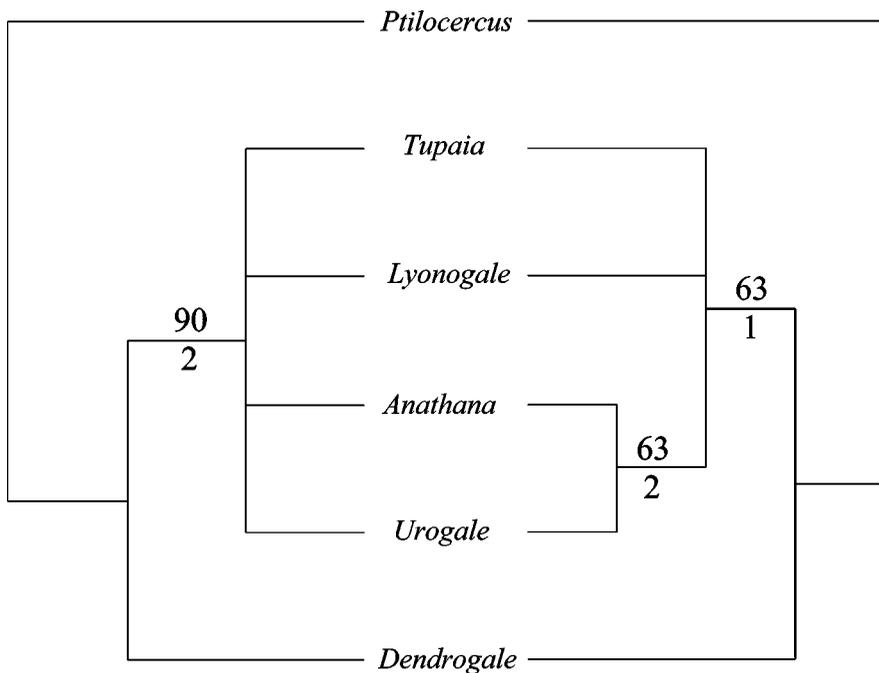
A heuristic tree search of the Steele (1973) data set with all characters treated as unordered resulted in 20,368 equally parsimonious trees (each 142 steps, consistency index (CI) = 0.338, retention index (RI) = 0.715). The strict consensus of these, shown in Figure 3, differs from Steele's original UPGMA tree (Figure 1) in several ways. First, *Tupaia minor* is recovered as the basal-most member of the Tupaiidae in parsimony analysis, a position occupied by *T. nicobarica* in Steele's tree. Second, whereas Steele's tree grouped specimens referred to *T. tana* as the sister taxon to *Urogale*, the former was not recovered as a monophyletic taxon in parsimony analyses, which instead weakly support paraphyly of *T. tana*. With few exceptions, relationships among the majority of the species in the genus *Tupaia* were not resolved by parsimony analysis of these data. Furthermore, support values for the majority of resolved clades are low. As in Steele's (1973) original analysis, *Tupaia* was not recovered as a monophyletic taxon, and the shortest trees from searches constrained to recover a monophyletic *Tupaia* were six steps longer (results not shown). In general, the Steele data set provides little phylogenetic resolution. Separate analyses treating Steele's characters 25 and 28 (hypocone development; see Appendix 2) as ordered resulted in essentially identical results (not shown).

### Butler (1980) Data

Parsimony analyses of the data derived from Butler (1980) are shown in Figure 4. Surprisingly, neither analysis recovered the topology favored by Butler in his fig. 12 (see Fig. 2a), in which *Dendrogale* was depicted as the sister to a *Tupaia* + *Lyonogale* clade.



**Fig. 3.** Strict consensus of 20,368 equally parsimonious trees resulting from a heuristic search using the data set in Steele (1973). All bootstrap values >50 are shown above the corresponding branches, while decay indices are given below. Tip labels as in Fig. 1.

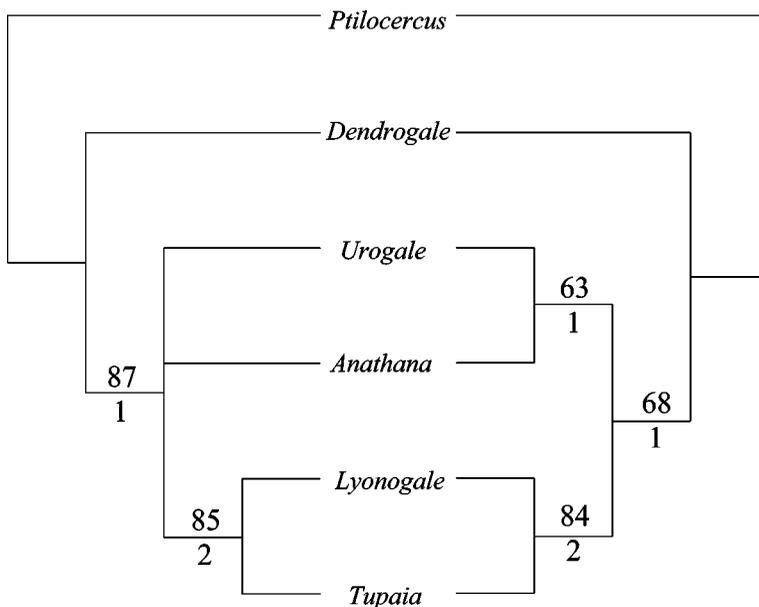


**Fig. 4.** Results of the parsimony analysis of the Butler (1980) data set. On the left is a strict consensus of four equally parsimonious trees resulting from the unordered analysis (25 steps, CI = 0.96, RI = 0.8). The strict consensus representation of the three shortest trees resulting from the ordered analysis is shown on the right (27 steps, CI = 0.89, RI = 0.63). Numbers above and below branches are as in Fig. 3.

Instead, all trees from both the unordered and ordered analyses recover *Dendrogale* as the basal-most tupaiaid genus. Whereas relationships among the remaining tupaiaid genera are unresolved by the unordered analysis, the ordered analysis favors an additional clade uniting *Anathana* with *Urogale* (a hypothesis likewise favored by Butler). Bootstrap support for the clade uniting all non-*Dendrogale* tupaiaids is relatively high (90%) in the unordered analysis, but considerably lower (63%) in the ordered analysis.

#### Luckett (1980) Data

Results of the analysis of the Luckett (1980) data are shown in Figure 5. As with the Butler (1980) data set, parsimony analysis of these data do not recover the tree presented in Luckett's original figure (see Fig. 2b). Whereas the unordered analysis does not resolve the position of *Anathana* among tupaiaid genera, the ordered analysis recovers an *Anathana* + *Urogale* clade, in contrast to Luckett's hypothesis of successively basal positions for *Anathana* and *Urogale* with respect to the *Tupaia* + *Lyonogale* clade (which was recovered in all parsimony analyses). Bootstrap support for the basal position of *Dendrogale* among tupaiaid genera was higher in the unordered analysis (87%) than in the ordered analysis (68%), with decay indices of one or two for all resolved clades.



**Fig. 5.** Results of the parsimony analysis of the Luckett (1980) data set, showing the strict consensus of three equally parsimonious trees on the left (12 steps, CI = 0.92, RI = 0.83) resulting from the unordered analysis, and the single most parsimonious tree resulting from the ordered analysis on the right (13 steps, CI = 0.85, RI = 0.75). Numbers as in Figs. 3 and 4.

## DISCUSSION

Our reanalysis of all three data sets recovered topologies different from those accompanying their original publications. This is not unexpected given that methods available today for phylogenetic analysis were not available at the time these authors presented their results. Furthermore, neither Steele (1973) nor Butler (1980) advocated their hypotheses as being the most parsimonious representations of their data, and the method behind Luckett's (1980, p. 18) "character phylogeny" was not explicitly stated. It is not our intent to criticize these authors. Instead, we simply wish to establish the point that their data (and, in the case of Butler, our interpretation of his data) do not support their phylogenetic hypotheses when analyzed under the explicit criterion of maximum parsimony.

Differences in taxon sampling (see below) preclude direct comparisons of our analysis of Steele's (1973) data set with analyses of those of Butler (1980) and Luckett (1980). The latter two authors, however, both considered each of the (then) recognized genera of treeshrews as individual operational taxonomic units. For both data sets, both unordered and ordered analyses recovered *Dendrogale* as the basal-most tupaiid genus. Because we used *Ptilocercus* to root all trees, however, this by itself is an invalid test of *Dendrogale*'s position relative to the remaining tupaiids. Davis (1938) argued that *Dendrogale*, rather than *Ptilocercus*, was the most primitive living treeshrew (and, by extension, the most basal), although subsequent authors have not endorsed this position. Luckett (1980) used the hypothetical ancestral eutherian condition in 15 characters to support the more widely accepted view that *Ptilocercus* represents the sister taxon to the remaining treeshrews (Lyon, 1913;

Le Gros Clark, 1926; Napier and Napier, 1967; Martin, 1968, 1990, 2001; Steele, 1973; Butler, 1980; Zeller, 1986a,b; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999; Sargis, 2000, 2001, 2002a,b,c,d, 2004, in press; contra Davis, 1938). However, this has never been tested using an outgroup taxon or taxa (see Nixon and Davis [1991]; Wiens [1998] for reviews of the problems associated with the use of hypothetical outgroups in phylogenetics). Relationships among the remaining tupaiid genera were not resolved by the unordered analysis of Butler's data (Fig. 4), but ordered analysis of both his and Lockett's data (Fig. 5) support *Anathana* + *Urogale* clade. Such a relationship, if valid, is not readily explicable from a biogeographic perspective. Finally, in contrast to the analyses of Lockett's data, *Tupaia* and *Lyonogale* were recovered as sister taxa in only one out of the three ordered and one out of four unordered most parsimonious trees on the basis of Butler's data. This is interesting, given that most recent authors have not recognized *Lyonogale* as distinct from *Tupaia* (Napier and Napier, 1967; Steele, 1973; Corbet and Hill, 1992; Wilson, 1993; Nowak, 1999; Helgen, in press). Both immunological distances (Dene *et al.*, 1978, 1980) and DNA hybridization (Han *et al.*, 2000) suggest a nested position of *T. tana* within *Tupaia* (*sensu lato*), as do cluster analyses of postcranial data (Sargis, 2002a,b,c, 2004). However, this is not unexpected since the only two apomorphies mapped as supporting the *Tupaia* + *Lyonogale* clade in Butler (1980) are also shown on the branch leading to *Urogale* + *Anathana*.

### Are Assumptions of Generic Monophyly Valid?

Because both Butler (1980) and Lockett (1980) presented their character data at the generic level, their data sets are not amenable to testing for monophyly of the polytypic genera *Dendrogale*, *Lyonogale* (see Introduction), or *Tupaia*. The monophyly of *Tupaia* (*sensu lato*; i.e., including the taxa formerly comprising *Lyonogale*), while widely assumed, has been either implicitly or explicitly questioned (Fiedler, 1956; Han *et al.*, 2000). The DNA hybridization study of Han *et al.* (2000), which included five species of *Tupaia* as well as *Urogale everetti*, recovered very short genetic distances between the two genera. These authors interpreted this as strongly suggesting paraphyly of the genus *Tupaia* with respect to *Urogale* (which is nested among species of *Tupaia* in cluster analyses of postcranial data; Sargis 2002a,b,c, 2004). We find it noteworthy that neither Steele's (1973) original UPGMA analysis, nor our parsimony analysis of his data support a monophyletic *Tupaia*. Indeed, heuristic searches constrained to recover a monophyletic *Tupaia* are six and seven steps longer than unconstrained searches in unordered and ordered analyses, respectively (not shown). Unfortunately, Steele (1973) was unable to code the monotypic genus *Anathana*, whose generic distinctiveness relative to *Tupaia* has also been questioned (e.g., Fiedler, 1956). Collectively, these results suggest that future studies should not assume monophyly of the relatively speciose genus *Tupaia*, and that published data sets making such a priori assumptions (e.g., Butler, 1980; Lockett, 1980) should be interpreted with great caution.

### Issues in Character Coding

In reviewing and comparing the three data sets analyzed in this study, we uncovered several instances of disagreement between authors, as well as inconsistencies within studies with respect to character coding. As previously stated, we did not verify codings using museum specimens for reasons given in the introduction. Certain controversial characters were, however, compared with other published accounts as discussed below.

### *Upper Canine*

Both Lockett (1980) and Butler (1980) coded *Dendrogale* as possessing a double-rooted upper canine, a condition likewise noted by Davis (1938) in his seminal monograph on this genus. Steele (1973) coded *Dendrogale* as having the single-rooted condition, yet this appears to be one of many inconsistencies between his character matrix (his fig. 4; Appendix 2 here) and corresponding discussions in his text. For example, he referred to *Dendrogale* (Steele 1973, p. 162) as being “the only genus within this subfamily that exhibited a double-rooted canine.” Interestingly, he went on to say that two of the seven specimens of *D. melanura* had single-rooted canines. For a separate character, Steele characterized the shape of the upper canine as being either a simple cone or premolariform, essentially identical to one of the characters Lyon (1913) and Lockett (1980) considered constant within each family. While agreeing with these authors that *Ptilocercus* possesses a premolariform upper canine, Steele also coded several *Tupaia* specimens and *Dendrogale murina* as exhibiting this condition. Whether this represents an error on Steele’s part or merely inherent differences in character state definitions is unknown.

### *Hypocone*

This character has featured prominently in the comparative morphology of treeshrews (e.g., Gregory, 1910; Lyon, 1913; Le Gros Clark, 1926). Both Lockett (1980) and Butler (1980) considered hypocone development as a single character with essentially identical states and codings among genera (Appendices 3 and 5). Steele (1973), on the other hand, characterized the condition of the hypocone separately for P4, M1, and M2, with varying combinations of states among different taxa (Appendices 1 and 2). There are, however, inconsistencies between Steele’s codings and the accompanying discussion. For example, the molars of *Tupaia minor* and *T. gracilis* are said in the text to “lack hypocones” (Steele, 1973, p. 166), yet *T. minor* was coded as having poorly developed hypocones on M1 and M2 and those of *T. gracilis inflata* were coded as being well-developed.

### *P3*

Steele (1973) coded P3 as being single-rooted in *Dendrogale*, in contrast to the double-rooted condition reported by Davis (1938). Steele (1973) also coded the parastyle of P3 as absent in *Urogale*, while Butler (1980) claimed that only *Ptilocercus* and some *Tupaia* lack this feature (although he did not consider its presence or absence among his apomorphies).

### *Mesostyle*

Presence of a mesostyle on one or more molars is considered a synapomorphy of Tupaiaidae (*sensu* Helgen, in press; Butler, 1980; Lockett, 1980). Steele (1973) considered the condition of the mesostyle (single versus bifid), when present, as separate characters for M1 and M2, with *Tupaia nicobarica nicobarica* coded as having single cusps and *T. n. surda* with bifid cusps for both teeth. Butler (1980) discussed this feature (but did not consider it among his apomorphies), noting that *T. nicobarica* possesses the single-cusp condition. It is unclear which subspecies (if not both) he had access to. Butler further

noted the single condition in *T. minor*, *T. gracilis*, and *T. javanica*; an intermediate (?) “ridge-like” condition in *Urogale*; and the bifid state in all other tupaiids. This is in contrast to Steele, who characterized *Dendrogale*, several subspecies of *T. glis*, and *T. montana* as having single, nonbifid mesostyles on both teeth considered. However, Steele (1973) was inconsistent, stating in the text (p. 166) that the mesostyle is “bifid in the majority of specimens examined” and “single only in *T. minor* and *T. gracilis*.”

#### *Lower Incisors*

One of Lockett’s (1980) 15 characters separating the two treeshrew families deals with the development of the first two lower incisors (a character first used by Lyon, 1913 to separate Tupaiinae from Ptilocercinae in his key). Lockett’s (1980, p. 17) states (“i2 subequal to i1” versus “i2 twice as large as i1”), fixed in Tupaiidae and *Ptilocercus*, respectively, are seemingly identical to those in Steele’s (1973, p. 169) character 4 (“i1 and i2 approximately equal in size” versus “i2 significantly larger than i1”). However, Steele also coded several tupaiids (*Dendrogale murina*, *Tupaia javanica*, and *T. minor*) along with *Ptilocercus* as possessing an enlarged i2.

#### *Fusion of the Scaphoid and Lunate*

There has been very little agreement concerning the fusion of the scaphoid and lunate in the carpus of various treeshrews. While most agree that these bones are fused in *Tupaia* (Flower, 1885; Gregory, 1910; Lyon, 1913; Carlsson, 1922; Davis, 1938; George, 1977), *Anathana*, and *Urogale* (George, 1977), Novacek (1980) coded them as being unfused in Tupaiinae (see Novacek, 1980, fig. 23; table 5). Le Gros Clark (1926) reported these bones as unfused in *Ptilocercus*. Davis’ (1938) comments concerning the fusion of the scaphoid and lunate in *Dendrogale* are confusing. His initial claim that the “the scaphoid and lunar [=lunate] are separate” is contradicted later in the same paragraph in his reference to “the fused condition of the scaphoid and lunar in *Dendrogale*” (p. 386). Lockett (1980) coded this feature as fused in *Tupaia* and *Anathana*, unfused in *Ptilocercus* and *Dendrogale*, and unknown in *Urogale* (contra George 1977; see above). Stafford and Thorington (1998) were in complete agreement with George (1977) in concluding that the scaphoid and lunate are fused into a scapholunate in *Tupaia*, *Urogale*, and *Anathana*, while these bones are unfused in *Dendrogale* (see Davis, 1938) and *Ptilocercus* (see Le Gros Clark, 1926). Stafford and Thorington (1998), however, did not attempt to disarticulate the *Ptilocercus* carpus in their care (which they have figured extremely well; see their fig. 2a). This is unfortunate because hypotheses concerning carpal fusion (in adults) are best tested by disarticulation.

Sargis (2002b) was able to examine the disarticulated wrists of several treeshrews, including those of *Ptilocercus* and *Dendrogale*, and the scaphoid and lunate of these taxa are fused, although not to the same degree as in *Tupaia*, *Anathana*, and *Urogale* (see his figs. 20, 21; contra Le Gros Clark, 1926; Davis, 1938; George, 1977; Lockett, 1980; Novacek, 1980; Stafford and Thorington, 1998). A groove remains on the scapholunate of *Ptilocercus* and *Dendrogale* (see arrows on his figs. 19–21), whereas it has been completely obliterated (fig. 21) in *Tupaia*, *Urogale*, and *Anathana*. Sargis (2002b) argued that the fusion of the scaphoid and lunate (i.e., presence of a scapholunate) is a synapomorphy that unites all living scandentians and, as such, is of little, if any, phylogenetic utility at the intraordinal level.

### *Cecum*

Peters (1864) used this character to separate members of the order Insectivora into groups possessing a cecum in the gut (Scandentia, Macroscelidea) or lacking one (Soricidae, Talpidae, Chrysochloridae, Tenrecidae, Erinaceidae, and Solenodontidae). This arrangement was subsequently adopted by Haeckel (1866), who proposed the suborders Menotyphla and Lipotyphla, respectively, to accommodate them. The historical importance of this feature calls for a careful consideration of Lockett's (1980) suggestion that cecum loss is an autapomorphy of *Lyonogale* (and therefore a synapomorphy uniting *Tupaia tana* and *T. dorsalis*; Table I). Lyon (1913) noted the absence of a cecum in *T. tana* as well as *T. picta*, citing the works of Garrod (1879) and Chapman (1904), respectively. Lyon himself personally dissected specimens of *T. glis*, *T. belangeri*, *T. chrysogaster*, and *T. nicobarica*, reporting the presence of a cecum in each. He further remarked on published accounts of a cecum in *T. splendidula* by Garrod (1879, cited in Lyon, 1913) and *Anathana* (Anderson, 1879, cited in Lyon, 1913). Davis (1938) discussed and figured a prominent cecum in *Dendrogale murina*, as did Le Gros Clark (1926) in *Ptilocercus*. To our knowledge (and consistent with Lockett, 1980), *Urogale*'s condition remains unknown. Thus, published accounts to date conflict with Lockett's (1980) notion of cecum loss occurring only in *Lyonogale*, given the additional account of its loss in *T. picta* (Chapman, 1904, as cited in Lyon, 1913) and the as yet unknown condition in *T. dorsalis* and *Urogale*. Lyon (1913, p. 14) concluded his discussion with the observation that "[i]t would not appear that the presence or absence of a cecum is a good character for determining larger groups," though he then reiterated its variable occurrence in the genus *Tupaia*. The continued controversy over the phylogenetic importance of cecal absence in mammals (e.g., MacPhee and Novacek, 1993) calls for a reinvestigation of this feature among treeshrew species.

In addition to the above issues related to character coding, our review of the studies of Steele (1973), Butler (1980), and Lockett (1980) identified several fundamental shortcomings that have yet to be overcome in the phylogenetic analysis of morphological data within Scandentia. The first, as mentioned above, deals with the a priori assumption of monophyly of the genus *Tupaia*. While both Butler and Lockett assumed *Tupaia* (*sensu stricto*) to be a natural group, neither Steele's data nor the molecular data of Han *et al.* (2000) support this. However, our critical examination of Steele's data suggests either numerous coding errors or misrepresentation of the coding for his fig. 4. Because none of the authors provided a list of specimens examined and the characters coded for each specimen, their results cannot be replicated. Given the often confusing taxonomic history of treeshrews, particularly for species in the genus *Tupaia*, future studies must include details of both specimens examined and variability within taxa. Finally, none of the three studies used outgroup taxa to root their trees. While few authors would suggest nonmonophyly of Tupaiidae (*sensu* Helgen, in press) given *Ptilocercus*' unequivocal distinctiveness (see Sargis, 2000, 2001, 2002a,b,c,d, 2004, in press), this has yet to be formally tested with outgroup taxa. In light of these shortcomings, we therefore suggest that studies assuming generic monophyly be provisionally used to guide future investigations, but that their results be interpreted with caution.

### **Can Morphology Resolve Interspecific Relationships among Treeshrews?**

The role of morphology in contemporary phylogenetic systematics (which is increasingly dominated by molecular data) has been both championed (e.g., Wiens, 2000) and

questioned (Scotland *et al.*, 2003) in recent years. Although a thorough review of this debate is beyond the scope of this study, we will nonetheless comment on this issue as it pertains to issues in the systematics of treeshrews. Scotland *et al.* (2003) reviewed several of the fundamental differences between molecular and morphological systematics. These include relatively fewer characters available for morphological studies (Hillis, 1987), averaging fewer than three per taxon in a recent survey (Scotland *et al.*, 2003). This is certainly the case for the studies reviewed here, which range from 0.88–3.5 characters/OTU (Table II). However, the list of characters included in these studies is by no means exhaustive. Countless potentially informative characters have been described in great detail for several taxa but have not been coded in the majority of treeshrew species; these include myological, postcranial, chondrocranial, and external soft tissue features (e.g., Lyon, 1913; Carlsson, 1922; Le Gros Clark, 1926; Davis, 1938; Zeller, 1986a,b; Wible and Zeller, 1994; Sargis, 2001, 2002b,c,d). We therefore strongly disagree with the general conclusion reached by Scotland *et al.* (2003, p. 545) that “much of the useful morphological diversity has already been scrutinized.” Indeed, we consider this an unsubstantiated claim for mammals as a whole despite their long history of intensive systematic and morphological study, and we offer treeshrews as a striking counterexample. Given the long-standing interest in treeshrews with respect to their phylogenetic position at the interordinal level and the continued debate over their putative relationship to primates (e.g., Lockett, 1980; Martin, 1990; MacPhee, 1993; Murphy *et al.*, 2001; Silcox, 2001; Bloch and Boyer, 2002; Sargis, 2002d, in press), one might assume that morphological variation within a taxon of such apparent widespread interest had long since been extensively and meticulously documented in comparative phylogenetic studies. Yet, as we have shown here, this is decidedly not the case. Indeed, we are of the opinion that no phylogenetic investigation that could truly be considered rigorous (including this one) has *ever* been conducted on the morphological diversity known to occur among living treeshrew species. Are we to abandon such efforts and instead rely on molecular variation to resolve all unresolved phylogenetic issues? While DNA sequence data will undoubtedly lend much-needed insight into treeshrew interrelationships (Olson, Sargis, and Martin, unpublished), the contention that “rigorous and critical anatomical studies of *fewer* morphological characters in the context of a molecular phylogeny is the way that integrated studies will and should develop” (Scotland *et al.*, 2003, p. 545; emphasis added) is misguided and unfounded in our view. There have, of course, been disagreements and inconsistencies with respect to character coding and character conceptualization in morphological studies, including those reviewed here. Nevertheless, we argue that the rigorous and critical examination of *more* characters is desperately needed, regardless of the amount of molecular character data for treeshrews published previously (very limited) or forthcoming in the foreseeable future. How else are we to improve our understanding of morphological diversification in treeshrews (or any morphologically variable taxon, for that matter) than by continuing to characterize and analyze such variation, with or without the “context of a molecular phylogeny” (Scotland *et al.*, 2003, p. 545). Simply mapping morphological characters ad hoc onto molecular trees without investigating their phylogenetic informativeness diminishes their explanatory power a priori and unjustifiably. Furthermore, while the fossil record for treeshrews is poor (see reviews in Sargis, 1999, 2004), only morphological data will allow us to make sense of the relationships of extinct treeshrews such as *Palaeotupaia*, *Prodendrogale*, and *Eodendrogale*.

We have attempted to review here the status of morphological phylogenetics in treeshrews and hope that a renewed interest in their evolutionary and biogeographical history will emerge. Certainly, much remains to be learned, and this can only be achieved by continuing to critically and rigorously collect, characterize, and analyze data from a wide variety of character systems, including morphology.

#### APPENDIX 1. Character Descriptions from Steele's Data Set

All of the character descriptions below were taken directly from Steele's (1973) Table II.

- 
1. *Relative length of upper incisors.* (0) I1 and I2 equal in length; (1) I1 longer than I2; (2) I2 longer than I1.
  2. *Relative size of upper canine.* (0) equal to P3; (1) greater than P3.
  3. *Relative size of P2.* (0) less than P3; (1) equal to P3.
  4. *Relative size of i1 and i2.* (0) i1 and i2 approximately equal in size; (1) i2 significantly larger than i1.
  5. *Relative length of i3.* (0) i3 less than 1/2 length of i2; (1) i3 greater than 1/2 length of i2.
  6. *Relative size of p2.* (0) smaller than p3; (1) greater than p3.
  7. *Shape of I2.* (0) simple cone; (1) premolariform; (2) caniniform.
  8. *I1 reflected mesially.* (0) no; (1) yes.
  9. *Shape of upper canine.* (0) simple cone; (1) premolariform.
  10. *Shape of cusps on M1.* (0) with well-defined cristae; (1) more bunodont.
  11. *Shape of lower canine.* (0) incisorform; (2) caniniform; (3) premolariform.
  12. *Upper canine has two roots.* (0) no; (1) yes.
  13. *Root number of P2.* (0) one root; (1) two roots.
  14. *Root number of P3.* (0) two roots; (1) three roots.
  15. *Root number of p3.* (0) one root; (1) two roots.
  16. *Protocone present on P3.* (0) no; (1) yes.
  17. *Parastyle present on P3.* (0) no; (1) yes.
  18. *Metastyle present on P3.* (0) no; (1) yes.
  19. *Preparacrista present on P3.* (0) no; (1) yes.
  20. *Postparacrista present on P3.* (0) no; (1) yes.
  21. *Stylar shelf present on P4.* (0) no; (1) yes.
  22. *Preparacrista present on P4.* (0) no; (1) yes.
  23. *Postparacrista present on P4.* (0) no; (1) yes.
  24. *Hypocone present on P4.* (0) no; (1) yes.
  25. *Hypocone present on M1.* (0) no; (1) present but poorly defined; (2) well developed. In ordered analyses these states were ordered 0–1–2.
  26. *Nature of mesostyle on M1.* (0) single; (1) bifid.
  27. *Internal cingulum present on M1.* (0) no; (1) yes.
  28. *Hypocone present on M2.* (0) no; (1) present but poorly defined; (2) well developed. In ordered analyses these states were ordered 0–1–2.
  29. *Nature of mesostyle on M2.* (0) single; (1) bifid.
  30. *Internal cingulum present on M2.* (0) no; (1) yes.
  31. *P2 has posterior fovea.* (0) no; (1) yes.
  32. *p3 has an anterior fovea.* (0) no; (1) yes.
  33. *p3 has a talonid shelf.* (0) no; (1) yes.
  34. *p4 has three cusps on trigonid.* (0) no; (1) yes.
  35. *p4 talonid divided.* (0) no; (1) yes.
  36. *m1 has an entoconulid.* (0) no; (1) yes.
  37. *m1 has a precingulum.* (0) no; (1) yes.
  38. *m1 has a cingulum.* (0) no; (1) yes.
  39. *m2 has an entoconulid.* (0) no; (1) yes.
  40. *m2 has a precingulum.* (0) no; (1) yes.
  41. *m2 has a cingulum.* (0) no; (1) yes.
  42. *m3 has a hypoconulid.* (0) no; (1) yes.
  43. *m3 has a precingulum.* (0) no; (1) yes.
-

## APPENDIX 2. Data Matrix From Steele (1973)

The data matrix from Steele (1973) is based on his figs. 3 and 4, arranged alphabetically by species in the genus *Tupaia* (above dotted line) and by species in other genera (below dotted line). Numbers at the beginning of each row correspond to Steele's labels, which are retained here to differentiate taxonomically identical specimens that were coded differently (see text). See Fig. 1 for a reconciliation of these names with the currently accepted taxonomy.

		1	1	2	3	4
		1	1	1	1	1
8.	<i>glis anambae</i>	0100100110	1011111101	1110110110	0111000001	011
19.	<i>glis batamana</i>	0100100100	1011111111	1110200200	0111100001	011
10.	<i>glis cambodiana</i>	0100100100	1011101111	1110210210	0111100001	011
26.	<i>glis chrysogaster</i>	0100100100	1011111100	0010210210	0111110011	011
6.	<i>glis clarissa</i>	0100100100	1011110101	1110210210	0111000001	011
12.	<i>glis demissa</i>	0100100110	1011111111	1110210210	0111100001	011
1.	<i>glis discolor</i>	0000100110	1011110111	1110210210	1111000001	011
9.	<i>glis ferruginea</i>	0100100100	1011110101	1110210210	0111000001	001
5.	<i>glis jacki</i>	0000100110	1011100101	1110210210	0111100001	011
16.	<i>glis kohtauensis</i>	0100100100	0011100111	1110210210	0111000001	011
18.	<i>glis lacernata</i>	0100100100	1011111111	1110200200	0111000001	011
20.	<i>glis laotum</i>	0100100110	1011111111	1110200200	0111000001	011
4.	<i>glis lepcha</i>	1100101110	1011111101	1110210210	1111110011	011
17.	<i>glis modesta</i>	1100101100	0011110111	1110210210	0111100011	011
22.	<i>glis olivaceous</i>	0100100100	0011110111	1110200200	0111100001	011
13.	<i>glis phaeniura</i>	0100100110	1011101101	1110210210	0111100001	011
14.	<i>glis phaeura</i>	0100100100	0011100101	1110210210	0111100001	011
3.	<i>glis salatana</i>	1100101100	1011111111	1110210210	0111000001	011
11.	<i>glis siaca</i>	1100101100	1011111111	1110110110	0111000000	010
23.	<i>glis sinus</i>	0100100100	0011100101	1110200200	0111000001	011
21.	<i>glis sordida</i>	0100100100	0011111111	1110200200	0111100001	011
15.	<i>glis ultima</i>	0100100100	0011101111	1110210210	0111100001	011
29.	<i>glis versurae</i>	0100100100	0011111111	1110200200	0111000000	010
7.	<i>glis wilkinsoni</i>	0100100100	0011110101	1110210210	0111000001	011
28.	<i>gracilis gracilis</i>	0000100100	0011110111	1110100100	0111000000	000
30.	<i>gracilis inflata</i>	0000100100	0011110111	1110200200	0111000000	000
42.	<i>javanica occidentalis</i>	0101000100	1011100101	1110100100	1111100001	011
41.	<i>minor malaccana</i>	1101001010	1000100111	1110100100	0111000001	011
40.	<i>minor minor</i>	1101001010	1000101111	1110100100	1111000001	011
24.	<i>montana baluensis</i>	0100100100	1011110111	1110100100	1111000001	011
25.	<i>Mulleri</i>	0100100110	1011100100	0010210210	0111000001	011
45.	<i>nicobarica nicobarica</i>	0100000000	1000101100	0010200200	1111110011	001
46.	<i>nicobarica surda</i>	0100000000	1000101100	0010110110	1111110010	000
39.	<i>Picta</i>	0000100110	1011110101	1110210210	1111010010	010
27.	<i>splendidula carimatae</i>	0100100100	1011111101	1110110110	1111000001	001
2.	<i>splendidula splendidula</i>	0100100110	1011111111	1110210210	1111100001	011
35.	<i>tana bunoe</i>	0100000100	1011110100	0010210210	0111000001	011
31.	<i>tana chrysura</i>	0100000100	1011111111	1110210210	0111000000	010
33.	<i>tana paitana</i>	0100000100	1011111110	0010210210	0111000001	011
32.	<i>tana sirhassensis</i>	0100100100	1011111101	1110110110	0111000000	010
34.	<i>tana tana</i>	0000100100	1011110100	0010210210	0111000000	010
36.	<i>tana utara</i>	0100100100	1011110100	0010210210	0111000001	011
.....						
44.	<i>Dendrogale frenata</i>	0101000110	0011111111	1110000000	1111100000	010
43.	<i>D. melanura baluensis</i>	0100000100	0011111111	1110000000	1111000000	010
37.	<i>Urogale everetti</i>	2100002100	1011110100	0010200200	0111000000	010
38.	<i>U. everetti</i>	2100002100	1011110100	0010200200	0111000000	010
47.	<i>Philocercus lowii</i>	1011011111	2111000001	1101201201	0000001101	111
48.	<i>P. lowii</i>	1011011111	2111000001	1101201201	0000001101	111
49.	<i>P. lowii</i>	1011011111	2111010011	1101201201	1000001101	111

### APPENDIX 3. Character Descriptions from Butler's (1980) Data Set

Character descriptions from Butler's (1980) data set are based on the text and fig. 12 of Butler (1980). Numbers were assigned in the present study, as Butler himself did not present a matrix or list of characters (see text). Likewise, as only apomorphies were labeled in his fig. 12, we have left the primitive "states" undefined unless otherwise noted.

- 
1. *Paracone*. (0) primitive; (1) buccal.
  2. *Buccal cingulum on lower molars*. (0) primitive; (1) present.
  3. *P3/p3*. (0) primitive; (1) reduced.
  4. *Mesostyle*. (0) primitive; (1) present but undivided; (2) divided. In ordered analyses, these states were ordered 0–1–2.
  5. *Metacone*. (0) primitive; (1) enlarged.
  6. *Hypoconulid*. (0) primitive; (1) lingual.
  7. *m3*. (0) primitive; (1) smaller.
  8. *Incisors*. (0) primitive; (1) smaller.
  9. *Preprotocone cingulum*. (0) primitive; (1) lost.
  10. *Hypocone*. (0) enlarged; (1) small but distinct; (2) reduced; (3) lost.  
States 0, 2, and 3 were explicitly identified as apomorphic by Butler; we inferred state one from his discussion in order to treat this character as ordered (0–1–2–3).
  11. *Anterior teeth*. (0) primitive; (1) simplified.
  12. *C1*. (0) primitive; (1) one root.
  13. *Diastemata*. (0) primitive; (1) present.
  14. *Face*. (0) primitive; (1) long.
  15. *M1/m1*. (0) primitive; (1) long.
  16. *I2, c1*. (0) primitive; (1) enlarged.
  17. *p4 hypoconid*. (0) primitive; (1) present.
  18. *Molars*. (0) primitive; (1) transverse.
  19. *P3 protocone*. (0) primitive; (1) large.
  20. *Metaconid and entoconid*. (0) primitive; (1) higher.
  21. *M2/m2*. (0) primitive; (1) larger.
- 

### APPENDIX 4. Data Matrix from Butler (1980)

The data matrix from Butler (1980) is based on the text and fig. 12 in Butler (1980; see Appendix 3 and text). States for characters coded as polymorphic are enclosed in braces.

	1	1	2
	1	1	1
<i>Ptilocercus</i>	111 0 0000 1	00 0 000000	0
<i>Tupaia</i>	000{12}11111{23}	11{01}0000000	0
<i>Lyonogale</i>	000 2 11111 2	11 0 1100000	0
<i>Urogale</i>	000 1 11111 0	11 1 1011000	0
<i>Anathana</i>	000 2 11111 0	11 1 0000111	1
<i>Dendrogale</i>	000 2 11111 3	00 0 0000000	0

### APPENDIX 5. Character Descriptions from Luckett (1980)

Character descriptions are modified from table 5 of Luckett (1980). Character states considered primitive by Luckett are assigned state zero here.

- 
1. *CI*. (0) double-rooted; (1) single-rooted.
  2. *Zygomatic foramen*. (0) small; (1) large.
  3. *Posterior palatal vacuities*. (0) absent; (1) large.
  4. *Scaphoid and lunata*. (0) unfused; (1) fused.
  5. *Hypocone*. (0) enlarged; (1) moderately developed; (2) lost; (3) enlarged. In ordered analyses these states were ordered 0–1–2–3.
  6. *Snout*. (0) moderately developed; (1) greatly elongated.
  7. *Incisor development*. (0) I2 subequal to I1, i3 moderately developed; (1) I2 larger than I1, i3 reduced and functionless.
  8. *Entoconid*. (0) somewhat lower than hypoconid; (1) elevated relative to hypoconid.
  9. *Cecum*. (0) present; (1) absent.
- 

### APPENDIX 6. Data Matrix from Luckett (1980)

The data matrix is based on fig. 7 and table 5 in Luckett (1980).

	123456789
<i>Lyonogale</i>	111121001
<i>Tupaia</i>	111120000
<i>Anathana</i>	100100010
<i>Urogale</i>	100?0110?
<i>Dendrogale</i>	000030000
<i>Ptilocercus</i>	000010000

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