

# New Views on Tree Shrews: The Role of Tupaiids in Primate Supraordinal Relationships

ERIC J. SARGIS

Tree shrews (Scandentia, Tupaiidae), or the mammals formerly known as primates, are known to most primatologists simply as “the outgroup.” Small-bodied mammals from South and Southeast Asia that superficially resemble squirrels (Fig. 1), tree shrews have long been considered to have close affinities with primates and are often used as an outgroup in analyses of relationships among primate taxa.<sup>3,4</sup> They were, in fact, included in the order Primates from the 1920s to the 1960s (Box 1), a period during which a considerable amount of research on tree shrews was conducted. After tree shrews were removed from the order Primates, comparatively little attention was paid to them until 1980,<sup>5</sup> and since then studies of tree shrews have been sporadic. Recently, however, research on this group has undergone something of a renaissance.<sup>6,7</sup> The year 2000, in fact, could be considered the Year of the Tree Shrew, heralding major advances in tree shrew genetics,<sup>8,9</sup> behavioral ecology,<sup>10</sup> and morphology.<sup>11</sup>

“[I]t is certain that the tree shrews represent a highly important group of mammals, and, for this reason, they demand an intensive study from all aspects.”

Le Gros Clark<sup>1</sup> (p. 255)

“Among living non-primates the tupaiids are apparently the closest primate relatives, and these conclusions in no way lessen the value of tupaiids to primatology.”

McKenna<sup>2</sup> (p. 9)

Although tree shrews are still re-

garded as close relatives of primates, their precise phylogenetic relationships are not clear. Both taxa are frequently included with flying lemurs (Dermoptera) and bats (Chiroptera) in the supraordinal grouping Archonta, assignments that are supported by morphological data.<sup>12–18</sup> Molecular studies support a clade uniting tree shrews and primates with flying lemurs, to the exclusion of bats; this group is called Euarchonta.<sup>19</sup> Within Archonta or Euarchonta, both tree shrews<sup>20,21</sup> and flying lemurs<sup>22</sup> have been proposed to be the closest relatives of primates, though more recent studies have shown that tree shrews may in fact be more closely related to flying lemurs than either is to Primates<sup>19,23–25</sup> (see Sargis<sup>25</sup> for a detailed history of the relationships of archontans and a review of morphological and molecular studies). Whether or not tree shrews are the sister taxon to Primates, they are still crucial to primate supraordinal relationships and represent a critical outgroup in studies of primate phylogenetics.<sup>4</sup> The goal of this paper is to summarize recent research that has improved our understanding of tree

shrews and their relationships to primates and other mammals.

## FOSSIL RECORD

While much has been learned to date about the biology of tree shrews, there remain substantial gaps in our knowledge. Our understanding of tupaiid evolutionary relationships has partly been hindered by their poor fossil record<sup>26</sup> (see Box 2). Most tree-shrew fossils have been found in the Siwaliks of India and Pakistan. In India, skull fragments and teeth similar to those of *Tupaia* were recovered from Miocene deposits,<sup>27,28</sup> and a complete rib cage possibly representing *Tupaia* was discovered in Pliocene sediments.<sup>29</sup> The Miocene fossils were attributed to a new taxon, *Palaeotupaia sivalicus*, within the subfamily Tupaiinae,<sup>27,28</sup> but Luckett and Jacobs<sup>30</sup> argued that these fossils should not be allocated to a new genus because they are virtually identical to *Tupaia*.<sup>12,26</sup> Additional skull fragments and teeth from the Miocene have been found in Pakistan. These fossils, which are about ten million years old, were discovered further west than the distribution of living tree shrews.<sup>31</sup> These specimens probably represent new taxa,<sup>26,32</sup> but they have never been named.

Tree shrew teeth have also been recovered from Miocene deposits in China and Thailand (Box 2). Fossil teeth were first found in China at Lufeng and assigned to a new taxon, *Prodendrogale yunnanica*, based on similarities to *Dendrogale*.<sup>32</sup> More *Prodendrogale* teeth were later found at Yuanmou but, perhaps more importantly, some of the unnamed material may represent the first fossil represen-

Eric J. Sargis is an Assistant Professor in the Department of Anthropology, Yale University. His research interests include primate supraordinal relationships, archontan systematics, and tupaiid and cercopithecoid functional postcranial morphology and systematics. E-mail: Eric.Sargis@yale.edu

Key words: Scandentia; *Ptilocercus*; phylogenetics; tree shrews; morphology

© 2004 Wiley-Liss, Inc.  
DOI 10.1002/evan.10131  
Published online in Wiley InterScience  
(www.interscience.wiley.com).

### Box 1. History of Tree Shrew Ordinal Designations

Order Insectivora	Wagner <sup>98</sup>
Order Menotyphla	Haeckel <sup>99</sup>
Order Primates	Gregory <sup>100</sup>
	Carlsson <sup>101</sup>
	Le Gros Clark <sup>39,63,102</sup>
	Simpson <sup>103</sup>
Removed from Order Primates	Napier and Napier <sup>89</sup>
	Van Valen <sup>104</sup>
	McKenna <sup>2</sup>
	Campbell <sup>105</sup>
	Martin <sup>106,107</sup>
Order Scandentia	Szalay <sup>45</sup>
	Butler <sup>108</sup>

tative of the *Ptilocercus* lineage.<sup>33</sup> In Thailand, a single molar was discovered and allocated to *Tupaia*, but it was attributed to a new species, *T. miocenica*.<sup>34</sup>

The earliest known tree shrew fossils are from middle Eocene beds at Henan, China.<sup>35</sup> These isolated teeth are similar to those of *Dendrogale* and were assigned to a new taxon, *Eodendrogale parvum*. While the fossil record of tree

shrews is poor, it certainly indicates that they had evolved by the middle Eocene, and that they once had a broader distribution than they do today.

#### VARIATION WITHIN TUPAIIDAE

Variation among tree shrews is rarely considered by either primate systematists or those studying mammalian supraordinal relationships, as the sole ge-

nus *Tupaia* is generally used to represent all of Scandentia in such studies (for example, Beard<sup>22</sup> and Murphy and coworkers<sup>19</sup>). In fact, there are five genera of tree shrews: *Tupaia*, *Anathana*, *Urogale*, *Dendrogale*, and *Ptilocercus* (Box 3). Of these, the arboreal *Ptilocercus* (Box 4), rather than *Tupaia*, has been considered to be the living tree shrew that most closely resembles the ancestral tupaiid in both its



Figure 1. *Tupaia minor*, an arboreal tupaiine (A), and *Ptilocercus lowii*, the only ptilocercine (B). *Ptilocercus* photo by Annette Zitzmann © 1995.

## Box 2. Tree Shrew Fossil Record

TAXON	EPOCH	LOCALITY	ELEMENTS	SOURCES
<i>Tupaia</i>	Pliocene	upper Siwaliks of India	rib cage	29
<i>Palaeotupaia</i> <sup>a</sup> <i>sivalicus</i>	Miocene	middle Siwaliks of India	skull fragment, left maxillary fragment, lower right second molar	27, 28
Tupaiainae <sup>b</sup>	Miocene	Siwaliks of Pakistan	skull fragment, lower left first molar, lower molar talonid	31
<i>Tupaia</i> <i>miocenica</i>	Miocene	Li Mae Long, Thailand	upper left second molar	34
<i>Prodendrogale</i> <i>yunnanica</i>	Miocene	Lufeng, China	seventeen isolated teeth	32
<i>Prodendrogale</i> and Ptilocercinae <sup>b</sup>	Miocene	Yuanmou, China	mandibular fragment with P4 and M1, 9 isolated teeth	33
<i>Eodendrogale</i> <i>parvum</i>	Eocene	Henan, China	upper left molar, upper right first and third molars, two lower molar talonids	35

<sup>a</sup> These specimens are indistinguishable from *Tupaia* and should not be separated into another genus.<sup>12,26,30</sup>

<sup>b</sup> These unnamed specimens may represent new genera and species.

ecology and its morphological attributes.<sup>10,11,16–18,23–25,36–45</sup>

*Ptilocercus* is included in a separate subfamily from *Tupaia* and its closest relatives (see Box 3), which are mostly terrestrial, and the two subfamilies are quite distinct in their postcranial morphology.<sup>11,25,41–44</sup> They also differ in their activity pattern, as *Ptilocercus* is nocturnal and all tupaiaines are diurnal. *Tupaia minor*, like *Ptilocercus*, is arboreal, while *T. tana* (commonly called the terrestrial tree shrew), *T. gracilis*, *T. longipes*, and *T. montana* are all terrestrial.<sup>10</sup> There is anecdotal evidence that *Dendrogale melanura* is terrestrial as well (Emmons, personal communication), but *D. murina* appears to be arboreal.<sup>46</sup> *Tupaia glis* has been shown to be much more terres-

trial than was previously believed,<sup>47–50</sup> and seems to escape predators on the ground.<sup>1,49</sup> *Urogale everetti*, which is considered to be one of the most terrestrial species,<sup>40,51</sup> has been shown to be a terrestrial digger in the wild.<sup>52</sup> Little is known about *Anathana ellioti*; Chorazyna and Kurup<sup>53</sup> stated that it is terrestrial, while Martin<sup>51</sup> claimed that it is semiterrestrial (Box 4).

In an attempt to make the postcranial variation among tree shrews more accessible to primatologists, I will review several differences between *Ptilocercus* and the tupaiaines, as well as several unique features of *Urogale*, which is a digger. This review represents a summary of several previous papers,<sup>41–43</sup> which should be consulted for more detailed assessments of these features.

## Tree Shrew Morphology

Although I will focus on postcranial morphology, the craniodental morphology of tree shrews is of interest because of various (convergent) similarities to that of primates. For instance, tree shrews possess a tooth comb for grooming similar to that of living strepsirhine primates, but tree shrews have a different dental formula than primates do. The tree shrew dental formula is I 2/3 C 1/1 P 3/3 M 3/3. Tree shrews also possess a postorbital bar like that of euprimates (Fig. 2). Although it has been proposed that this character is a synapomorphy uniting these two groups,<sup>20,21</sup> it is perhaps more likely that this feature evolved independently. The orbits of the arboreal *Ptilocercus* are

Box 3. Classification of Tree Shrews<sup>a</sup>

Order Scandentia  
 Family Tupaiidae  
 Subfamily Tupaiinae  
*Tupaia* (14 species)  
*Dendrogale* (2 species)  
*Anathana ellioti*  
*Urogale everetti*  
 Subfamily Ptilocercinae  
*Ptilocercus lowii*

<sup>a</sup> From Wilson,<sup>91</sup> but several other classifications of tree shrews exist.<sup>51,89,90,92</sup>

## Box 4. Tree Shrew Substrate Preferences

TAXON	SUBSTRATE PREFERENCE	SOURCES
<i>Ptilocercus lowii</i>	Arboreal	10, 38, 109
<i>Anathana ellioti</i>	Terrestrial or Semiterrestrial	51, 53
<i>Dendrogale melanura</i>	Terrestrial?	Emmons (personal communication)
<i>Dendrogale murina</i>	Arboreal	46
<i>Tupaia glis</i>	Terrestrial or Semiterrestrial (Scansorial)	47–50, 110
<i>Tupaia gracilis</i>	Terrestrial	10
<i>Tupaia longipes</i>	Terrestrial	10
<i>Tupaia minor</i>	Arboreal	10, 74, 110
<i>Tupaia montana</i>	Terrestrial	10
<i>Tupaia nicobarica</i>	Arboreal to Semiterrestrial	111 51
<i>Tupaia palawanensis</i>	Terrestrial	112
<i>Tupaia tana</i>	Terrestrial	10, 74, 110
<i>Urogale everetti</i>	Terrestrial	52

also relatively similar to those of euprimates in that they face forward, but the orbits of all other tree shrews face laterally.<sup>40</sup> Another cranial similarity that has been proposed as a synapomorphy uniting tree shrews and euprimates is the enclosure of the middle-ear arteries in bony canals.<sup>20,21</sup> Not every aspect of the ear region, however, is similar between these groups. Euprimates have a petrosal bulla, while tree shrews have an entotympanic bulla (Fig. 2).

While tupaiid craniodental morphology has been relatively well-studied,<sup>36,54–59</sup> tupaiid postcranial morphology was, until recently, poorly known and had not been studied from a functional perspective.<sup>11</sup> The following sections provide a general review of the main differences among tree shrews with respect to their postcranial morphology. Appreciation of this diversity is critical not only for understanding the evolution of this ancient group, but also for properly evaluating its phylogenetic position among placental mammals.

### Axial Skeleton

The axial skeleton of *Ptilocercus* differs in several ways from that of tupaiines in that it is adapted for stability, while the vertebral column of tupaiines is much more mobile.<sup>41</sup> For instance, the atlas vertebra of *Ptilocercus* has a broad dorsal surface and the

other cervical vertebrae articulate tightly, both of which restrict mobility in the neck.<sup>41</sup> Furthermore, the spine of the axis vertebra is oriented cranially in *Ptilocercus*,<sup>41</sup> which seems to limit extension of the neck.<sup>60</sup>

The ribs of *Ptilocercus* are cranio-caudally expanded relative to those of tupaiines. All of the species of *Tupaia*, *Anathana*, *Dendrogale*, and *Urogale* have thin ribs. Jenkins<sup>61</sup> discussed how thickened ribs may facilitate slow climbing and bridging in loroid primates by increasing “the stability of the thorax, which, in turn, increases the stability of the vertebral column” (p. 288). While *Ptilocercus* is not a slow climber, it may require this increased stability to “bridge” gaps between branches<sup>41</sup> and/or climb on vertical supports.<sup>10</sup>

The spinous processes of the thoracic vertebrae of *Ptilocercus* are short

and wide, whereas in tupaiines they are long and thin.<sup>41</sup> The lumbar spinous processes of *Ptilocercus* are also short as compared to those of tupaiines.<sup>41</sup> Gambaryan<sup>62</sup> demonstrated in his comparisons of ungulates, which have stable vertebral columns, and carnivorans, which have mobile vertebral columns, that wide spinous processes restrict vertebral mobility. The short, wide spinous processes of *Ptilocercus*, therefore, may restrict spinal mobility by decreasing intervertebral space, while the long, thin spinous processes of tupaiines may allow greater spinal mobility by increasing intervertebral space. Again, the restricted mobility in the vertebral column of *Ptilocercus* may be related to bridging and/or vertical climbing,<sup>10</sup> while the greater mobility in the vertebral column of tupaiines contributes to increased stride length.

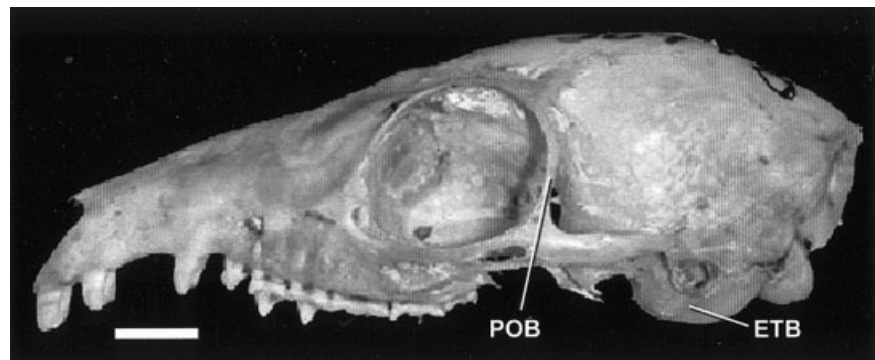


Figure 2. Skull of *Tupaia glis*. ETB, entotympanic bulla; POB, postorbital bar. Scale bar is 5.01 mm. Note the postorbital bar like that of euprimates.

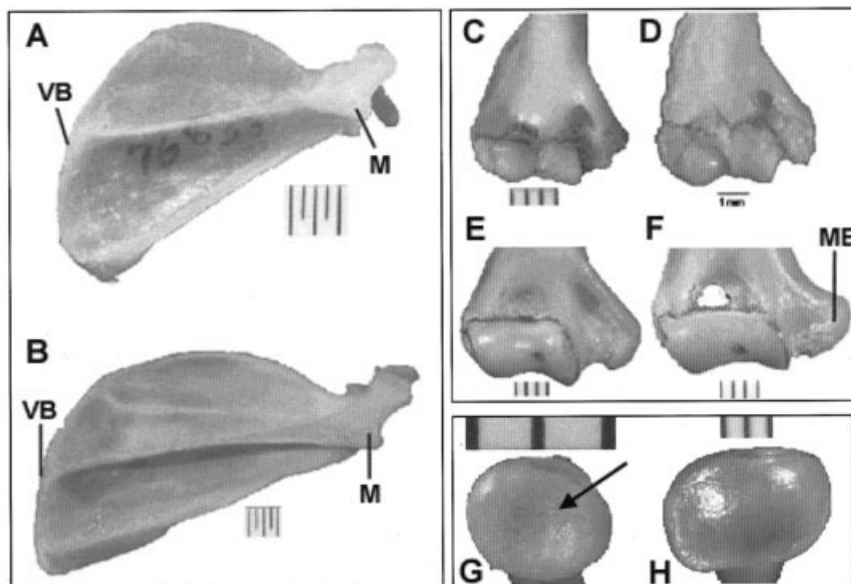


Figure 3. Scapulae of *Ptilocercus* (A) and *Tupaia tana* (B). M, metacromion; VB, vertebral border. Subdivisions on scale are 0.5 mm. Note the short, wide scapula and the cranial angulation of the metacromion of *Ptilocercus*. Distal humeri of *Ptilocercus* (C, D), *Tupaia tana* (E), and *Urogale* (F). ME, medial epicondyle. Subdivisions on scale are 0.5 mm. Note the rounded capitulum, which is separated from the trochlea, in *Ptilocercus*. Radial head (proximal view) and central fossa of *Ptilocercus* (G). Subdivisions on scale are 1.0 mm. Radial head (proximal view) and central fossa of *Tupaia tana* (H). Subdivisions on scale are 0.5 mm. Note the more circular radial head and central fossa of *Ptilocercus*.

The length of the thoracic and lumbar spinous processes is also significant in that these processes act as bony levers for vertebral extensor muscles.<sup>39,63,64</sup> The increased length of these processes in tupaiines gives the extensor muscles a greater mechanical advantage for powerful extension during terrestrial running, for which a great deal of vertebral flexion and extension are important to increase stride length.

### Forelimb

The scapula of *Ptilocercus* is short and relatively wide, while that of tupaiines is longer and narrower (Fig. 3a–b). *Ptilocercus* also has an elongated vertebral border and a cranially angled metacromion (Fig. 3a, b). The more cranial orientation of the metacromion in *Ptilocercus* may provide better leverage for the deltoid muscle during arm elevation.<sup>42,65</sup> The vertebral border, which is long relative to the length of the scapula, may increase the mechanical advantage of the serratus anterior and rhomboideus,<sup>42,66</sup> the muscles that attach to

this border, which must resist the turning of the scapula during climbing.<sup>66</sup> The relatively long vertebral border in *Ptilocercus* is, therefore, likely to be related to climbing during arboreal locomotion.

The narrow humeral heads of the terrestrial *T. palawanensis*, *T. tana*, and *Urogale* restrict shoulder mobility principally to the parasagittal plane.<sup>65</sup> The humeral head of all tree shrews projects above the greater and lesser tuberosities, thus allowing greater mobility in the shoulder joint.<sup>42,67–69</sup>

The elbow of *Ptilocercus* is quite distinct from that of tupaiines, reflecting differences between the two subfamilies in substrate preference. The rounded, globular (more spherical) capitulum and more circular radial head of *Ptilocercus* (Fig. 3c, d, g) allow the radius to rotate more freely than it does in tupaiines, thus providing more mobility in the elbow joint.<sup>42,65,67,70–72</sup> The distinct separation of the capitulum from the trochlea in *Ptilocercus* allows both the radius and ulna greater freedom of movement.<sup>42,65</sup> On the other hand, the continuity between the trochlea and

capitulum of tupaiines keeps the ulna and radius tightly packed together, restricting both their range of motion and the general mobility of the elbow joint. This, in combination with the flatter, more spindle-shaped capitulum and more rectangular radial head (Fig. 3e, f, h), provides more stability by restricting radial rotation, while allowing flexion and extension in the parasagittal plane.<sup>42,65,67,72</sup>

The increased length of the trochlea in the terrestrial tupaiines is found in the medial trochlear keel (Fig. 3e, f). A more pronounced version of this feature is found in several cursorial mammals,<sup>73</sup> as well as terrestrial cercopithecines.<sup>67,71</sup> The proximodistally longer medial trochlear keel of terrestrial tupaiines better resists the torques produced in semi-flexed and flexed pronated postures, and hence increases stability in the elbow joint.<sup>42,67,71,73</sup> It also restricts movements more to the parasagittal plane during terrestrial quadrupedal walking and running,<sup>42,67,73</sup> thereby increasing the efficiency of terrestrial locomotion.

It is interesting that *Ptilocercus*, the smallest and most arboreal tree shrew, and *Urogale*, the largest and most terrestrial tree shrew, both have a long medial epicondyle (Fig. 3c, d, f), especially considering the fact that they represent two different clades. They clearly possess this feature in relation to very different biological roles. The medial epicondyle is the site of origin for the wrist and digital flexors. A long medial epicondyle, therefore, provides a larger area of attachment for an enlarged flexor muscle mass. These muscles are particularly important to arboreal mammals for flexion of the digits during grasping of branches. This makes sense in the case of *Ptilocercus* because it is capable of grasping (A. Zitzmann, personal communication).<sup>74</sup> A shorter medial epicondyle is common in many cursorial mammals<sup>73</sup> and is also found in terrestrial cercopithecines.<sup>66,67</sup> The reduction of the medial epicondyle in terrestrial mammals is related to a relative reduction in the size of the flexor musculature.<sup>66,67,73,75</sup>

If terrestrial mammals often have short medial epicondyles, why does

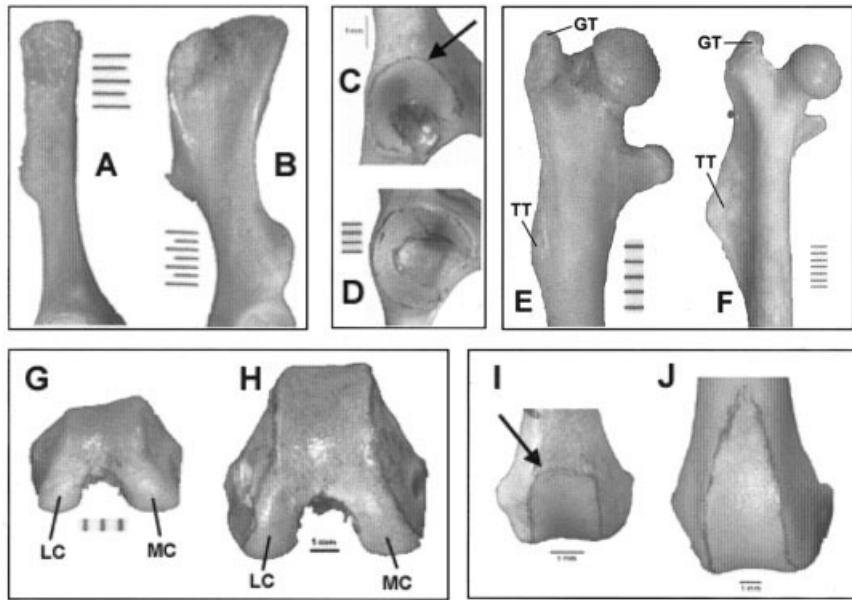


Figure 4. Lateral view of the ilia of *Ptilocercus* (A) and *Tupaia tana* (B). Subdivisions on scale are 0.5 mm. Note the narrow ilium of *Ptilocercus*. Acetabulum of *Ptilocercus* (C) and *Tupaia tana* (D). Subdivisions on scale are 0.5 mm. Note the elliptical acetabulum and expansion of the cranial portion of the articular surface in *Ptilocercus*. Proximal femora of *Ptilocercus* (E) and *Tupaia tana* (F). GT, greater trochanter; TT, third trochanter. Subdivisions on scale are 0.5 mm. Note the small greater and third trochanters of *Ptilocercus*. Distal view of femora of *Ptilocercus* (G) and *Tupaia tana* (H). LC, lateral condyle; MC, medial condyle. Subdivisions on scale are 0.5 mm. Note the shallow condyles of *Ptilocercus*. Distal femora of *Ptilocercus* (I) and *Tupaia tana* (J). Note the short, wide patellar groove of *Ptilocercus*.

*Urogale* have an elongated medial epicondyle? Wharton<sup>52</sup> reported that *Urogale* nests in burrows and was observed rooting and digging. In fact, Wharton<sup>52</sup> stated that *Urogale* “exhibited tendencies to root and dig like miniature pigs” (p. 353). This explains the large medial epicondyle of *Urogale*: powerful flexion of the digits and wrist by the flexor musculature that originates at the medial epicondyle is important in scratch-digging,<sup>76</sup> which involves the use of the claws of the hands for digging.<sup>76</sup> *Urogale* also exhibits rooting and digging adaptations in its skull<sup>40,51</sup> and claws (see below).<sup>51</sup>

The long olecranon process of the terrestrial *Urogale* and the short olecranon process of the arboreal *Ptilocercus* and *Tupaia minor* could be interpreted as relating to substrate preference because arboreal and terrestrial didelphid marsupials also exhibit these differences.<sup>69,75</sup> The olecranon process is the insertion site for the triceps brachii muscle, an extensor of the antebrachium. The longer olecranon process of *Urogale* provides a longer lever arm and

larger attachment area for the triceps muscle. Hence, the long olecranon process of *Urogale* might be related to powerful extension of the forearm by the triceps brachii muscle for propulsion during terrestrial locomotion.<sup>75</sup> It is more likely, however, that the length of this process is related to *Urogale*'s digging habits<sup>42,52</sup> because digging requires very powerful extension of the antebrachium, and scratch diggers are characterized by a long olecranon process.<sup>42,76</sup> The shorter olecranon process of *Ptilocercus* and *Tupaia minor* is probably related to the fact that these arboreal taxa do not require powerful extension of the forearm in arboreal locomotion.<sup>42,75</sup> They typically employ flexed arm postures in an attempt to keep their center of gravity close to the branch they are moving on.<sup>77,78</sup>

Martin<sup>51</sup> discussed the relationship between claw length and substrate preference in tree shrews. Arboreal tree shrews have shorter and deeper claws, while terrestrial tree shrews have longer and shallower claws for rooting.<sup>51</sup> *Urogale* has particularly long claws and ungual phalan-

ges<sup>11,42,43</sup> that are likely adaptations for scratch digging, as long claws and unguals are typical of diggers.<sup>42,43,70,76</sup> The manual and pedal ungual phalanges of the arboreal *Ptilocercus* are short and deep, while those of tupaiines are longer and more shallow. This is probably related to differential substrate use, as arboreal mammals usually have shorter, deeper unguals, while terrestrial mammals typically have longer, shallower unguals.<sup>70</sup> The short, deep ungual phalanges of *Ptilocercus* and other arboreal mammals are dorsopalmarly reinforced to resist bending loads,<sup>79</sup> especially those incurred during claw clinging and climbing on vertical supports.<sup>80</sup>

## Hindlimb

The ilium of *Ptilocercus* is longer and narrower than that of tupaiines (Fig. 4a, b). The wider ilium of tupaiines provides a broad area of attachment for the gluteal muscles, which may, in turn, indicate powerful extension of the thigh by these muscles for propulsion during terrestrial running.<sup>43,81</sup> Taylor<sup>81</sup> stated that mammals with wide ilia and a proximally projecting greater trochanter (another feature that tupaiines exhibit; see below) can extend the thigh more powerfully in the latter stages of retraction.

The more circular acetabulum of tupaiines (Fig. 4d) restricts the mobility of the hip joint and limits movements more to the parasagittal plane, which increases the efficiency of terrestrial locomotion. The more elliptical acetabulum of *Ptilocercus* (Fig. 4c), on the other hand, allows more mobility at the hip joint<sup>69</sup> so that greater ranges of abduction and lateral rotation are possible at this joint.<sup>79</sup> This is particularly important for an arboreal climber like *Ptilocercus*. The expansion of the cranial portion of the articular surface in *Ptilocercus* reflects loads incurred during climbing on vertical supports,<sup>79</sup> an activity that *Ptilocercus* commonly engages in.<sup>10</sup>

On the femur of tupaiines, the greater and third trochanters project farther proximally and laterally, respectively, than do those of *Ptilocercus* (Fig. 4e, f). Just as the expanded ilium of tupaiines provides a broader area of origin for the

gluteal muscles, the large greater and third trochanters in this group provide longer lever arms about which these muscles can act. This may indicate powerful extension of the thigh by these muscles for propulsion during terrestrial running. The more proximal projection of the greater trochanter in tupaiines also restricts the mobility of the hip joint, which particularly limits the range of abduction. This, in turn, makes the parasagittal hindlimb movements of terrestrial locomotion more efficient. Just as a low greater tuberosity allows more mobility in the shoulder joint,<sup>42,68</sup> a less projecting greater trochanter like that of *Ptilocercus* allows greater mobility in the hip joint, especially for abduction of the thigh in arboreal quadrupedalism and climbing.

The medial and lateral femoral condyles of *Ptilocercus* are relatively shallow anteroposteriorly, while those of tupaiines are relatively deep (Fig. 4g, h). The deeper condyles of tupaiines increase the moment arm of the tendon of the quadriceps femoris muscle, an extensor of the leg, which, in turn, increases the leverage and mechanical advantage of the quadriceps femoris muscle for knee extension.<sup>43,82</sup> The “deep knee” of tupaiines, therefore, allows powerful extension of the knee by the quadriceps femoris for propulsion during terrestrial running.<sup>43,82</sup> The shallower knee of *Ptilocercus* is indicative of a more flexed hindlimb and a slower form of arboreal quadrupedalism in which powerful extension of the leg is less common. Among tupaiines, *Urogale* has the deepest knee, which may be related either to the fact that *Urogale* is the most terrestrial tree shrew or to its digging behavior.<sup>42,43,52</sup> Powerful extension of the knee would likely be important for digging if *Urogale* uses its hindlimbs for this behavior.

The patellar groove of *Ptilocercus* is short and relatively wide, while that of tupaiines is longer and narrower (Fig. 4i, j). It is likely that the tupaiine condition is related to extensive excursions of the knee<sup>79</sup> during fast terrestrial running, while the condition seen in *Ptilocercus* may be related to a slower form of arboreal quadrupedalism and climbing, as this condition is also seen in lorisids.<sup>43,79</sup>

Most of the details of the tupaiid tarsus are far too complex to include

here. Szalay and Drawhorn<sup>16</sup> pointed out that the tupaiid foot, both in the way it is used in locomotion and in its morphology, provides strong evidence for the arboreal ancestry of tree shrews, and other features of the postcranium corroborate this hypothesis (see below).<sup>42,43</sup> First, it appears that all tree shrews, including terrestrial taxa like *Tupaia tana*, are capable of some degree of hindfoot reversal, which they use when descending inclined substrates.<sup>16,74,83–85</sup> However, terrestrial tree shrews like *T. tana* perform this behavior relatively infrequently<sup>74</sup> and are incapable of the same degree of hindfoot reversal as is possible for arboreal tree shrews.<sup>85</sup> It is likely that the capacity for hindfoot reversal in the terrestrial species is retained from the arboreal ancestral tupaiid. The morphology of the tarsus also indicates an arboreal ancestor of the family because even terrestrial taxa such as *T. tana* and *Urogale* are characterized by a relatively mobile tarsus that facilitates inversion of the foot.<sup>16,43</sup> This is an extremely important movement for arboreal locomotion, particularly on small branches. The ancestral tupaiid, therefore, was probably arboreal and had a tarsus like that of *Ptilocercus*. Terrestrial tupaiines likely retain some tarsal mobility due to this arboreal ancestry,<sup>16,43</sup> but it appears that some of the capacity for inversion was lost in the transition to tupaiine terrestriality.

While Szalay and Drawhorn<sup>16</sup> were mistaken concerning the lack of a grasping hallux in tree shrews, Szalay and Dagosto<sup>86</sup> correctly noted *Ptilocercus*' capacity for pedal grasping.<sup>43,74</sup> In *Ptilocercus*, the distal facet of the entocuneiform for articulation with the first metatarsal has a wider dorsal surface than does that of tupaiines. In addition, the proximal facet of the first metatarsal is more globular and less restricted mediolaterally in *Ptilocercus* than it is in tupaiines. This allows *Ptilocercus* a greater range of abduction of the hallux for pedal grasping.<sup>86</sup> In tupaiines, on the other hand, the capacity for hallucial abduction is reduced by their restricted entocuneiform-first metatarsal joint. The condition of the hallucial tarsometatarsal joint (and grasping) in *Ptilocercus* may be primitive for tupai-

ids. The condition found in tupaiines is likely related to their terrestrial ancestry because there is less need for hallucial abduction during locomotion on the ground. The fact that *Tupaia minor* is capable of grasping and habitually abducts its hallux,<sup>74</sup> yet is not capable of as great a range of abduction at the tarsometatarsal joint as is *Ptilocercus*, implies that *T. minor* achieves hallucial abduction at the metatarsophalangeal joint. This form of abduction of the hallux, which Jenkins<sup>83</sup> has described in *T. glis*, may indicate that *T. minor* and *Ptilocercus* grasp in different ways. It is therefore unlikely that grasping is homologous in *Ptilocercus* and *T. minor*. It is likely, rather, that grasping is primitive for tupaiids and that the ancestral tupaiid was similar to *Ptilocercus* in its grasping behavior (Box 5). That *T. minor*'s grasping ability represents the primitive condition for the subfamily Tupaiinae is unlikely based on a host of postcranial features that reflect the likely terrestrial and nongrasping nature of the ancestral tupaiine. Grasping, therefore, probably evolved secondarily in *T. minor*. It may have evolved first in a *Ptilocercus*-like ancestral tupaiid as an arboreal adaptation for moving on small, terminal branches. If the ancestral tupaiine was indeed terrestrial and had lost its ability to grasp, then grasping must have evolved secondarily in *T. minor* when this species began exploiting fine branches as part of a return to an arboreal lifestyle.

## EVOLUTION OF THE POSTCRANIUM IN SCANDENTIA

As stated earlier, *Ptilocercus* has been considered to be the most primitive living tree shrew. Consequently, many of the features I have discussed that characterize *Ptilocercus* may also have been present in the ancestral tupaiid, which was likely arboreal.<sup>41–44</sup> The arboreal ancestry of tupaiids is also supported by numerous features shared by all tupaiids, including the arboreal *Ptilocercus* and the most terrestrial tupaiines. These features include, for example, a humeral head that projects above the tuberosities, an anteriorly curved proximal ulna, a high femoral neck angle, and several features of the foot.<sup>16,43</sup>

### Box 5. Tree Shrew Grasping and Models for Early Primates

The ability to grasp with the feet and hands has been proposed as one of the defining features of primates<sup>40</sup> and is therefore a crucial feature in any discussion of primate origins.<sup>95,113</sup> Arboreal tree shrews such as *Tupaia minor*, and especially *Ptilocercus lowii*, are capable of grasping as well. It was for this reason, contrary to Lemelin<sup>114</sup> that I suggested that they represent better models for “early primates” than do didelphid marsupials.<sup>74</sup> Schmitt and Lemelin,<sup>115</sup> however, strongly disagreed with me, arguing instead that *Caluromys* is a better model for “primate origins” than are tree shrews.

There is, in fact, good reason for this disagreement. When I referred to “early primates,”<sup>74</sup> I was referring to plesiadapiforms (i.e., Primates, *sensu lato*). In fact, I stated that “[t]upaiids can, at the very least, be used as living models for the extinct plesiadapiforms be-

cause both groups are clawed mammals and they share similarities in their entocuneiform morphology” (p. 488).<sup>74</sup> In other words, I believe that tree shrews represent an appropriate extant model with which we can make paleobiological inferences about the extinct plesiadapiforms, which I consider to be “early primates.” Schmitt and Lemelin,<sup>115</sup> on the other hand, were likely referring to the ancestral euprimate (i.e., Primates, *sensu lato*) when they referred to “primate origins.” That said, I am not sure how a taxon like *Caluromys* can be a model for an event like the origin of primates. The postcranium of *Caluromys*, although it is adapted for arboreality,<sup>69,75</sup> is not very similar to that of the earliest known euprimates, adapids and omomyids. Furthermore, it is certainly more similar to other marsupials than to euprimates in its ankle and knee morphology.<sup>69</sup>

The history of grasping within Archonta appears to be complex, but the type of grasping seen in an arboreal tree shrew like *Ptilocercus* may represent the antecedent condition to that seen in primates.<sup>74</sup> Grasping capabilities similar to those of *Ptilocercus* may be primitive for Archonta,<sup>43,74,86,113</sup> and the powerful grasping of primates may not have evolved until later in primate evolution.<sup>95,113</sup> Evidence for this lies in the similarity between the hallucial tarsometatarsal joint morphology of *Ptilocercus* and *Plesiadapis*, which implies that *Plesiadapis* was capable of *Ptilocercus*-like, but not euprimate-like, grasping<sup>25,43,74,86,113</sup> (contra Beard<sup>22</sup>). *Carpolestes*, on the other hand, is a plesiadapiform that was most certainly capable of euprimate-like grasping.<sup>95,113</sup>

On the other hand, it appears equally likely that the origin of tupaiines coincided with a shift to more terrestrial locomotion and that the ancestral tupaiine was terrestrial.<sup>41–44</sup> This would imply that the features of tupaiines that I have discussed are most likely derived. The fact that even the most arboreal tupaiines, such as *Tupaia minor* (Box 4), exhibit numerous similarities to all other tupaiines, all of which are more terrestrial, suggests that the ancestral tupaiine was probably terrestrial<sup>41–44</sup> and that *T. minor* is constrained by this terrestrial heritage. If the ancestral tupaiid was arboreal and had several *Ptilocercus*-like postcranial features, then the evolution of Tupaiinae was characterized by numerous postcranial changes in response to a shift to terrestriality.<sup>41–44</sup> The terrestrial ancestry of tupaiines is supported by too many features to list here, but see Sargis.<sup>41–44</sup>

#### TAXONOMIC IMPLICATIONS

In addition to the qualitative and univariate analyses discussed above, some

multivariate analyses have also been performed on tree shrew postcranial data. The results of these analyses may have implications for the taxonomy of the family Tupaiidae.<sup>44</sup> A cluster analysis of the variables included in forty-seven forelimb and hindlimb indices shows that *Ptilocercus* is quite distinct from tupaiines in its limb morphology (Fig. 5). The nesting of *Tupaia tana* (formerly *Lyonogale*) among *Tupaia* species in the cluster analysis (Fig. 5) is, perhaps, another reason to include *T. tana* in *Tupaia* rather than in the separate genus *Lyonogale*. *Tupaia tana* is also similar to other species of *Tupaia* in its dentition (see figures in Butler<sup>36</sup>; Szalay, personal communication), and is part of the *Tupaia* ingroup in molecular phylogenies of tupaiids.<sup>8,87,88</sup> The inclusion of *T. tana* in *Tupaia*, therefore, certainly seems warranted<sup>8,42–44,55,87–91</sup> despite the fact that this species is sometimes separated from *Tupaia*<sup>92</sup> into *Lyonogale*.<sup>36,40,51,93</sup>

*Dendrogale* and *Urogale* are also nested among species of *Tupaia* in the cluster analysis (Fig. 5). It is interesting that *Urogale* is nested among *Tupaia* species because Han,

Sheldon, and Stuebing<sup>8</sup> recently suggested, based on DNA hybridization and morphometric analysis of external characters, that *Urogale everetti*, originally described as *Tupaia everetti* Thomas, 1892,<sup>91</sup> should be included within *Tupaia*. This possibility was previously difficult to assess due to missing limb measurements.<sup>42,44</sup> Now that those measurements have been taken, it appears that the evidence from the limb morphology supports this suggestion (Fig. 5). Thus, inclusion of *Urogale* in *Tupaia* does seem warranted based on postcranial evidence (contra Sargis<sup>43,44</sup>). The paraphyly of *Tupaia* with respect to *Urogale*, which is supported by several phenetic measures, is currently being tested with mitochondrial and nuclear DNA sequence data (Olson, Sargis, and Martin, in preparation).

#### PHYLOGENETIC IMPLICATIONS

As stated above, there has been a great deal of recent debate about the relationships among archontan mammals. For example, it has been proposed that tree shrews are closely re-



## Forelimb and Hindlimb Cluster Analysis (UPGA)

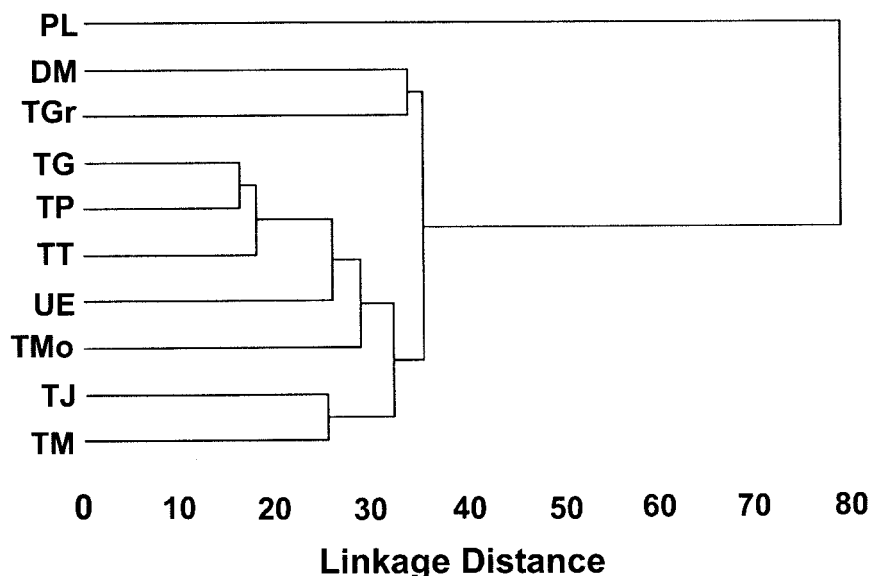


Figure 5. Cluster analysis (unweighted pair-group average) of the variables included in 47 forelimb and hindlimb indices. Tree is shown with Euclidean distance. PL, *Ptilocercus lowii*; DM, *Dendrogale* sp.; TGr, *Tupaia gracilis*; TG, *T. glis*; TP, *T. palawanensis*; TT, *T. tana*; UE, *Urogale everetti*; TMo, *T. montana*; TJ, *T. javanica*; TM, *T. minor*. Note the difference between *Ptilocercus* and the tupaiines. Also note the positions of *Urogale* and *T. tana*.

lated to both euprimates<sup>20,21</sup> and flying lemurs.<sup>19,23–25</sup> Alternatively, Beard<sup>22</sup> argued that flying lemurs are the closest relatives of primates, based mostly on his analysis of postcranial characters. Postcranial data, therefore, are an important body of evidence in the debate on archontan relationships.

As noted, the postcranial morphology of *Ptilocercus* is clearly extremely different from that of tupaiines. In all of these features, *Ptilocercus* is more similar to other archontans (flying lemurs, bats, plesiadapiforms, and early euprimates) than are tupaiines.<sup>25,41–43</sup> Postcranial data from *Ptilocercus*, therefore, may significantly alter the supportive evidence for proposed relationships within Archonta. Such relationships include both a Chiroptera-Dermoptera clade, called Volitantia, and a Primates-Dermoptera clade, called Primatomorpha.<sup>22,79</sup>

For Volitantia, using *Ptilocercus* to represent Scandentia affects only three features used to support this clade.<sup>25</sup> These three characters represent only two of Szalay and Lucas'<sup>17,18</sup>

seven diagnostic character complexes of the protovolitantiian and only three of the seventeen volitantiian synapomorphies listed by Simmons.<sup>94</sup> The use of *Ptilocercus* rather than *Tupaia* to represent Scandentia, therefore, does not greatly reduce the evidence for Volitantia.<sup>25</sup>

The evidence used to support Primatomorpha, on the other hand, is considerably reduced by the inclusion of *Ptilocercus* in the analysis.<sup>25</sup> My re-examination of Beard's<sup>22</sup> twenty-two postcranial characters showed that twelve of them should be interpreted differently when *Ptilocercus*, rather than *Tupaia*, is used to represent Scandentia.<sup>25</sup> This greatly reduces the evidence for Primatomorpha. Beard,<sup>22,79</sup> on the other hand, used *Tupaia* to represent Scandentia. However, my inclusion of *Ptilocercus* allowed a more robust character analysis, with greater taxonomic sampling, to be performed on primatomorphan and volitantiian features in light of an understanding of the polymorphic nature of the tupaiid postcranium. This character analysis showed that several

of the features proposed to be unique to volitantiians or primatomorphans are also found in *Ptilocercus*. Such features, therefore, may represent primitive archontan characters rather than synapomorphies of Volitantia or Primatomorpha.

Furthermore, several recent phylogenetic analyses have outright rejected the Primatomorpha hypothesis.<sup>23,24,95–97</sup> These studies have supported a Plesiadapiformes-Euprimates clade (Primates, *sensu lato*), as well as Volitantia (when bats are included in the analysis) or a Scandentia-Dermoptera clade (when bats are excluded from the analysis). The Scandentia-Dermoptera clade is also supported by molecular evidence.<sup>19</sup> Consequently, the closest relatives of flying lemurs may in fact be tree shrews rather than either primates or bats.

In summary, the most recent research on tree shrews has shown *Ptilocercus* to be quite distinct from *Tupaia* and the other tupaiines with respect to its postcranial morphology. This research has also supported the notion that *Ptilocercus* is the more plesiomorphic of these taxa, a hypothesis that has been proposed previously by numerous others.<sup>10,11,16–18,23–25,36–45</sup> The polymorphic nature of the tupaiid postcranium is an essential consideration in supraordinal phylogenetic analyses that include Scandentia. In such studies, the more plesiomorphic *Ptilocercus* should certainly be included in the analysis, especially if postcranial features are being considered.<sup>11,25,42,43</sup> This would also apply to any phylogenetic analyses that use Scandentia as an outgroup, such as studies examining the relationships among primates. In this regard, tree shrews are still vital to primate phylogenetics. Even if most primatologists regard them only as “the outgroup,” tree shrews are clearly indispensable to primatology and will likely remain so in the future.

## ACKNOWLEDGMENTS

I thank John Fleagle both for inviting me to contribute this paper and for all his help with the manuscript. I thank Larissa Swedell for critiquing several drafts of this paper. The comments of Dr. Fleagle and Dr. Swedell greatly improved this manuscript. I

thank Fred Szalay, Eric Delson, Rich Cifelli, and John Wahlert for critically reviewing an earlier version of the manuscript. I thank Annette Zitzmann for providing the photo of *Ptilocercus* in Figure 1. The use of the equipment of the AMICA facility at Hunter College allowed me to carry out this research. This work was funded by a National Science Foundation Doctoral Dissertation Improvement Grant (SBR-9616194), a Field Museum of Natural History Visiting Scholarship, a Sigma Xi Scientific Research Society Grant-in-Aid of Research, and a New York Consortium in Evolutionary Primatology graduate fellowship. Finally, I am grateful to all of the curators and collection managers who provided access to specimens in their care.

## REFERENCES

- 1 Le Gros Clark WE. 1927. Exhibition of photographs of the tree shrew (*Tupaia minor*): remarks on the tree shrew, *Tupaia minor*, with photographs. Proc Zool Soc Lond 1927:254–256.
- 2 McKenna MC. 1966. Paleontology and the origin of the primates. Folia Primatol 4:1–25.
- 3 Seiffert ER, Simons EL, Attia Y. 2003. Fossil evidence for an ancient divergence of lorises and galagos. Nature 422:421–424.
- 4 Shoshani J, Groves CP, Simons EL, Gunnell GF. 1996. Primate phylogeny: morphological vs molecular results. Mol Phylogenet Evol 5:102–154.
- 5 Luckett WP, editor. 1980. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press.
- 6 Endo H, Rerkamnuaychoke W, Kimura J, Sasaki M, Kurohmaru M, Yamada J. 1999. Functional morphology of the locomotor system in the northern smooth-tailed tree shrew (*Dendrogale murina*). Ann Anat 181:397–402.
- 7 Schilling N, Fischer MS. 1999. Kinematic analysis of treadmill locomotion of tree shrews, *Tupaia glis* (Scandentia: Tupaiidae). Z Säugetierkunde 64:129–153.
- 8 Han K-H, Sheldon FH, Stuebing RB. 2000. Interspecific relationships and biogeography of some Bornean tree shrews (Tupaiidae: Tupaia), based on DNA hybridization and morphometric comparisons. Biol J Linnean Soc 70:1–14.
- 9 Schmitz J, Ohme M, Zischler H. 2000. The complete mitochondrial genome of *Tupaia belangeri* and the phylogenetic affiliation of Scandentia to other eutherian orders. Mol Biol Evol 17:1334–1343.
- 10 Emmons LH. 2000. Tupai: a field study of Bornean treeshrews. Berkeley: University of California Press.
- 11 Sargis EJ. 2000. The functional morphology of the postcranium of *Ptilocercus* and tupaiines (Scandentia, Tupaiidae): implications for the relationships of primates and other archontan mammals. Unpublished doctoral dissertation, City University of New York.
- 12 McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York: Columbia University Press.
- 13 Novacek MJ, Wyss AR. 1986. Higher-level relationships of the recent eutherian orders: morphological evidence. Cladistics 2:257–287.
- 14 Shoshani J, McKenna MC. 1998. Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. Mol Phylogenet Evol 9:572–584.
- 15 Szalay FS. 1977. Phylogenetic relationships and a classification of the eutherian Mammalia. In: Hecht MK, Goody PC, Hecht BM, editors. Major patterns in vertebrate evolution. New York: Plenum Press. p 315–374.
- 16 Szalay FS, Drawhorn G. 1980. Evolution and diversification of the Archonta in an arboreal milieu. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 133–169.
- 17 Szalay FS, Lucas SG. 1993. Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In: MacPhee RDE, editor. Primates and their relatives in phylogenetic perspective. New York: Plenum Press. p 187–226.
- 18 Szalay FS, Lucas SG. 1996. The postcranial morphology of Paleocene *Chriacus* and *Mixodectes* and the phylogenetic relationships of archontan mammals. Bull New Mex Museum Nat Hist Sci 7:1–47.
- 19 Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling EC, Ryder OA, Stanhope MJ, de Jong WW, Springer MS. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294:2348–2351.
- 20 Kay RF, Thewissen JGM, Yoder AD. 1992. Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. Am J Phys Anthropol 89:477–498.
- 21 Wible JR, Covert HH. 1987. Primates: cladistic diagnosis and relationships. J Hum Evol 16:1–22.
- 22 Beard KC. 1993. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: Szalay FS, Novacek MJ, McKenna MC, editors. Mammal phylogeny: placentals. New York: Springer-Verlag. p 129–150.
- 23 Sargis EJ. 2001. The phylogenetic relationships of archontan mammals: postcranial evidence. J Vertebrate Paleontol 21(suppl to No. 3):97A.
- 24 Sargis EJ. n.d. The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae) and its implications for primate supraordinal relationships. In: Ravosa MJ, Dagosto M, editors. Primate origins and adaptations: a multidisciplinary perspective. New York: Plenum Press. In press.
- 25 Sargis EJ. 2002. The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae): an analysis of primatomorphan and volitanti characters. J Mammal Evol 9:137–160.
- 26 Sargis EJ. 1999. Tree shrews. In: Singer R, editor. Encyclopedia of paleontology. Chicago: Fitzroy Dearborn. p 1286–1287.
- 27 Chopra SRK, Kaul S, Vasishat RN. 1979. Miocene tree shrews from the Indian Sivaliks. Nature 281:213–214.
- 28 Chopra SRK, Vasishat RN. 1979. Sivalik fossil tree shrew from Haritalyangar, India. Nature 281:214–215.
- 29 Dutta AK. 1975. Micromammals from Sivaliks. Indian Minerals 29:76–77.
- 30 Luckett WP, Jacobs LL. 1980. Proposed fossil tree shrew genus *Palaetotupaia*. Nature 288:104–104.
- 31 Jacobs LL. 1980. Sivalik fossil tree shrews. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 205–216.
- 32 Qiu Z. 1986. Fossil tupaiid from the hominoid locality of Lufeng, Yunnan. Vertebrata PalAsiatica 24:308–319.
- 33 Ni X, Qiu Z. 2002. The micromammalian fauna from the Leilao, Yuanmou hominoid locality: implications for biochronology and paleoecology. J Hum Evol 42:535–546.
- 34 Mein P, Ginsburg L. 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: Systématique, biostratigraphie et paléoenvironnement. Geodiversitas 19:783–844.
- 35 Tong Y. 1988. Fossil tree shrews from the Eocene Hetaoyuan Formation of Xichuan, Henan. Vert PalAsiatica 26:214–220.
- 36 Butler PM. 1980. The tupaiid dentition. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 171–204.
- 37 Campbell CBG. 1974. On the phyletic relationships of the tree shrews. Mamm Rev 4:125–143.
- 38 Gould E. 1978. The behavior of the moonrat, *Echinorex gymmurus* (Erinaceidae) and the pentail tree shrew, *Ptilocercus lowii* (Tupaiidae) with comments on the behavior of other Insectivora. Z Tierpsychol 48:1–27.
- 39 Le Gros Clark WE. 1926. On the anatomy of the pen-tailed tree shrew (*Ptilocercus lowii*). Proc Zool Soc Lond 1926:1179–1309.
- 40 Martin RD. 1990. Primate origins and evolution. Princeton: Princeton University Press.
- 41 Sargis EJ. 2001. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. J Zool Lond 253:473–483.
- 42 Sargis EJ. 2002. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. J Morphol 253:10–42.
- 43 Sargis EJ. 2002. Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. J Morphol 254:149–185.
- 44 Sargis EJ. 2002. A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. Mammalia 66:579–598.
- 45 Szalay FS. 1969. Mixodectidae, Microsypidae, and the insectivore-primate transition. Bull Am Museum Nat Hist 140:193–330.
- 46 Timmins RJ, Duckworth JW, Robson CR, Walston JL. 2003. Distribution, status and ecology of the mainland slender-tailed treeshrew *Dendrogale murina*. Mammal Rev 33:272–283.
- 47 Kaufmann JH. 1965. Studies on the behavior of captive tree shrews (*Tupaia glis*). Folia Primatol 3:50–74.
- 48 Kawamichi T, Kawamichi M. 1979. Spatial organization and territory of tree shrews (*Tupaia glis*). Anim Behav 27:381–393.
- 49 Langham NPE. 1982. The ecology of the common tree shrew *Tupaia glis* in peninsular Malaysia. J Zool Lond 197:323–344.
- 50 Vandenbergh JG. 1963. Feeding, activity and social behavior of the tree shrew, *Tupaia glis*, in a large outdoor enclosure. Folia Primatol 1:199–207.
- 51 Martin RD. 1984. Tree shrews. In: Macdonald D, editor. The encyclopedia of mammals. New York: Facts on File. p 440–445.
- 52 Wharton CH. 1950. Notes on the Philippine tree shrew, *Urogale everetti* Thomas. J Mammal 31:352–354.
- 53 Chorazyna H, Kurup GU. 1975. Observations

- on the ecology and behavior of *Anathana ellioti* in the wild. In: Kondo S, Kawai M, Ehara A, editors. Contemporary primateology. Basel: Karger. p 342–344.
- 54 Cartmill M, MacPhee RDE. 1980. Tupaiid affinities: the evidence of the carotid arteries and cranial skeleton. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 95–132.
- 55 Steele DG. 1973. Dental variability in the tree shrews (Tupaiaidae). In: Zingesser MR, editor. Craniofacial biology of primates: Symposium of the IVth International Congress of Primatology, vol. 3. Basel: Karger. p 154–179.
- 56 Wible JR, Zeller UA. 1994. Cranial circulation of the pen-tailed tree shrew *Ptilocercus lowii* and relationships of Scandentia. *J Mammal Evol* 2: 209–230.
- 57 Wohrman-Repenning A. 1979. Primate characters in the skull of *Tupaia glis* and *Urogale everetti* (Mammalia, Tupaiiformes). *Senckenberg Biol* 60:1–6.
- 58 Zeller UA. 1986. Ontogeny and cranial morphology of the tympanic region of the Tupaiidae, with special reference to *Ptilocercus*. *Folia Primatol* 47:61–80.
- 59 Zeller UA. 1986. The systematic relations of tree shrews: Evidence from skull morphogenesis. In: Else JG, Lee PC, editors. Primate evolution. Cambridge: Cambridge University Press. p 273–280.
- 60 Evans FG. 1939. The morphology and functional evolution of the atlas-axis complex from fish to mammals. *Ann NY Acad Sci* 39:29–104.
- 61 Jenkins FA, Jr. 1970. Anatomy and function of expanded ribs in certain edentates and primates. *J Mammal* 51:288–301.
- 62 Gambaryan PP. 1974. How mammals run. New York: John Wiley & Sons.
- 63 Le Gros Clark WE. 1924. The myology of the tree shrew (*Tupaia minor*). *Proc Zool Soc Lond* 1924:461–497.
- 64 Shapiro LJ. 1993. Functional morphology of the vertebral column of primates. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. Dekalb: Northern Illinois University Press. p 121–149.
- 65 Gebo DL, Sargis EJ. 1994. Terrestrial adaptations in the postcranial skeletons of guenons. *Am J Phys Anthropol* 93:341–371.
- 66 Jolly CJ. 1967. The evolution of the baboons. In: Vagtborg H, editor. The baboon in medical research, vol. 2. Austin: University of Texas Press. p 23–50.
- 67 Harrison T. 1989. New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *J Hum Evol* 18:3–54.
- 68 Larson SG. 1993. Functional morphology of the shoulder in primates. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. Dekalb: Northern Illinois University Press. p 45–69.
- 69 Szalay FS, Sargis EJ. 2001. Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. *Geodiversitas* 23:139–302.
- 70 MacLeod N, Rose KD. 1993. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. *Am J Sci* 293-A:300–355.
- 71 Rose MD. 1988. Another look at the anthropoid elbow. *J Hum Evol* 17:193–224.
- 72 Szalay FS, Dagosto M. 1980. Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia Primatol* 34:1–45.
- 73 Jenkins FA, Jr. 1973. The functional anatomy and evolution of the mammalian humero-ulnar articulation. *Am J Anat* 137:281–298.
- 74 Sargis EJ. 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J Zool Lond* 253:485–490.
- 75 Argot C. 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *J Morphol* 247:51–79.
- 76 Hildebrand M. 1985. Digging of quadrupeds. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge, MA: Belknap. p 89–109.
- 77 Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge, MA: Belknap. p 73–88.
- 78 Napier JR. 1967. Evolutionary aspects of primate locomotion. *Am J Phys Anthropol* 27:333–342.
- 79 Beard KC. 1989. Postcranial anatomy, locomotor adaptations, and paleoecology of Early Cenozoic Plesiadapidae, Paromomyidae, and Microomyidae (Eutheria, Dermoptera). Unpublished doctoral dissertation, Johns Hopkins University.
- 80 Hamrick MW, Rosenman BA, Brush JA. 1999. Phalangeal morphology of the Paromomyidae (?Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. *Am J Phys Anthropol* 109:397–413.
- 81 Taylor ME. 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). *J Morphol* 148:227–254.
- 82 Kappelmann J. 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. *J Morphol* 198:119–130.
- 83 Jenkins FA, Jr. 1974. Tree shrew locomotion and the origins of primate arborealism. In: Jenkins FA, Jr., editor. Primate locomotion. New York: Academic Press. p 85–116.
- 84 Jenkins FA, Jr., McClearn D. 1984. Mechanisms of hind foot reversal in climbing mammals. *J Morphol* 182:197–219.
- 85 Sorenson MW. 1970. Behavior of tree shrews. In: Rosenblum LA, editor. Primate behavior: developments in field and laboratory research, vol. 1. New York: Academic Press. p 141–193.
- 86 Szalay FS, Dagosto M. 1988. Evolution of hallucial grasping in the primates. *J Hum Evol* 17: 1–33.
- 87 Dene H, Goodman M, Prychodko W. 1978. An immunological examination of the systematics of Tupaiodea. *J Mammal* 59:697–706.
- 88 Dene H, Goodman M, Prychodko W, Matsuda G. 1980. Molecular evidence for the affinities of Tupaiidae. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 269–291.
- 89 Napier JR, Napier PH. 1967. A handbook of living primates. London: Academic Press.
- 90 Nowak RM. 1999. Walker's mammals of the world. 6th ed. Baltimore: Johns Hopkins University Press.
- 91 Wilson DE. 1993. Order Scandentia. In: Wilson DE, Reeder DM, editors. Mammal species of the world: a taxonomic and geographic reference. Washington, D.C.: Smithsonian Institution Press. p 131–133.
- 92 Lyon MW. 1913. Tree shrews: an account of the mammalian family Tupaiidae. *Proc US Nat Museum* 45:1–188.
- 93 Luckett WP. 1980. The suggested evolutionary relationships and classification of tree shrews. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 3–31.
- 94 Simmons NB. 1995. Bat relationships and the origin of flight. *Symp Zool Soc Lond* 67:27–43.
- 95 Bloch JJ, Boyer DM. 2002. Grasping primate origins. *Science* 298:1606–1610.
- 96 Bloch JJ, Silcox MT, Sargis EJ. 2002. Origin and relationships of Archonta (Mammalia, Eutheria): re-evaluation of Eudermoptera and Primatomorpha. *J Vertebrate Paleontol* 22(suppl to No. 3):37A.
- 97 Silcox MT. 2001. A phylogenetic analysis of Plesiadapiformes and their relationship to euprimates and other archontans. Unpublished doctoral dissertation, Johns Hopkins University.
- 98 Wagner JA. 1855. Die Säugethiere in Abbildungen nach der Natur. Leipzig: Weiger.
- 99 Haeckel E. 1866. Generelle Morphologie der Organismen. Berlin: Georg Reimer.
- 100 Gregory WK. 1910. The orders of mammals. *Bull Am Museum Nat Hist* 27:1–524.
- 101 Carlsson A. 1922. Über die Tupaiidae und ihre Beziehungen zu den Insectivora und den Prosimia. *Acta Zool* 3:227–270.
- 102 Le Gros Clark WE. 1925. On the skull of *Tupaia*. *Proc Zool Soc Lond* 1925:559–567.
- 103 Simpson GG. 1945. The principles of classification and a classification of mammals. *Bull Am Museum Nat Hist* 85:1–350.
- 104 Van Valen LM. 1965. Tree shrews, primates, and fossils. *Evolution* 19:137–151.
- 105 Campbell CBG. 1966. Taxonomic status of tree shrews. *Science* 153:436.
- 106 Martin RD. 1966. Tree shrews: unique reproductive mechanism of systematic importance. *Science* 152:1402–1404.
- 107 Martin RD. 1968. Reproduction and ontogeny in tree shrews (*Tupaia belangeri*), with reference to their general behavior and taxonomic relationships. *Z Tierpsychol* 25:409–532.
- 108 Butler PM. 1972. The problem of insectivore classification. In: Joysey KA, Kemp TS, editors. Studies in vertebrate evolution. Edinburgh: Oliver and Boyd. p 253–265.
- 109 Lim BL. 1967. Note on the food habits of *Ptilocercus lowii* Gray (pentail tree shrew) and *Echinosorex gymmurus* (Raffles) (Moonrat) in Malaya with remarks on "ecological labelling" by parasite patterns. *J Zool Lond* 152:375–379.
- 110 D'Souza F. 1974. A preliminary field report on the lesser tree shrew *Tupaia minor*. In: Martin RD, Doyle GA, Walker AC, editors. Prosimian biology. London: Duckworth. p 167–182.
- 111 Prashanth M, Veenakumari K. 1996. Perspectives on the zoogeography of the Andaman and Nicobar Islands, India. *Malay Nat J* 50:99–106.
- 112 Dans ATL. 1993. Population estimate and behavior of Palawan tree shrew, *Tupaia palawanensis* (Scandentia, Tupaiidae). *Asia Life Sci* 2:201–214.
- 113 Sargis EJ. 2002. Primate origins nailed. *Science* 298:1564–1565.
- 114 Lemelin P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J Zool Lond* 247:165–175.
- 115 Schmitt D, Lemelin P. 2002. Origins of primate locomotion: gait mechanics of the Woolly Opossum. *Am J Phys Anthropol* 118:231–238.