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## Pelvic Shape in Gliding Rodents: Implications for the Launch

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### Abstract

*We used thin-plate splines to explore pelvic shape in 23 species of pteromyine, anomalurid, and pedetid rodents. A principal components analysis of partial warp scores produced an ordination of species which reflects the distinct phylogenetic histories of the Pteromyinae, Anomaluridae, and Pedetidae. Pedetes, Anomalurus, and Idiurus occupy distinct quadrants in the shape space, while the pteromyines form two distinct clusters with large Petaurista and Aeromys in one cluster. Regression analysis revealed relative length of the ilium to increase significantly with increasing pelvic girdle size in Petaurista, but decrease in Anomalurus. The results suggest important differences in the locomotor architecture of anomalurid and pteromyine gliders, and among small and large gliders.*

### Keywords

*Pteromyinae, Anomaluridae, thin-plate splines, leaping, locomotor morphology.*

### 1. Introduction

Gliding locomotion appears to be a relatively common evolutionary event. It has evolved in the Mammalia at least 8 times (Pteromyinae, Anomaluridae, Eomyidae [36], Myoxidae, Dermoptera, Petauridae, Pseudocheiridae, Acrobati-

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dae), in the Reptilia at least 6 times (*Icarosaurus*; [7], *Daedelosaurus*; [12], *Sharovipteryx*; [13], perhaps *Longisquama*; [34], *Ptychozoon* (Gekkonidae), *Draco* (Agamidae), *Kuehneosaurus*, *Weigeltisaurus*, *Podopteryx*; [33], and *Chryseopelia* (Colubridae); [22], in the Amphibia (*Rhacophorus*: Rhacophoridae; [10]; [9]) and in the Fishes (*Thoracopteridae*, *Exocoetidae*; [33]). In spite of the novelty of this locomotory mode, there has been relatively little study of its evolutionary form or function. Notable exceptions include work by Emerson [9] on gliding frogs, work by Runestad and Ruff [29] on gliding mammals, Thorington and Heaney [38] on the skeletal morphology of sciurid gliders, and comparative studies of the myology of mammalian gliders [16, 23]. We know very little about the phylogenetic history of mammalian gliders, and even less about the selective forces that led to the evolution of gliding.

Descriptions of glides by Scholey [32] suggest large gliders like *Petaurista* launch by dropping from a trunk or branch, accelerating during a fall, and then gliding at a relatively high speed. However, film footage provided by the BBC as well as observations by Takeo Kawamichi suggest otherwise. We know from field and lab observations that *Glaucomys* uses a leaping launch, at least when launching from a branch. We have observed launches from tree trunks, but have not filmed them and can not say if the animals leap or drop from trunks. Our observations of *Glaucomys* suggest this glider leaps during its launch without using a drop/descent phase for acceleration. Also, accounts of anomalurid glides by Tom Macintyre and Lynn Robbins (personal communication) strongly suggest that *Anomalurus* uses a leaping launch.

A leaping launch adds to the energetic cost of gliding [17], but increases take off velocity and consequently improves avoidance of arboreal predators. Shape and size may have a substantial influence on launch velocity. Animals that have identical shapes but different sizes can be expected to have similar performance [14]. That is, small leapers move less mass and accelerate through shorter distances, but achieve jumps of equal height or distance to that of larger animals, which move greater mass, but accelerate through greater distances.

Shape of the pelvic girdle together with muscular architecture determine to a large extent the ability of gliders to accelerate during launch. Clearly, high acceleration enhances predator avoidance and maximizes glide range. Shortening of the ilium [8, 15, 19] and arrangements of origins and insertions of hip extensors determine to a large extent the force of extension and angular acceleration of the femur during launch. Jumping animals like *Pedetes* and *Dipodomys* have a relatively shorter ilium than nonjumpers (perhaps because the mechanical advantage of hip extensors and hip flexors is optimized, or the ischium is proportionately longer, providing more surface or improved mechanics for hip extensors).

Detailed studies of the myology and function of the hind limb [5, 30] have not been conducted for pteromyine or anomalurid rodents, and it is unclear how pelvic girdle design influences body mechanics of leaping and launching. However, some aspects of girdle design suggest leaping. For example,

increased surface area of the ischial tuberosity may indicate greater muscle mass of the major hip extensors (biceps femoris, semitendinosus, quadratus femoris). Also, increased surface area of the lateral surface of the ilium may provide increased area for origins of the gluteus medius and minimus, thereby increasing the potential force of abduction of the femur. This may improve the ability of small gliding rodents to rotate the hind limb during descent on a tree trunk. Large gliders appear to descend backwards, without rotation of the hind limbs. Clearly, the musculature functions over a broad range of locomotor activities. However, comparison of a diversity of glider designs may provide some insight to function.

Recent comparative studies of sciurid morphology [11, 28, 37] have used geometric morphometric techniques [3, 4, 27] to explore shape changes, and have attempted to determine level of morphological integration within a specific structure. The techniques are useful in interpreting ecomorphological patterns [1] in an historical context. In this paper, we use thin-plate splines to explore the structure of pelvic girdles in pteromyine and anomalurid gliders. Our objective is to use the limited data we have on launching dynamics in gliders, and relate it to the structure of one propulsive component. Although no reliable phylogeny has been published for the Anomaluridae or the Pteromyinae, our analysis may provide additional clues to the history of these groups. Our results are used to launch questions about the biology and natural history of an interesting group.

## 2. Methods

Pteromyine and anomalurid specimens deposited at the Field Museum of Natural History (FMNH), the Carnegie Museum of Natural History (CMNH), the American Museum of Natural History (AMNH), and the U.S. National Museum (NMNH) were examined (see Appendix). Pelvic girdles from 85 specimens representing 23 species were photographed using Kodak Tmax 100 film with a 35 mm camera and a 100 mm macro lens stopped down to f32 to maximize depth of field. Film was developed in Tmax developer, and negatives digitized using a Minolta Snappy frame grabber. Digitized images were imported to SigmaScan (SPSS Inc., 444 N. Michigan Ave., Chicago, IL 60611), where coordinates of homologous and Type III landmarks [3, 35] were established. Orientation and size of each pelvic girdle were standardized within QuatroPro (Borland International Inc., Scotts Valley, Calif., USA). The ventralmost margin of the tuberosity of the ischium and the anterior most point of the spine of the ilium were chosen as the baseline of the girdle, and assigned coordinates (0,0) and (1,0) respectively. All remaining landmarks were scaled to these coordinates and exported to TpSpline 1.02 (Michigan Morphometrics Workshop: [www.life.bio.sunysb.edu/morph/](http://www.life.bio.sunysb.edu/morph/)) for tps analysis.

Twelve landmarks were chosen in an effort to reflect functional components of pelvic shape (Fig. 1). Landmarks included (1 and 2) the tuberosity of the ischium (most ventral and most dorsal margins), (3) spine of the ischium,

(4) posterior inferior spine of the ilium, (5) most dorsal edge, (6) most anterior point, and (7) most ventral edge of the crest of the ilium, (8) iliopectineal eminence, (9) pubic tubercle, (10) most posterior and (11) most anterior margins of the obturator foramen, and (12) center of the acetabulum. Mean values for each coordinate across all species means were used to define a reference specimen for the thin-plate spline analysis. No effort was made here to characterize the phylogenetic history or relationships of the species studied. Hence, choice of a reference specimen served only to center the point of view in shape space towards all other species (for discussion, see [26]). In this context, results of the analysis are not sensitive to choice of reference shape.

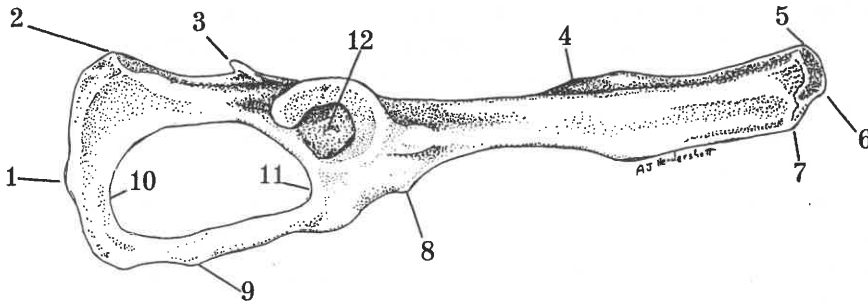


Fig. 1. Diagram of a sciurid pelvic girdle illustrating the landmarks used in the thin-plate spline analysis. 1 = ventral margin of the Tuberosity of the Ischium, 2 = dorsal margin of the Tuberosity of the Ischium, 3 = Spine of Ischium, 4 = Posterior Inferior Spine, 5 = dorsal margin of the Crest of the Ilium, 6 = anterior margin of the Crest of the Ilium, 7 = ventral margin of the Crest of the Ilium, 8 = Iliopectineal Eminence, 9 = Pubic Tubercle, 10 = posterior margin of the Obturator Foramen, 11 = anterior margin of the Obturator Foramen, 12 = Acetabulum.

Thin-plate splines [2, 3] permit exploration of size-free shape changes from one specimen to the next. Briefly, landmarks on the reference species are 'tacked' to a hypothetical, infinitely large thin steel plate, where the expected shape of the girdle landmarks represent a solution to the biharmonic equation [2]. Successive deformations of the thin steel plate for the reference specimen are principal warps. They are eigenfunctions of the bending-energy matrix for the spline. Deformations of the spline for the reference specimen to each other species are represented by partial warps, and are eigenvectors of the bending-energy matrix. These represent the 'bending' necessary to warp the reference shape into that of the new species. The first partial warp represents the most localized deformation, and that which has the greatest bending energy, the last partial warp is the most global deformation, and has the least bending energy.

A principal components analysis of partial warp scores (a relative warp analysis, [25]) was used to characterize the shape space, and identify major axes of shape change across all species. Shapes of various species within the principal components space were visualized using total splines from the reference species to individual elements.

Length of the ilium relative to total pelvic girdle length was computed using the distance of the ilium from the center of the acetabulum to the anterior most point of the crest of the ilium. The total length of the pelvic girdle was computed as the distance from the anterior most point on the crest of the ilium, to the most ventral edge of the tuberosity of the ischium. Linear regression was used to assess the relationship between the log transformed relative length of the ilium and overall length of the pelvic girdle.

### 3. Results

Pelvic girdles of 23 species were photographed and digitized (see Appendix). Many species were represented by only one or a few specimens, while material for many pteromyine species was not available at the institutions visited. Although large sample sizes are desirable, all available material was used in the analysis. The general patterns observed here should not be affected strongly by sample size.

Principal warps for the reference specimen are presented in Table 1. It is clear from the table that the first principal warp characterizes bending energy applied to the reference specimen at the iliac crest, the second is associated with posterior bending of the posterior margin of the obturator foramen, the third involves rotation of the tuberosity of the ischium, and the fourth defines a posteroventral rotation of the acetabulum and an anterodorsal rotation of the iliopectineal eminence. The fifth principal warp is associated with posterior movement of the pubic tubercle and anterodorsal movement of the posterior margin of the obturator foramen, while the sixth defines bending along the anterior margin of the iliac crest. The seventh principal warp is characterized by posterior movement of the spine of the ischium and forward bending of the iliopectineal eminence. Principal warps 8 and 9 define large scale bending along the longitudinal axis of the girdle. The principal warps indicate nothing about the biology of the reference specimen. They only characterize the fit of the reference shape to the biharmonic equation, and provide a point of reference for the other species.

The principal components analysis of the partial warp space (Table 2) required 5 eigenvectors to account for 90 % of the variance in the shape space. Of these, the first 2 components explained nearly 60 % of the variance. These principal components were loaded most heavily by the ninth and seventh partial warps (PC1 and PC2). This space produced an ordination of species (Fig. 2) with anomalurids at the extreme right, with *Anomalurus* and *Idiurus* separated along PC2. *Pedetes* is at the extreme lower left. The pteromyines are concentrated at the left hand portion of the space, with *Iomys* and *Glaucomys* at

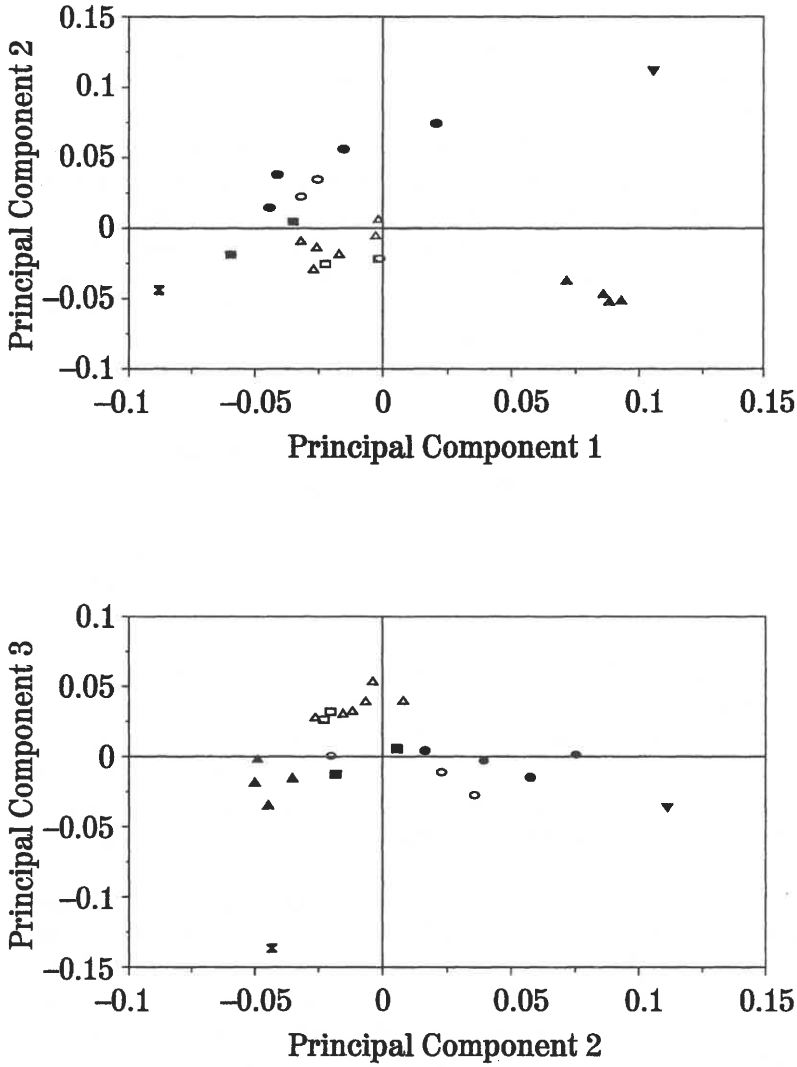


Fig. 2. Distribution of species within the principal components shape space. The PCA was performed on partial warp scores for each species. Closed 'up' triangles = *Anomalurus*, closed 'down' triangles = *Idiurus*, closed hourglass = *Pedetes*, Open triangles = *Petaurista*, open rectangles = *Aeromys*, closed ovals = *Glaucomys*, *Pteromys*, *Iomys*, and *Belomys*, Open ovals = *Hylomys* and *Eoglaucomys*, and closed rectangles = *Trogopterus*. Note the overlap of *Aeromys thomasi* and *Eoglaucomys fimbriatus*. Splines of representative species within the space are illustrated in Figure 3.

Table 1

Principal warps for the mean reference shape. Twelve landmarks were used in the analysis, and hence there are 9 eigenvectors. The eigenvectors proceed from local to global shape changes.

Warp	1	2	3	4	5	6	7	8	9
Eigenvalue	26.2	23.56	21.59	12.08	6.47	4.71	3.36	1.66	0.37
Landmark									
Tuberosity of Ischium 1	-0.052	-0.263	0.573	-0.183	0.069	-0.176	0.348	0.129	-0.363
Tuberosity of Ischium 2	0.053	0.261	-0.604	-0.027	-0.352	-0.042	0.233	-0.068	-0.195
Spine of Ischium	-0.019	-0.085	0.287	0.320	-0.155	0.418	-0.415	-0.371	0.228
Posterior Inferior Spine	-0.122	-0.063	-0.039	0.016	-0.052	0.212	0.054	0.782	0.387
Crest of Ilium (upper margin)	0.533	-0.005	0.064	0.071	-0.047	-0.529	-0.337	0.039	-0.115
Crest of Ilium (ant. margin)	-0.759	0.071	-0.035	-0.028	0.021	-0.141	-0.090	-0.184	-0.244
Crest of Ilium (lower margin)	0.337	-0.064	-0.013	-0.052	0.046	0.574	0.377	-0.168	-0.270
Iliopectineal Eminence	-0.015	0.362	0.208	0.517	-0.118	-0.257	0.404	-0.089	0.305
Pubic Tubercle	-0.006	0.056	0.080	-0.335	-0.516	0.073	-0.364	0.144	-0.130
Obturator Foramen (post.)	0.015	0.124	-0.207	0.313	0.625	0.096	-0.288	0.214	-0.324
Obturator Foramen (ant.)	-0.030	-0.752	-0.352	0.003	0.074	-0.195	0.082	-0.200	0.290
Acetabulum	0.065	0.357	0.039	-0.614	0.404	-0.033	-0.003	-0.226	0.430

the top and *Petaurista leucogenys* at the bottom. The splines (Fig. 3) show that *Anomalurus beecrofti* exhibits expansion along an axis defined by the spine of the ischium and the pubic tubercle. There is some compression of the tuberosity of the ischium. At the top right of the shape space, *Idiurus macrotis* shows some compression of the tuberosity of the ischium, but no expansion along the axis defined by the spine of the ischium and the pubic tubercle. There is some forward movement of the iliopectineal eminence. *Iomys* shows some rotation about the tuberosity of the ischium, and extension of the posterior inferior spine and the anterior margin of the crest of the ilium. *Pedetes* shows contraction between the acetabulum and the iliopectineal eminence, and expansion of the tuberosity of the ischium and the crest of the ilium.

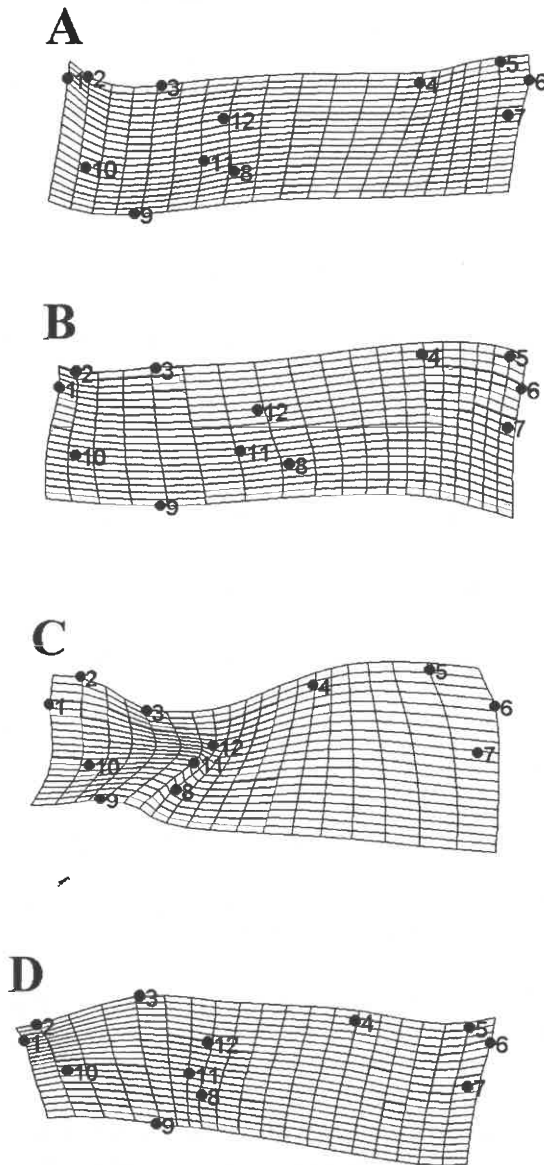


Fig. 3. Splines of species relative to the mean reference shape. A = *Iomys horsefieldi*, B = *Idiurus macrotis*, C = *Pedetes capensis*, D = *Anomalurus beecrofti*.



Table 2

Eigenvectors for the principal components analysis of partial warp scores for the deformation from the mean reference shape to each other species. There were 9 partial warps, represented here by x1 through y9. Highest loadings of horizontal or vertical aspects of warps on a principal component are indicated by an asterisk.

Warp	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Var.	.362	.585	.778	.869	.919	.953	.965	.975	.983
x1	-0.012	0.017	0.165	0.349	0.123	-0.027	0.090	-0.272	0.253
y1	-0.090	0.043	0.054	-0.005	-0.249	0.177	-0.284	0.190	0.049
x2	-0.071	0.051	0.215	0.137	-0.288	-0.147	-0.099	0.177	-0.162
y2	-0.005	-0.017	0.076	0.107	-0.171	-0.062	0.143	0.497	0.173
x3	0.197	0.021	0.137	0.132	0.152	-0.207	0.277	0.077	0.042
y3	0.118	0.143	0.029	-0.116	0.190	-0.126	0.385	0.073	0.125
x4	-0.236	0.347	0.124	0.256	0.245	0.017	0.080	0.518	-0.141
y4	0.102	-0.075	-0.016	0.197	-0.072	-0.041	0.280	0.109	-0.268
x5	-0.216	0.094	-0.533*	0.097	0.554	0.272	0.003	0.123	-0.006
y5	0.161	-0.078	0.071	0.140	0.109	-0.237	0.430	-0.214	-0.178
x6	-0.081	-0.252	-0.094	-0.357	0.146	0.007	0.124	0.026	0.349
y6	0.046	-0.099	0.278	0.297	0.108	0.139	-0.083	-0.022	0.661
x7	-0.314	0.554*	-0.065	0.108	-0.338	0.124	0.263	-0.205	0.247
y7	-0.285	0.374	0.226	-0.169	0.141	-0.039	-0.035	-0.401	-0.176
x8	0.335	0.309	0.386	-0.552*	0.143	0.274	0.084	0.183	0.037
y8	0.071	-0.008	-0.386	-0.126	-0.424	0.255	0.431	0.027	0.095
x9	0.672*	0.444	-0.331	0.185	-0.013	-0.102	-0.300	-0.054	0.079
y9	0.195	-0.143	0.212	0.271	0.023	0.752	0.103	-0.130	-0.264

Within the shape space formed by PC1 and PC2, the anomalurids (*Anomalurus* and *Idiurus*) are at the extreme positive end of PC1, and differ within the group along PC2. *Pedetes capensis* occupies the extreme negative position on PC1. The ordination along PC1 is suggestive of changes associated with leaping. *Pedetes* possesses a broad blade for the ilium, and expanded ischial tuberosity. Both *Anomalurus beecrofti* and *Idiurus* show apparent contraction of the ischial tuberosity. The ordination along PC2 suggests contraction of the distance between the iliopectineal eminence and pubic tubercle in *A. beecrofti*, and expansion in *Idiurus*.

The space defined by PC2 and PC3 provides a further ordination of species. The third principal component is defined primarily by the fifth partial warp. This warp involves a posterior movement of the pubic tubercle and an antero-

dorsal movement of the posterior landmark for the obturator foramen. *Petaurista* spp. and *Aeromys* occupy positive positions along PC3, while the remaining species are near zero or negative portions of this axis. *Pedetes* occupies the most negative position along PC3.

Relative size of the ilium increases significantly (Table 3, Fig. 4) with pelvic girdle size in *Petaurista* ( $p = .037$ ), but not in the Pteromyinae without *Petaurista* ( $p = .169$ ). In both cases, the regressions have positive slope, indicating a general increase in relative ilium length with increasing size of the animal. However, within *Anomalurus*, the relative size of the ilium decreases significantly ( $p = .001$ ) with increasing pelvic girdle size. Thus, as pteromyines become larger, they seem to have girdles which are less typical for a leaping design. *Anomalurus* on the other hand, follows the expected pattern.

**Table 3**

Linear regression results for relative ilium lengths of three groups of gliding mammals.

Group	$b_0$	$b_1$	df	F	P-value
<i>Anomalurus</i>	0.6335	-0.0067	1,19	14.6639	0.0011
<i>Pteromyinae</i>	0.6329	0.0031	1,20	2.0320	0.1694
<i>Petaurista</i>	0.6078	0.0068	1,10	5.7635	0.0373

#### 4. Discussion

The thin-plate spline analysis produced a characterization of shapes which illustrates clear differences between anomalurid and pteromyine gliders, and between *Pedetes* and the gliders. Differences between anomalurid and pteromyine gliders are confounded with their independent evolutionary histories, and care must be taken to avoid confusing functional differences with phylogenetic differences. Unfortunately, the phylogenetic histories of the Pteromyinae, *Pedetes*, and Anomaluridae have not been determined conclusively [21], and detailed analysis of functional patterns are not possible at present with the current data. Furthermore, the present analysis is limited both by the absence of data on non-gliding sciurids, and, an incomplete view of the propulsive machinery of the hind limbs. That is, there has been no dissection of musculature associated with leaping, nor have limb bones been analyzed. However, the present analysis provides an initial exploration of the pelvic girdle, and illustrates differences between pelvic girdles of anomalurid and pteromyine gliders that may influence gliding locomotion.

The principal warps (Table 1) illustrate regions of the pelvic girdle where bending energy is applied to the spline, and progress from small scale changes involving higher levels of bending energy, to large scale changes requiring less bending energy. Partial warps represent deformations relative to each princi-

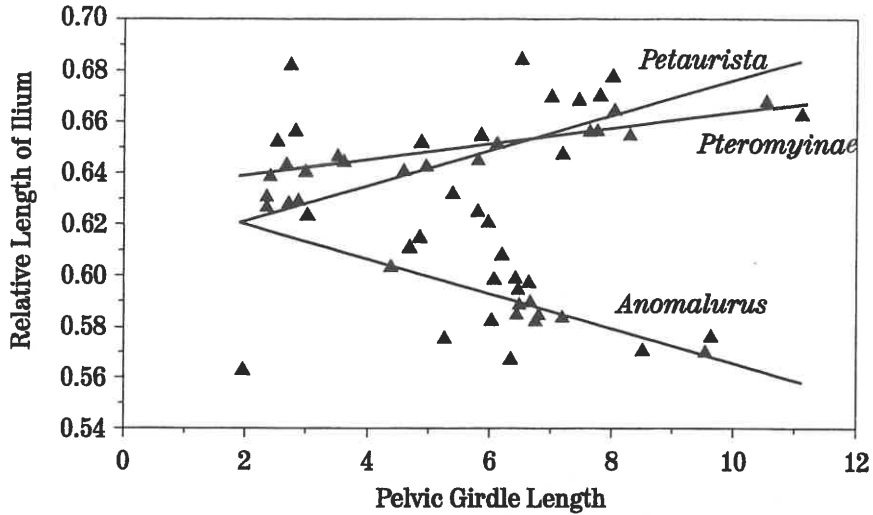


Fig. 4. Scatter plot and regressions of ln relative ilium length against ln pelvic girdle length, for the Pteromyinae, the genus *Petaurista*, and the genus *Anomalurus*.

pal warp, and do not reveal any explicit biological information regarding function. However, the partial warp scores are useful in an explicit analysis of shape using principal components analysis.

The principal components analysis (Table 2, Fig. 2) and corresponding total splines (Fig. 3) provide an overall ordination of shapes. Within this space, the uniqueness of the anomalurids and *Pedetes* is clear. *Anomalurus*, *Idiurus*, and *Pedetes* occupy extreme positions relative to the pteromyines. Furthermore, the differences between *Idiurus* and the larger *Anomalurus* species is considerable. Although *Pedetes* is not an anomalurid, it may share a common ancestor with the anomalurids ([21]; L. Heaney, personal communication). The fact that it is saltatorial and terrestrial results in an expectation that its pelvic morphology is different from those of the gliders.

Differences between *Idiurus* and *Anomalurus* are more interesting, and may reflect both an early evolutionary divergence between the genera, and/or fundamental differences in the way small and large gliders move. *Idiurus* is small (25–35 g) relative to *Anomalurus* [18], and probably leaps with considerable acceleration reaching terminal velocity at low speeds. By contrast, the work of Keith et al. [17] suggests that larger gliders, perhaps including *Anomalurus*, probably accelerate less during leaps but reach higher gliding speeds. The fact that pelvic shape is so different between these genera suggests potential differences in their respective locomotor dynamics. It is unknown if these differences are strictly the result of evolutionary divergence, or include size

effects associated with leaping launches, movement along branches, or the physics of climbing [39].

Our observations of small marsupial feather-tail gliders, *Acrobates pygmaeus* (10–14 g), in a zoo setting suggest this species leaps readily over short distances. It is possible that *Idiurus* too leaps readily from branch to branch. While there are no field observations of *Idiurus macrotis*, *Idiurus zenkeri* (14–17.5 g), or the larger nongliding idiurine *Zenkerella insignis* (180–220 g), analysis of their pelvic shapes may help discern phylogenetic effects as well as size and shape effects associated with the physics of leaping.

*Idiurus zenkeri* and *Zenkerella insignis* were not included in this analysis. *Zenkerella* is especially interesting because it is larger than *Idiurus* (180 to 220 g; [18]), and because it does not glide. Gliding appears to have been lost secondarily in this species. Unfortunately, very little is known about the distribution or ecology of *Zenkerella*. This information together with an understanding of the morphology of *Zenkerella* may provide some insight to the evolution and loss of gliding locomotion.

The principal component shape space reveals a dichotomy within the Pteromyinae. *Petaurista* spp. and *Aeromys* spp. form a relatively tight cluster within the spaces defined by principal components 1, 2, and 3 (Fig. 2). This cluster includes *Eoglaucomys* in the PC1 vs PC2 space. The remaining pteromyine species form a looser cluster. The fact that *Eoglaucomys* falls within the *Petaurista* and *Aeromys* cluster in the space defined by PC1 and PC2 is surprising. Unpublished work by V.L. Roth suggests a close phylogenetic relationship between *Eoglaucomys* and *Glaucomys*, although her preliminary analysis did not include *Aeromys*.

The association of *Petaurista*, *Aeromys*, and *Eoglaucomys* may indicate functional similarity. *Petaurista* and *Aeromys* are relatively large gliders, while the remaining pteromyine species are smaller. This space characterizes large scale bending of the girdle, and expansion of the ischium along PC1, and forward movement of the iliopectineal eminence and posterior movement of the spine of the ischium along PC2. These changes may be associated primarily with abduction of the femur, and secondarily with femoral extension.

The third principal component is associated with movement of the pubic tubercle. Positive regions along this axis indicate anterior movement, while negative regions indicate posterior movement. *Pedetes* occupies the extreme negative position along this axis, while *Petaurista* spp. occupy the extreme positive portion. This region of the pelvis is involved in adduction of the thigh, and changes in orientation of the pubic tubercle may reflect changes in the mechanical advantage of adduction. That is, the large pteromyines (*Petaurista* and *Aeromys*) have high wing loadings and partial adduction of the hind limb may be necessary to maintain the trailing edge of the airfoil.

Regression results suggest different patterns in the Pteromyinae and *Anomalurus*. While the relative length of the ilium in *Anomalurus* decreases with increasing size, suggestive of a leaping morphology, the opposite is true for *Petaurista*. It is possible that these groups possess unique designs within

the skeletal and muscular architecture of the hip, and both achieve powerful leaps in different ways. Changes in the length of the ilium can be compensated via alternative designs within the femur and tibia. Detailed investigation of the skeletal and muscular design within hind limbs is necessary. At present, data pertaining to muscle insertions for the femur and tibia have not been analyzed for either group.

It is interesting to note that work by Robins and Scheibe [24] illustrates positive allometry in the hind limbs of *Glaucomys volans*. This too has been hypothesized as a correlate of leaping animals. Similarly, Keith et al., [17] have computed some aspects of the energetics of launching in *G. volans*, and determined that it adds little to the overall cost of gliding in this species [31]. However, they speculate, based on data and models of Scholey [32] and Caple et al. [6], that *Petaurista petaurista* probably experiences considerable energetic cost associated with a leaping launch. If this is true, *Petaurista* may initiate glides very differently from other pteromyines, and perhaps Scholey's descriptions of launches by *Petaurista* are correct.

The different pattern observed for *Anomalurus* suggests that larger anomalurids rely more heavily on leaping launches than large pteromyines, although no field observations have been reported which would allow confirmation. It is unknown if anomalurids are faced with more extensive predation, or if the overall energetics of gliding differs significantly from that of *Petaurista*. *Idiurus* too seems to possess a leaping morphology within the girdle, perhaps reflecting a locomotor strategy similar to that of *Aerobates*.

Without detailed study of the musculature and limbs, or an understanding of the phylogenetic relationships between the groups, it is impossible to imply functional similarities or differences between genera and families. For example, the close association between *Petaurista*, *Aeromys*, and perhaps *Eoglaucomyis* may indicate some level of phylogenetic similarity. It is possible that partial warp scores may be useful in cladistic analyses [20], and may ultimately lead to new hypotheses for the relationships within the Pteromyinae and Anomaluridae. The data presented suggest size and shape play an important role in the ecology of gliding rodents. Furthermore, anomalurids and pteromyines possess different solutions to the functional problems posed by gliding locomotion. It is unclear what roles history and habitat structure have played in the evolution of their different designs. The speculation provided in this paper is offered as an impetus for careful study of the locomotor morphology of gliders, and development of hypotheses concerning the evolution of gliding locomotion. The hypothesized differences are consistent with ideas presented by Keith et al. [17], and warrant careful scrutiny.

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## References

- [1] Birch, J.M., (1997): Comparing wing shape of bats: the merits of principal-components analysis and relative-warp analysis. *Journal of Mammalogy* 78: 1187–1198.
- [2] Bookstein, F.L., (1989): Principal warps: Thin-plate splines and the decomposition of deformations. *I.E.E.E. Transactions on Pattern Analysis and Machine Intelligence* 11: 567–585.
- [3] Bookstein, F.L., (1991): Morphometric tools for landmark data. Cambridge University Press, Cambridge, United Kingdom.
- [4] Bookstein, F.L., (1996): Combining the tools of geometric morphometrics. Pp. 131–151 in: *Advances in Morphometrics* (L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor and D.E. Slice, eds.). NATO Advanced Science Institutes Series, Series A: Life Sciences Vol. 284. Plenum Press, New York and London.
- [5] Brown, I.A., T.L. Liinamaa, and G.E. Loeb (1996): Relationships between range of motion,  $L_0$ , and passive force in five strap-like muscles of the feline hind limb. *Journal of Morphology* 230: 69–77.
- [6] Caple, G., R.P. Balda, and W.R. Willis (1983): The physics of leaping animals and the evolution of preflight. *American Naturalist* 121: 455–476.
- [7] Colbert, E.H., (1970): The Triassic gliding Reptile *Icarosaurus*. *Bulletin of the American Museum of Natural History* 143: 85–142.
- [8] Emerson, S.B., (1985): Jumping and leaping. Pp. 57–72, in: *Functional Vertebrate Morphology* (M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds.). Cambridge, Mass: Belknap Press of Harvard University Press.
- [9] Emerson, S.B., (1991): The ecomorphology of Bornean tree frogs (family Rhacophoridae). *Zoological Journal of the Linnean Society* 101: 337–357.
- [10] Emerson, S.B., and M.A.R. Koehl (1990): The interaction of behavioral and morphological change in the evolution of a novel locomotor type: “flying” frogs. *Evolution* 44: 1931–1946.
- [11] Essner, R.L., Jr. and J.S. Scheibe (this volume): A comparison of scapular shape in flying squirrels using relative warp analysis (Rodentia: Sciuridae). In: *The Biology of Gliding Mammals* (R.L. Goldingay and J.S. Scheibe, eds.). Filander Press, Germany.
- [12] Evans, S., (1987): A review of the upper Permian genera *Coelurosaurus*, *Weigeltisaurus*, and *Gracilisaurus* (Reptilia: Diapsida). *Zoological Journal of the Linnean Society* 90: 275–303.

- [13] Gans, C., I. Darevski, and L.P. Tartinov (1987): *Sharovipteryx*, a reptilian glider? *Paleobiology* 13: 415–426.
- [14] Hill, A.V., (1950): The dimensions of animals and their muscular dynamics. *Science Progress* 38: 209–230.
- [15] Howell, A., (1932): The saltatorial rodent *Dipodomys*: the functional and comparative anatomy of its muscular and osseous systems. *Proceedings of the American Academy of Arts and Sciences* 67: 377–536.
- [16] Johnson-Murray, J.L., (1987): The comparative myology of the gliding membranes of *Acrobates*, *Petauroides* and *Petaurus* contrasted with the cutaneous myology of *Hemibelideus* and *Pseudocheirus* (Marsupialia: Phalangeridae) and with selected gliding Rodentia (Sciuridae and Anomaluridae). *Australian Journal of Zoology* 35: 101–113.
- [17] Keith, M.M., J.S. Scheibe, and A.J. Hendershott (this volume): Launch dynamics in *Glaucomys volans*. In: *The Biology of Gliding Mammals* (R.L. Goldingay and J.S. Scheibe, eds.). Filander Press, Germany.
- [18] Kingdon, J., (1997): *The Kingdon Field Guide to African Mammals*. London: Academic Press.
- [19] Maynard Smith, J., and R.J.G. Savage (1956): Some locomotory adaptations in mammals. *Journal of the Linnean Society of London (Zoology)* 42: 603–622.
- [20] Naylor, G.J.P., (1996): Can partial warp scores be used as cladistic characters? Pp. 519–530, in: *Advances in Morphometrics* (L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor and D.E. Slice, eds.) NATO ASI series, Plenum Press, New York.
- [21] Nedbal, M.A., R.L. Honeycutt, and D.A. Schlitter (1996): Higher-level systematics of rodents (Mammalia, Rodentia): Evidence from the mitochondrial 12S rRNA gene. *Journal of Mammalian Evolution* 3: 201–237.
- [22] Norberg, U.M., (1990): *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology, and Evolution*. Zoophysiology, Vol. 27. Berlin, Heidelberg, New York: Springer-Verlag.
- [23] Peterka, H.E., (1936): A study of the myology and osteology of tree sciurids with regard to adaptation to arboreal, glissant and fossorial habits. *Transactions of the Kansas Academy of Science* 39: 313–332.
- [24] Robins, J.H., and J.S. Scheibe (this volume): Sexual size dimorphism and allometry in southern flying squirrels, *Glaucomys volans*. In: *The Biology of Gliding Mammals* (R.L. Goldingay and J.S. Scheibe, eds.). Filander Press, Germany.
- [25] Rohlf, F.J., (1993): Relative warp analysis and an example of its application to mosquito wings. Pp. 131–159, in: *Contributions to Morphometrics* (L.F. Marcus, E. Bello and A. Garcia-Valdecasas, eds.). Monografias del Museo Nacional de Ciencias Naturales, 8. Madrid.
- [26] Rohlf, F.J., Loy, A. and Corti, M. (1996): Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. *Systematic Biology* 45: 344–362.

- [27] Rohlf, F.J., and F.L. Marcus (1993): A revolution in morphometrics. *Trends in Ecology and Evolution* 8: 129–132.
- [28] Roth, V.L., (1996): Cranial integration in the Sciuridae. *American Zoologist* 36: 14–23.
- [29] Runestad, J.A., and C.B. Ruff (1995): Structural adaptations for gliding in mammals with implications for locomotor behavior in paromomyids. *American Journal of Physical Anthropology* 98: 101–119.
- [30] Sacks, R. D., and R.R. Roy (1982): Architecture of the hind limb muscles of cats: functional significance. *Journal of Morphology* 173: 185–195.
- [31] Scheibe, J.S., and J.H. Robins (1998): Morphological and performance attributes of gliding mammals. Pp. 131–144, in: *Ecology and Evolutionary Biology of Tree Squirrels* (M.A. Steele, J.F. Merritt and D.A. Zegers, eds.). Special Publication, Virginia Museum of Natural History 6.
- [32] Scholey, K., (1986): The climbing and gliding locomotion of the giant red flying squirrel *Petaurista petaurista* (Sciuridae). *Biona-report* 5: 187–204.
- [33] Schaller, D., (1984): Wing evolution. Pp. 333–348, in: *The Beginnings of Birds* (M.K. Hecht, J.H. Ostrom, G. Viohl and P. Wellnhofer, eds.). Proceedings of the International Archaeopteryx Conference. Eichstatt, 1984. Freunde des Jura-Museums Eichstatt, Willibaldsburg.
- [34] Sharov, A.G., (1971): An unusual reptile from the lower Triassic of Fergana. *Paleontological Journal* 1: 127–130.
- [35] Slice, D.E., F.L. Bookstein, L.F. Marcus, and F.J. Rohlf (1996): A glossary for geometric morphometrics. Pp. 531–551, in: *Advances in Morphometrics* (L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor and D.E. Slice, eds.). NATO Advanced Science Institutes Series, Series A: Life Sciences Vol. 284. Plenum Press, New York and London.
- [36] Storch, G., B. Engesser, and M. Wuttke (1996): Oldest fossil record of gliding in rodents. *Nature* 379: 439–441.
- [37] Swiderski, D.L., (1993): Morphological evolution of the scapula in tree squirrels, chipmunks, and ground squirrels (Sciuridae): an analysis using thin-plate splines. *Evolution* 47: 1854–1873.
- [38] Thorington, R. W., Jr. and L.R. Heaney (1981): Body proportion and gliding adaptations of flying squirrels (Petauristinae). *Journal of Mammalogy*, 62: 101–114.
- [39] Thorington, R. W., Jr. and E.M. Thorington (1989): Posterian proportions of *Microsciurus* and *Sciurillus*, the american pygmy tree squirrels. Pp. 125–136, in: *Advances in Neotropical Mammalogy*. (K.H. Redford and J.F. Eisenberg, eds.). Gainesville, FL, USA: The Sandhill Crane Press.



**Appendix**

Specimens examined:

*Aeromys tephromelas*: AMNH 229, NMNH 196743.

*Aeromys thomasi*: FMNH 90437.

*Anomalurus beecrofti*: AMNH 52101, NMNH 466118.

*Anomalurus derbianus*: AMNH 52100, 52102, 89389, 150411, 150412, 150446, 241148, 241149, CMNH 41140, FMNH 148383, NMNH 466119, 466120, 466121.

*Anomalurus pelii*: CMNH 69351, FMNH 62223, NMNH 399470, 429832, 466126.

*Anomalurus pusillus*: AMNH 51015, 52103, 52138, 52137.

*Belomys pearsonii*: CMNH 88179, 88180.

*Eoglaucomyys fimbriatus*: FMNH 140397, 140399, 140400, 140401, NMNH 173361, 173363, 173365, 353243.

*Glaucomyys sabrinus*: CMNH 7523, 13647, 19600, 22762, 25271, 27231, 31603, 31604, 62562, FMNH 150983.

*Hylomys nigripes*: FMNH 63031, 63030.

*Hylomys phayrei*: AMNH 106701, 106702, CMNH 88181.

*Idiurus macrotis*: AMNH 236384, CMNH 41142.

*Iomys horsfieldi*: NMNH 292654.

*Pedetes capensis*: FMNH 129464, NMNH 295258.

*Petaurista alborufus*: AMNH 184933, 187082, NMNH 332937.

*Petaurista elegans*: FMNH 114369, 114370, 114371, 114372, NMNH 292647.

*Petaurista leucogenys*: NMNH 20941.

*Petaurista magnificus*: FMNH 114364, 114365, 114366.

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*Petaurista petaurista*: FMNH 68784, 98533, NMNH 49660, 173374, 174079,  
174080, 197320.

*Petaurista philippensis*: AMNH 43183, 112975, FMNH 32396, 46647, NMNH  
307073.

*Pteromys volans*: CMNH 92170.

*Trogopterus edithae*: NMNH 258520.

*Trogopterus xanthipes*: NMNH 254807, 268872.