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A Comparison of Scapular Shape in Flying Squirrels (Rodentia: Sciuridae) Using Relative Warp Analysis

Abstract

Gliding locomotion has evolved repeatedly in the Mammalia and appears to be an important evolutionary theme. Nevertheless, morphological aspects of the transition from nongliding to gliding forms have rarely been investigated. This study focuses on the scapula because of its role as a transitional element between the forelimbs and body. We use relative warp analysis and least squares Procrustes superimposition to explore historical, functional, and allometric patterns of scapular morphology in Sciurus and nine pteromyine species. An analysis of the uniform component of shape change revealed that large and small flying squirrels have diverged with regard to shearing and scapular width. Relative warp analysis revealed that flying squirrels have longer coracoids and shorter metacromions than Sciurus. North American squirrels have shorter acromions than Asian squirrels, and large squirrels have an expanded supraspinous region. A cluster analysis of overall morphological distances was consistent with currently accepted phylogenetic relationships. Relative warp analysis highlights regions of the scapula that contain the most variation among forms, and suggests potentially fruitful directions for future functional studies. Furthermore, it provides a tractable means for making testable biomechanical predictions, a fundamental step in relating morphology and ecology.

Keywords

flying squirrels, gliding, morphometrics, scapula

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1. Introduction

Gliding has evolved independently at least eight times in the Mammalia. Eutherian groups include the Sciuridae, Anomaluridae, Myoxidae, Eomyidae, and Cynocephalidae, while marsupials include the Pseudocheiridae, Petauridae, and Acrobatidae [16, 17, 26, 29, 36]. Clearly, gliding represents an important, iterative theme in mammalian evolution. Nevertheless, morphological aspects of the transition from nongliding to gliding forms have rarely been investigated [but see 26, 34, 36, 37]. Lack of insight into morphological variation presents a major barrier in attempts to link form and function in gliding mammals.

One skeletal element that deserves special attention is the scapula. As the interface between the forelimbs and body, the scapula has the potential to contribute substantially to our understanding of locomotion. Not surprisingly, a number of studies have examined the link between its form and function in mammals [14, 19, 20, 28, 31, 32, 39]. Because gliding mammals inhabit a complex three-dimensional environment, the scapula must be a multifunctional element, able to accomplish a diverse set of tasks. Its role is likely to be especially complicated in gliding mammals due to the large number of muscle attachment sites [37] and the relative complexity of gliding locomotion [1].

Flying squirrels (subfamily Pteromyinae) are a model group for exploring the evolutionary shift in morphology associated with gliding. Unlike many glider taxa, the evolutionary relationships of pteromyines have received at least some attention, making it possible to use an historical perspective when examining variation in this group. Two concerns that must be addressed are: (1) monophyly of the in-group, and (2) identification of an appropriate outgroup. Although phylogenetic relationships within the Pteromyinae are not fully resolved [37], there are sufficient data in the literature to confront these concerns.

Several morphological and molecular studies provide support for monophyly of the Pteromyinae, as well as for a close evolutionary relationship between flying squirrels and tree squirrels. Thorington [34] argued that the Pteromyinae form a monophyletic clade based on synapomorphies of the wrist and patagium, and he provided evidence that tree squirrels and flying squirrels are sister taxa. More recently, a cladistic analysis of cranial characters by Roth and Dishop [25] revealed a close phylogenetic relationship between flying squirrels and tree squirrels. In their study, *Glaucomys* formed a monophyletic clade within tree squirrels, while ground squirrels and chipmunks were sister taxa. Hight *et al.* [11] used immunological data to investigate phylogenetic relationships within the Sciuridae. They demonstrated an affinity between *Sciurus* and the flying squirrels and, with the exception of *Iomys,* all flying squirrels they examined (*Glaucomys, Petinomys, Pteromys,* and *Petaurista*) were more similar to one another than to other squirrels. Finally, Oshida *et al.* [18] used molecular sequences obtained from mitochondrial 12S ribosomal RNA to demonstrate that tree squirrels and flying squirrels are more closely related to each other than either is to the chipmunk lineage. Thus, evidence supports the monophyly of Pteromyinae and a close phylogenetic relationship between tree squirrels and flying squirrels.

In addition to providing a description of morphological variation between non-gliding and gliding forms, this study explores variation within the Pteromyinae. Ideally, morphological patterns discerned from this investigation would be evaluated against a well-resolved phylogeny. Given that a phylogeny is unavailable, we evaluate morphological variation in light of the pteromyine taxonomy, as well as the suite of interspecific hypotheses that have been proposed. While we do not attempt to construct a phylogeny for the group, we hope that morphological variation uncovered with this approach will be useful in the search for phylogenetically informative characters. The final goal is to demonstrate how a precise description of scapular shape can be utilized for construction of biomechanical predictions necessary for future functional studies [40].

2. Methods

2.1 Thin-Plate Splines and Relative Warps

We used relative warp analysis to explore scapular shape in pteromyines. Relative warp analysis is essentially a principal components analysis of the covariance matrix of partial warp scores produced by thin-plate splines. The technique uses the descriptive power of thin-plate splines to produce a visualization of morphospace via the transformation grids of Thompson [33]. This allows clear representation of shape characteristics associated with various regions of morphospace.

A primary strength of relative warp analysis is its unique ability to provide both a descriptive and a quantitative description of shape. Birch [2] illustrated the utility of the technique by exploring wing shape differences in bats that differ ecologically. Others have used relative warps to investigate phylogenetic patterns of morphology [12, 23, 38].

Thin-plate splines are based on a mathematical model in which a thin metal plate mapped onto a reference form is deformed into a final form. Any consequent shape deformation involves two major components. First, the deformation is decomposed into a single uniform component, which describes shape change that occurs over the entire form. This can be visualized by imagining the metal plate as a grid of rectangles overlaying the reference shape. As the reference shape is deformed into the final shape, some change will involve only rotation and elevation of the entire grid. In this global or affine transformation, all rectangles change in a manner that allows parallel lines on the reference form to remain parallel on the final form. The result is a depiction of large-scale integrated shape change [2].

The second component of deformation involves that portion of shape change that requires bending of the reference form. Bending can be further decomposed, based on energy required to perform the deformation, into a series of smaller non-uniform components that describe progressively more global shape change. These non-uniform components are principal warps, and describe geometric regions of the reference form. The contributions of each principal warp to the actual landmark displacements are expressed as vectors called partial warps [30]. Technical descriptions of the method are provided by Bookstein [3, 4].

2.2 Data Acquisition

Adult specimens (n = 102) were obtained from the American Museum of Natural History [AMNH], British Museum of Natural History [BMNH], Carnegie Museum of Natural History [CMNH], Field Museum of Natural History [FMNH], United States National Museum [USNM], and the University of Kansas Museum of Natural History [KUMNH] and are listed along with geographic distributions and size ranges in the appendix. Specimens were chosen in an effort to represent geographic ranges and maximize intraspecific variation. Scapulae were filmed either with a Sony Handycam 8 mm camcorder mounted on a tripod, or a 35 mm camera with a 100 mm macro lens mounted on a copy stand. Scapulae were oriented parallel to the plane of focus, with the lateral surface facing the lens.

Video images were converted to digital images with a Play Inc. SNAPPY framegrabber. Photographs were converted into digital images with a UMAX Astra 300P scanner. Digital images were subsequently imported to TPSDIG version 1.08 [22] for digitization. Eleven landmarks were identified on each scapula and (x,y) coordinates obtained for each specimen in the manner of Swiderski [30] (Fig. 1). Coordinates were imported into SHAPE version 1.03 [7], providing translation, rotation, and rescaling of landmarks with reference to a specified baseline. Landmarks 7 and 10 defined the baseline in this study and were assigned fixed coordinates (0,0 and 1,0 respectively). The coordinates of all other landmarks were adjusted relative to this baseline. This produced landmarks which were size independent and analyzed only for shape differences. The transformed landmarks are shape coordinates [4].

Right scapulae were used whenever possible. Four specimens had right scapulae that were either missing or unusable. Therefore, we used left scapulae on these specimens and assumed no significant scapular asymmetry. Left scapulae coordinates were imported to ASYMM [24] which reflected the landmarks across the baseline. This transformation produced mirror images of the original forms.

2.3 Data Analysis

Mean shapes for each species were determined by averaging shape coordinates for each landmark with SHAPE. Means were then imported to TPSRELW version 1.13 [22], for relative warp analysis. TPSRELW averages all specimens in the analysis to calculate the reference or consensus form. This is necessary because thin-plate splines produce only pairwise comparisons. Thus, mean shapes for each species are compared to the reference form to generate partial

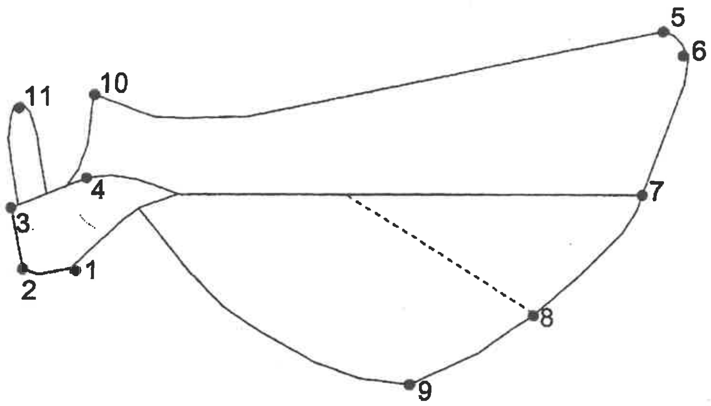

Fig. 1. Eleven landmarks for the consensus configuration of nine flying squirrels and one tree squirrel: (1) dorsal end of acromio-clavicular articulation; (2) ventral end of acromio-clavicular articulation; (3) flexure marking the boundary between acromion and metacromion; (4) ventral end of caudal margin of metacromion; (5) caudal end of vertebral border on teres fossa; (6) intersection of axillary ridge and vertebral border between teres fossa and infraspinous fossa; (7) intersection of spine and vertebral border between infraspinous fossa and supraspinous fossa; (8) projection of subscapular ridge to vertebral border; (9) maximum curvature along anterior border; (10) dorsal end of glenoid fossa; (11) tip of coracoid process. Note: Scapula is shifted 90o from correct anatomical position due to filming constraints.

warps on the same principal warps. Shape differences for each species are then revealed by examination of associated partial warps in the transformation grids.

To model the deformation of one shape to another with thin-plate splines, a superimposition method was used to calculate the "best fit" between the two shapes. We used least squares within TPSPLINE version 1.14 [22] to superimpose two forms. Least squares fit was computed using euclidean distances between corresponding landmarks on the forms. The resultant metric described overall morphological distance between forms, and was the Procrustes distance. Least squares methods work well when differences between two forms are general rather than localized to one region. We used this technique because we had no *a priori* reason to expect localized differences. A matrix of interspecific pairwise Procrustes distances based on mean shapes was constructed using TPSPLINE. A UPGMA (unweighted pair-group method using averages) cluster analysis was performed on the resultant matrix to explore patterns of scapular shape.

3. Results

3.1 Uniform Component

A scatter plot of the uniform component reveales patterns of global shape change (Fig. 2). Shape change along the x-axis indicates positive or negative shearing; whereas shape change along the y-axis indicates expansion or compression. Two trends are apparent. *Glaucomys* is negatively sheared, while giant flying squirrels (*Aeromys* and *Petaurista*) are positively sheared. Medium-sized flying squirrels and *Sciurus* are located centrally and exhibit little shearing. *Glaucomys* is laterally compressed, whereas giant flying squirrels show expansion. Again, *Sciurus, Eoglaucomys,* and *Hylopetes* are intermediate in position with little change from the consensus shape.

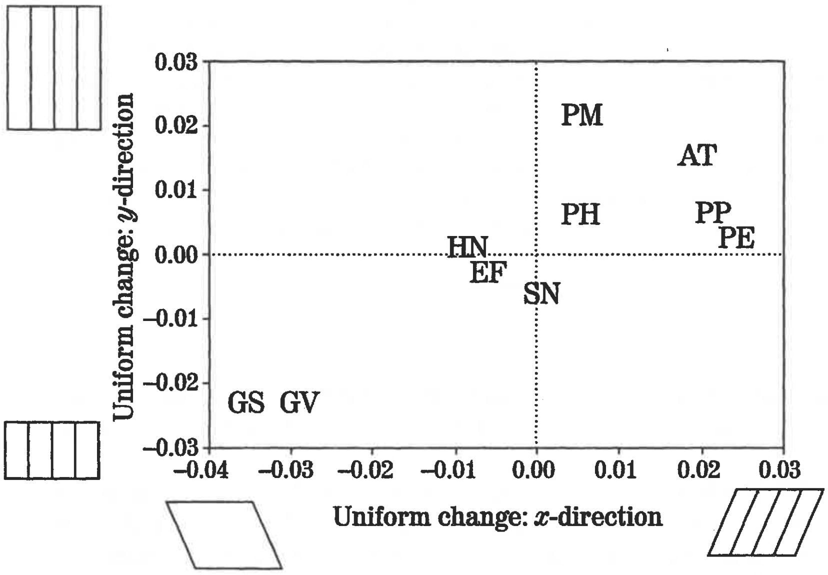

Fig. 2. Scatter plot of the uniform component of shape change illustrating a global transformation involving all landmarks. Shape change along the x-axis indicates shearing along the long axis of the scapula in the positive or negative direction; whereas, shape change along the y-axis indicates either expansion or compression along the long axis of the scapula. AT, *Aeromys tephromelas*; EF, *Eoglaucomys fimbriatus*; GS, *Glaucomys sabrinus*; GV, *Glaucomys volans*; HN, *Hylopetes nigripes*; PE, *Petaurista elegans*; PM, *Petaurista magnificus*; PP, *Petaurista petaurista*; PH, *Petaurista philippensis*; SN, *Sciurus niger*.

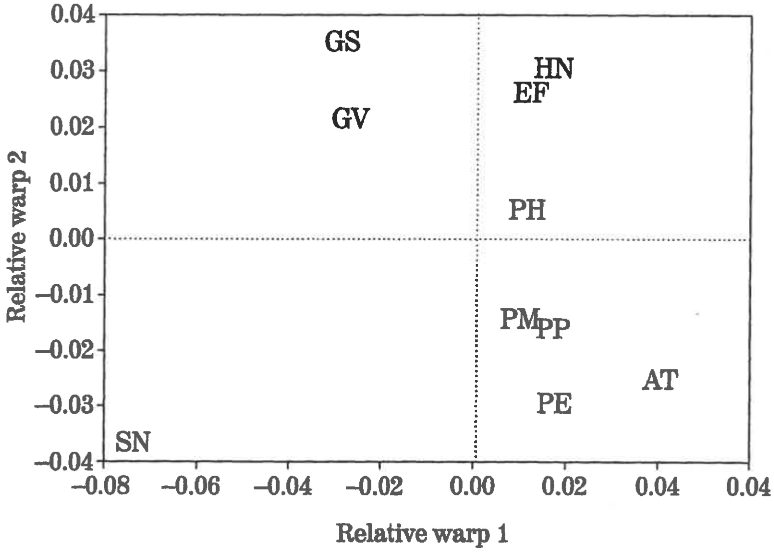

Fig. 3. Scatter plot for the relative warp scores including uniform and non-uniform components. AT, *Aeromys tephromelas*; EF, *Eoglaucomys fimbriatus*; GS, *Glaucomys sabrinus*; GV, *Glaucomys volans*; HN, *Hylopetes nigripes*; PE, *Petaurista elegans*; PM, *Petaurista magnificus*; PP, *Petaurista petaurista*; PH, *Petaurista philippensis*; SN, *Sciurus niger*.

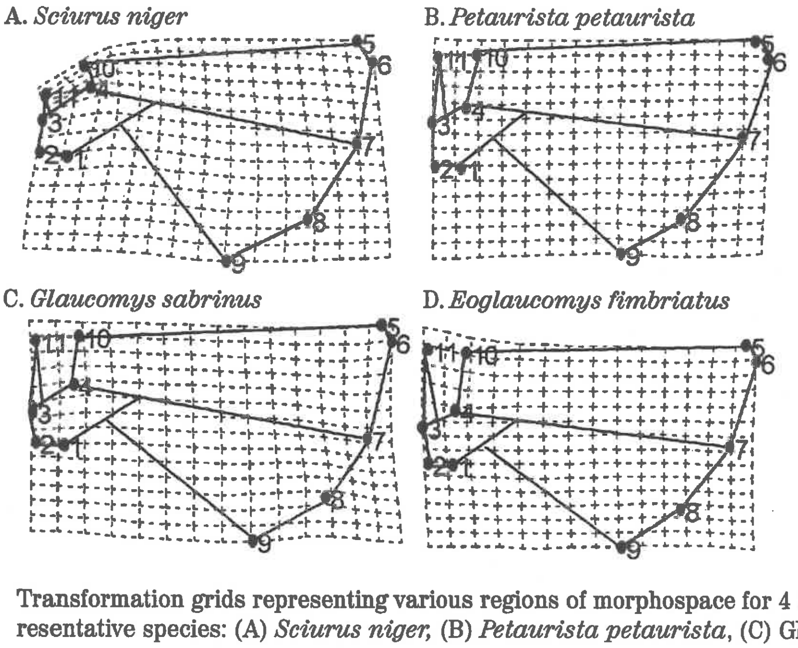

Fig. 4. Transformation grids representing various regions of morphospace for 4 representative species: (A) *Sciurus niger*, (B) *Petaurista petaurista*, (C) *Glaucomys sabrinus*, (D) *Eoglaucomys fimbriatus*.

3.2 Relative Warps

The scatter plot for relative warp scores, including uniform and nonuniform components, reveals additional patterns of shape change (Fig. 3). The first relative warp explains 47 % of the shape variation in the sample and discriminates *Sciurus* from pteromyines as well as North American species from Asian species. *Sciurus* differs from flying squirrels by having an expanded metacromion (landmark 4) and a shortened coracoid (landmark 11) (Fig. 4 A). North American squirrels (*Glaucomys* and *Sciurus*) differ from Asian squirrels (*Aeromys, Eoglaucomys, Hylopetes,* and *Petaurista*) by sharing a subtle contraction of the acromion (landmark 2; Fig. 5).

The second relative warp explains 32 % of the shape variation in the sample and discriminates between large squirrels (*Aeromys, Petaurista,* and *Sciurus*) and small to medium squirrels (*Eoglaucomys, Glaucomys,* and *Hylopetes*; Fig. 3). This can be attributed to an expanded supraspinous region (landmarks 7, 8, and 9) in the large squirrels (Fig. 4 A, B). Notably, *Petaurista philippensis* lacks the expanded supraspinous region causing it to approach the small/medium squirrel range (Fig. 3). Also, there appears to be a strong historical signal with respect to scapular shape since species group with congeners (former congeners in the case of *Eoglaucomys* and *Hylopetes*) [35].

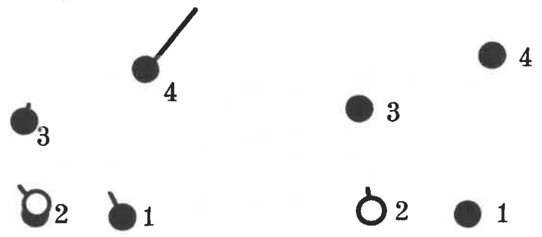
A. *Sciurus niger* B. *Glaucomys sabrinus*

Fig. 5. Vector displacements in the acromion/metacromion region in (A) *Sciurus niger* and (B) *Glaucomys sabrinus*. Open circle at ventral end of acromioclavicular articulation (landmark 2) identifies location of shared contraction.

3.3 Cluster Analysis

The UPGMA cluster analysis of Procrustes distances (Fig. 6) reveals that species cluster more or less taxonomically. *Sciurus* clusters as an outgroup to the Pteromyinae. Within the Pteromyinae, *Hylopetes* and *Eoglaucomys* form a cluster, as well as *Petaurista*. As in the relative warp plot, North American *Glaucomys* form a cluster distinct from Asian flying squirrels. *Aeromys* is joined distally to a *Hylopetes/Eoglaucomys* and *Petaurista* cluster.

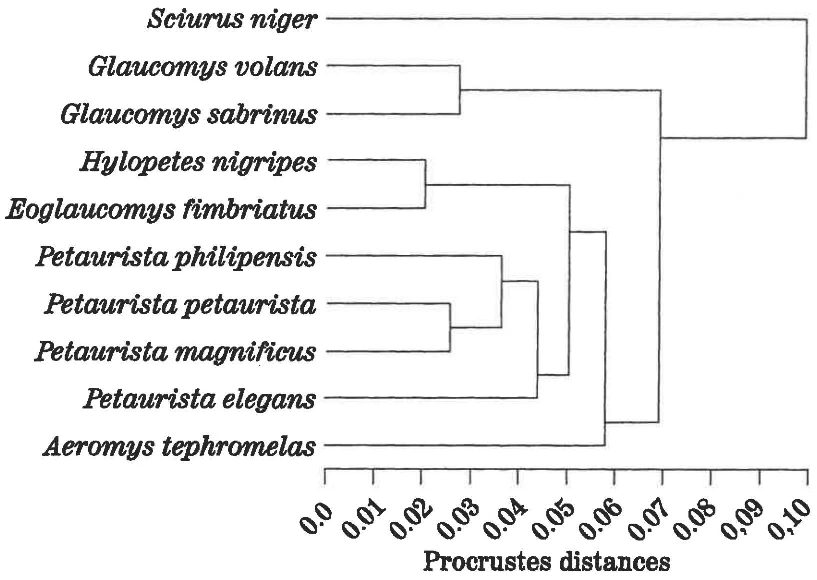

Fig. 6. UPGMA (unweighted pair-group method using averages) cluster analysis of overall morphological (Procrustes) distances.

4. Discussion

4.1 Species Comparisons

As expected, based upon currently accepted phylogenetic relationships, both relative warp and cluster analyses reveal differences between *Sciurus* and the pteromyines. Of note is the fact that *Glaucomys volans* and *G. sabrinus* are consistently similar in scapular shape. Burt [6] hypothesized that *G. sabrinus* is actually more closely related to *Hylopetes* than to *G. volans* on the basis of bacular morphology. The present study demonstrates that scapular shape between the two species of *Glaucomys* is nearly identical. More recent work by Thorington *et al.* [35] supports the monophyly of *Glaucomys*.

Relative warp analysis distinguishes North American squirrels from Asian forms, primarily on the basis of acromion shape (Fig. 3). The reduced acromion of *Glaucomys* was first noted by Bryant [5] and may be a plesiomorphic character for the tree squirrel/flying squirrel clade since *Sciurus* and *Glaucomys* are morphologically conservative taxa [10, 13].

Relative warp and cluster analyses reveal a close association between *Eoglaucomys fimbriatus* and *Hylopetes nigripes* (Fig. 3, 6). Until recently these species were congeners, but were separated by Thorington *et al.* [35] due to a lack of shared derived characters in cranial and postcranial morphology. This study supports a close phenetic relationship between the two groups.

Also, it illustrates that *Eoglaucomys* is far removed from the *Glaucomys* clade. This differs from the work of McKenna [15] who hypothesized a close relationship between *Glaucomys* and *Eoglaucomys* based primarily on dentition, the otic region of the skull, and the baculum.

We found that *Petaurista* is closely associated with *Aeromys* in the relative warp analysis, but is closer to *Hylopetes* and *Eoglaucomys* in the cluster analysis. Ellermann [9] noted that *Aeromys* is similar to *Petaurista* in external characters such as tail and interfemoral patagium morphology, but is most similar to *Hylopetes* in tooth morphology.

4.2 Functional Inference

The first relative warp reveals that *Sciurus* has an enlarged metacromion and shorter coracoid compared to the pteromyines (Fig. 3, 4 A). These observations are consistent with those of Bryant [5] who noted these differences between *Sciurus* and *Glaucomys*. The enlarged metacromion may be plesiomorphic for sciurids given its presence in a wide array of distantly related nongliding sciurids [37].

Both the *trapezius* and the *atlantoscapularis ventralis* attach at the metacromion [37]. The *trapezius* draws the vertebral border of the scapula medially, while the *atlantoscapularis ventralis* draws the scapula cranially [8]. There is little variation in the origin or insertion of the *atlantoscapularis ventralis* among squirrels [37]. The same appears to hold true for the *trapezius*. It is unclear why there is such morphological disparity between *Sciurus* and pteromyines.

Pteromyines exhibit lengthening of the coracoid process (Fig. 4 B–D). Muscles associated with the coracoid include the *biceps brachii*, a flexor of the antibrachium, and the *coracobrachialis*, an adductor of the humerus [8, 37]. It is difficult to understand fully the implications of an elongated coracoid without careful dissection and functional analysis in living animals. Nevertheless, as an example of the utility of relative warp analysis for making testable biomechanical predictions we could infer that increased length of the coracoid would increase the moment arm of the *coracobrachialis*, resulting in greater angular acceleration and torque when driving claws into bark during climbing. Perhaps even more importantly, it may aid landing after a glide by enabling an effective hold on the substrate, or assist in keeping the forelimbs in a fixed position during gliding in order to counter the upward force of air. While these hypotheses remain untested, relative warp analysis has provided a useful mechanism for generating them.

4.3 Allometry

Size has been shown to be an important component of morphological variation in flying squirrels. Thorington and Heaney [36] investigated body proportions and gliding adaptations in pteromyines and found that large-bodied flying squirrels are proportionately more gracile than either small flying squirrels or tree squirrels. Also, they have longer tails than small flying squirrels, albeit not as long as the largest tree squirrels (*e.g., Ratufa*).

A possible allometric pattern was revealed in this study by the uniform component of shape change (Fig. 2). Apparently, large and small flying squirrels have diverged with respect to relative scapular compression. As noted by Bryant [5], compared to other squirrels *Glaucomys* has a narrower scapula relative to vertebral column length. This observation was verified by the location of *Glaucomys* in the scatter plot. By comparison, large flying squirrels have a relatively wide scapula, while medium flying squirrels and *Sciurus* are located in an intermediate position.

The second relative warp reveals an allometric signal in the supraspinous region of the scapula (Fig. 3). In large squirrels, this region of the scapula is expanded relative to small and medium-sized squirrels (Fig. 4 A, B). The *supraspinatus* attaches here and is responsible for extending the humerus [8]. It seems likely that the *supraspinatus* is important in climbing. These differences likely reflect the need to generate greater force (proportional to muscle cross-sectional area) in order to move a relatively larger mass.

5. Conclusion

Several of the patterns discussed here have been described previously only in a qualitative manner [5, 37]. This study demonstrates the efficacy of relative warp analysis for exploratory studies of morphology by suggesting potentially fruitful directions for future functional studies. Relative warp analysis highlights regions of a form that explain the majority of morphological variation among taxa, thereby facilitating the generation of functional, allometric, and historical hypotheses. Furthermore, it provides a tractable means for making testable biomechanical predictions, a fundamental step in relating morphology and ecology.

Several key features of the scapula have evolved in interesting ways in pteromyines. However, definitive statements about form/function relationships in these regions are premature without thorough analysis of locomotion. These elements are prime candidates for analysis of function using locomotor kinematics together with electromyography of associated muscles. A biodynamic analysis of climbing, running, and gliding may elucidate behavioral consequences of morphological variation [21].

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Appendix A

Specimens examined:

Aeromys tephromelas: AMNH229, BMNH77.2886, 77.55, NMNH196743.

Eoglaucomys fimbriatus: BMNH1721.a, FMNH140399, 140400, NMNH173361, 173363, 173365, 353243.

Glaucomys sabrinus: CMNH13647, 19600, 62562, FMNH145945, KUMNH6959, 15079, 37519, 91106, 101036, 130428, 138573, 142380, 145230, 145291.

Glaucomys volans: FMNH41656, 124579, 127263, KUMNH2943, 8759, 8760, 8779, 9648, 9823, 11916, 61315, 61316, 61317, 61318, 63757, 66572, 66573, 68347, 68348, 68452, 68833, 77949, 119970, 130427, 143921.

Hylopetes nigripes: FMNH63025, 63030, 63031.

Petaurista elegans: BMNH77.2891, 1979.2891, FMNH114369, 114370, 114372, NMNH292647.

Petaurista magnificus: BMNH1845.1.12.5.28, 1848.11.20.11, FMNH114364, 114365, 114366.

Petaurista petaurista: BMNH77.2887, 77.2888, 77.2890, 79.3443, 1879.7.2.1, 1897.3.10.3, 1960.8.4.5, 1977.2889, FMNH32396, 68784, NMNH173374, 174079, 174080, 197320.

Petaurista philippensis: AMNH112975, BMNH1977.463, NMNH257844, 307073.

Sciurus niger: KUMNH4302, 5138, 5259, 6206, 6266, 6638, 8273, 8784, 8848, 9172, 11523, 12114, 12115, 13448, 76918, 119478, 140082, 140087, 140163, 143957.

Appendix B

Number of individuals, geographic distribution, and size range for each species represented in the study. Size ranges were obtained from Silva and Downing [40].

Species	Number of individuals	Geographic distribution	Size range (kg)
Aeromys tephromelas	4	Asia	1.0–1.5
Eoglaucomys fimbriatus	7	Asia	.51
Glaucomys sabrinus	14	North America	.13–.19
Glaucomys volans	25	North America	.04–.11
Hylopetes nigripes	3	Asia	.53
Petaurista elegans	6	Asia	.92–1.6
Petaurista magnificus	5	Asia	1.8
Petaurista petaurista	14	Asia	1–3.2
Petaurista philippensis	4	Asia	—
Sciurus niger	20	North America	.43–1.2