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GEOMETRIC MORPHOMETRICS AND THE DEVELOPMENT OF COMPLEX STRUCTURES: ONTOGENETIC CHANGES IN SCAPULAR SHAPE OF DASYPODID ARMADILLOS.

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ABSTRACT - The ontogenetic development of the scapula of *Euphractus sexcinctus* and *Dasypus novemcinctus* was studied using geometric morphometrics techniques. The relative importance of uniform, large, and small scale shape changes on ontogenetic development was assessed both by multivariate regression of shape on size and by relative warps analysis. The scapular development in both species is very similar and is characterized (and dominated) by an enlargement of the teres major process. This process serves **as** origin for the teres major muscle, which is responsible for limb retraction (an important function for digging behavior). There **is** also **a** global increase in relative anteroposterior length, increasing the moment arm of this muscle. The uniform shape changes during development are responsible for **a** small percentage of the size-based shape variation in *Euphractus*, and for a large percentage in *Dasypus*. The large scale localized shape changes (which depict the teres major process enlargement) are responsible for **a** large percentage of size-based shape variation. The region of the coracoid process and glenoid cavity are almost unaltered during the ontogeny in both species.

Key words: geometric morphometrics, ontogeny, scapula, complex structures.

INTRODUCTION

The mammalian scapula is a complex morphological structure (Atchley and Hall, 1991). It represents the ontogenetic fusion of two ossification centers (morphogenetic components) initially formed from cartilage templates: a scapular plate and a coracoid plate (Goodrich, 1986). Particularly in Xenarthran mammals, a suture between the coracoid plate and the scapular blade can be discerned late in ontogeny.

There is considerable controversy concerning the ontogenetic and evolutionary determinants of shape in the mammalian scapula. Evidence from the literature points mainly to a functional influence (Lehmann, 1963; Oxnard, 1968; Leamy and Atchley, 1984). However, Swiderski (1993) found no functional influence in the evolutionary differentiation of the scapula in squirrels. Monteiro and Abe (1999) quantified the influence of locomotor behavior and phylogeny in the scapular morphology of Xenarthran mammals and found that both factors contribute significantly to shape differentiation. Leamy and Atchley (1984) showed that in terms of interlandmark distances, the scapula of rats was a highly integrated structure and function was a major causal factor for shape differentiation. Ventura (1992) studied the on-

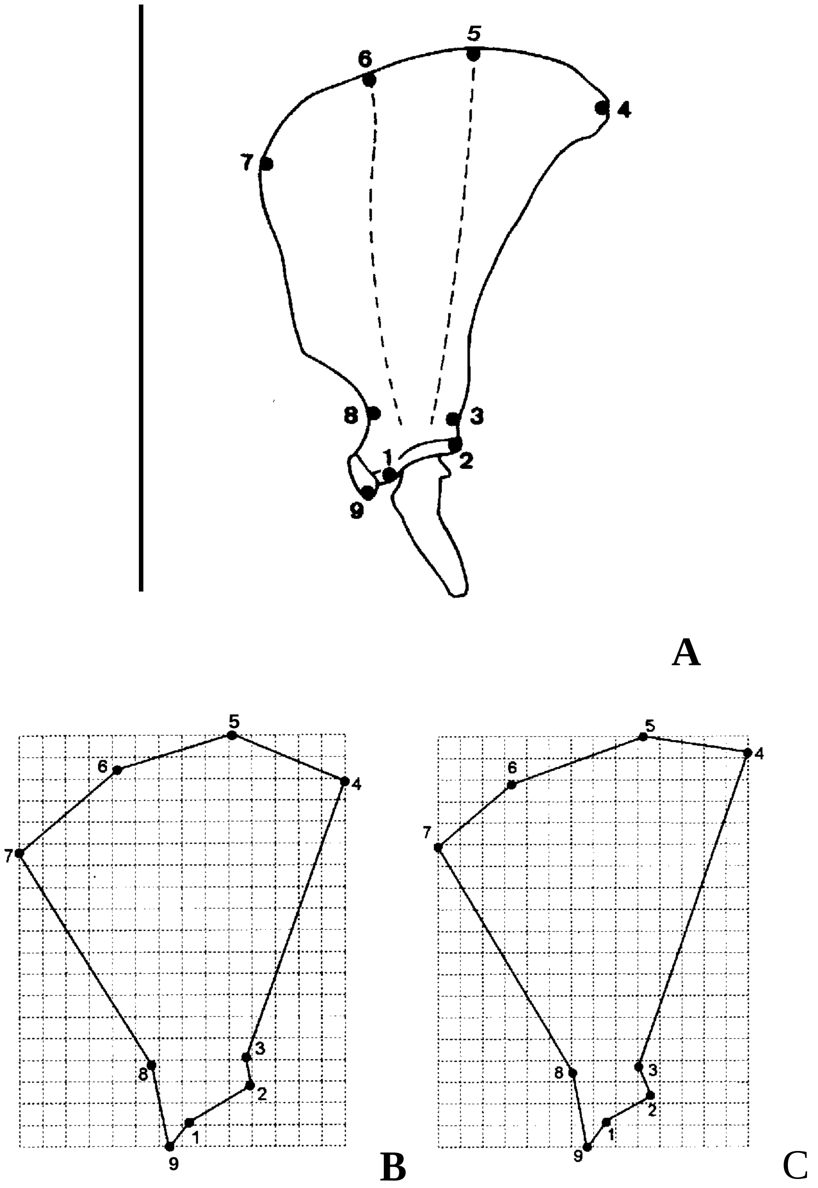

Figure 1. **A)** Scapula of *Euphractus sexcinctus* in medial view showing the landmarks used in this study. Scale bar is 10 cm long. Landmarks are defined as follows: : 1 - anterior extremity of glenoid cavity; 2 - posterior extremity of glenoid cavity; 3 - depression between glenoid cavity and infraspinoun fossa; 4 - teres major process: 5 - intersection between scapular crest and posterior scapular border: 6 - intersection between scapular spine and scapular border between supraspinous and infraspinous fossa; 7 - cranial extreme of insertion of muscle serratus magnus; 8 - coracoidean groove: 9 - coracoid process extremity B) Consensus configuration for the sample of *Euphractus* with a superimposed grid. C) Consensus configuration for the sample of *Dasypus* with **a** superimposed grid.

togenetic variation of scapular shape in *Arvicola*, but his discussion about shape variation was very limited because of the small number of variables used.

The six-banded armadillo (*Euphractus sexcinctus*) occupies a large geographic range lrom the Amazon Basin in Brazil to Northern Argentina (Nowak, 1991). Its preferred habitat are dry savannah or drier parts of wet savannah. The individuals of this species are solitary most of the time, they continually dig the ground searching for food (plant material and insects) and build their own burrows, which are usually one or two meters deep (Nowak, 1991). The long-nosed or nine-banded armadillo (*Dasypus novemcinctus*) is found in the Americas, from south-central and southeastern United States to Peru and Northern Argentina (Nowak, 1991). It constructs burrows 0.5-3.5 m deep which are up to 7.5 m long. The long-nosed armadillos eat mostly animal matter, particularly insects such as beetles and ants (Nowak, 1991). Only older individuals of both species are known to dig regularly for shelter (Ruiz Miranda, pers. obs.).

Monteiro and Abe (1999) have identified different large scale and small scale regions in the scapula of Xenarthran mammals under important functional and phylogenetic influence. respectively. The shape of the scapular blade (a large scale region where most muscles insert and originate) is dependent on functional demands. whereas the shape of the coracoid region (a small scale region) is phylogenetically conservative. The aim of this study is to assess the ontogenetic shape changes in the scapula of a Xenarthran species specialized for digging, and to determine which scapular regions (the large scale functionally important or the small scale phylogenetic conservative) are important in ontogenetic differentiation.

MATERIALS AND METHODS

The sample of scapulae consisted of *27* specimens (14 males. 8 females, and 5 indeterminate) of *Euphractus sexcinctus* from a single locality in the middle of the geographic range of the species (Anápolis, State of Goias, inidwestern Brazil), and 10 specimens (indeterminate sex) of *Dasypus novemcinctus* froni midwestern Brazil, all housed in the mastozoological collection of the Museu Nacional do Rio de Janeiro. The scapulae were photographed in medial view (Fig. 1A). The photographs were digitized by a flatbed scanner and coordinates of 9 landmarks were obtained using the TpsDig program (Rohlf, 1998). Heretofore, I will refer to a configuration of landmarks as a specimen. In the absence of better estimators, centroid size (square root of summed squared distances from each landmark to the configuration mean point. Bookstein, 1991) of the scapulas was used as indicator of specimen age. The *Euphractus* sample ranged from 5.6 to 10.8 in centroid size, whereas the *Dasypus* sample ranged from 5.7 to 11.0 cm in centroid size. Thus. the largest scapula in both samples was approximately twice as large as the smallest one. The specimens were uniformly distributed throughout their size ranges.

Specimens were superimposed using generalized least squares (Rohlf and Slice, 1990) and consensus landmark configurations for each species were estimated (Fig. 1B and 1C). These average shapes were used to construct the tangent space of partial warps and uniform components (Rohlf, 1996) for each species. Global shape variation was estimated by the uniform component scores proposed by Bookstein (1996). Localized shape changes were estimated by partial warp scores (Bookstein, 1991).

To assess sexual dimorphism in scapular shape (for *Euphractus* only), two MANOVAs were performed using sex as an independent variable and the partial warp and uniform component scores as dependent variables. The scores were tested separately to assess differences in uniform (global) versus localized shape changes. Two MANCOVAs were also performed to check for

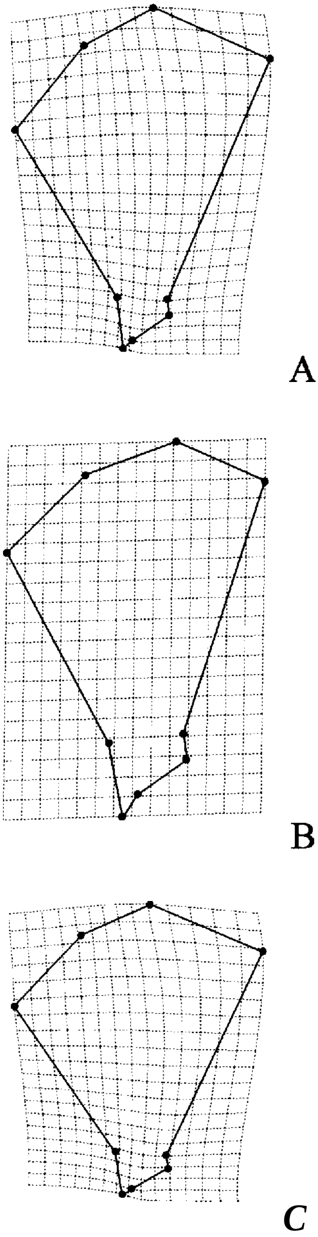

Figure 2. Multivariate regression results of shape on size for the *Euphractus* sample showing predicted shapes for large sizes (magnified 10 times for clarity) for: A) The entire tangent space (partial warps + uniform components). B) The uniform components (uniform subspace) only. C) The partial warps (localized subspace) only.

sexual dimorphism in the ontogenetic shape trajectories, using sex as the independent variable, the partial warps and uniform components as dependent variables, and centroid size as covariate. An ANOVA was used to test for sexual dimorphism in centroid size (also for *Euphractus* only).

The ontogenetic shape changes in the scapula of both species were assessed by a multivariate regression of the partial warp (**W** matrix) and uniform component scores on centroid size. The relative importance of global and localized shape changes was determined by comparing the results of the regression of the partial warps only (localized changes subspace) with the regression of the uniform components added to the **W** matrix of partial warp scores (total tangent shape space). The percentage of shape variance (estimated by Procrustes distances, Monteiro, 1999) explained by size variation was used as a measure of fit of the multivariate regression.

RESULTS

The MANOVAs and MANCOVAs testing for significant differences due to sexual dimporhism in scapular shape and ontogenetic trajectories, respectively. were not significant for either partial warp or uniform component scores (Table 1). *Euphractus* did not show significant differences in size due to sexual dimorphism ($P = 0.1789$). Because of the absence of dimorphism, the males and females were combined in a single sample for subsequent analyses.

The multivariate regression (Table 2) showed significant associations betweem shape variables and size, but the percentages of shape variation explained by size are low. For *Euphractus*, the partial warps alone depict 18.3% of ontogenetic shape variation, whereas the uniform component scores depict only 7.8% of ontogenetic shape variation. The visualization of shape changes linked to ontogenetic transformations are shown in Figure *2*. The most conspicuous scapular shape change in *Euphractus* ontogeny is a localized

Table 1. Results of MANOVAs and MANCOVAs on the *Euphractus* scapular landmarks data set (Sex as factor, Centroid Size as covariate). PW = partial warps; UCOMP = uniform components

Dependent variables	Wilks'Λ	df_1	df_2	*P*
MANOVA				
PW	0.288705	12	9	0.181197
UCOMP	0.781664	2	9	0.096315
MANCOVA				
PW	0.305124	12	8	0.282145
UCOMP	0.852234	2	8	0.237203

Table 2. Results of multivariate regression of scapular shape on centroid size. PW = partial warps: UCOMP = uniform components. The coefficient of determination (R^2) is shown as a percentage of explained shape variation for each model.

W matrix	R^2 (%)	*F*	df_1	df_2	*P*
Euphractus					
PW+UCOMP	26.1	8.7666	14	350	< 0.00001
PW only	18.3	5.5673	12	300	< 0.00001
Dasypus					
PW+UCOMP	25.8	2.7906	14	112	0.0013
PW only	16.5	1.5907	12	96	0.1071

relative expansion of the infraspinal fossa, particularly, the teres major process, which corresponds to the site of origin of the teres major muscle. responsible for limb retraction. The other localized shape change is the relative reduction of the coracoid process, which indicates a reduced growth rate associated with this region. The most important uniform shape change in *Euphractus* is a global anteroposterior elongation of the scapula. In the *Dasypus* sample. the relative contributions are very similar to *Euphractus* (Table 2). However, the uniform components probably plays a more important role in ontogenetic shape changes for *Dasypus*, because when they are removed from the **W** matrix of partial warp and uniform component scores, the regression is no longer significant. The shape changes associated with ontogenetic differentiation in *Dasypus* (Fig. 3) is very similar to the *Euphractus* pattern. The common feature between the two species is the development of the teres major process and the absence of shape changes related to the coracoid region and glenoid cavity. The differences between the ontogenetic trajectories of the two species are found mostly in the uniform components. In *Euphractus*, the uniform components depict an anteroposterior scapular elongation, whereas in *Dasypus* they show a shearing where landmarks in the anterior border are displaced forward and landmarks in the posterior border are displaced backwards.

DISCUSSION

The absence of sexual dimorphism in scapular size and shape is not uncommon in mammals (Taylor and Siegel, 1995; Ventura, 1992). However, Petrov (1992) found

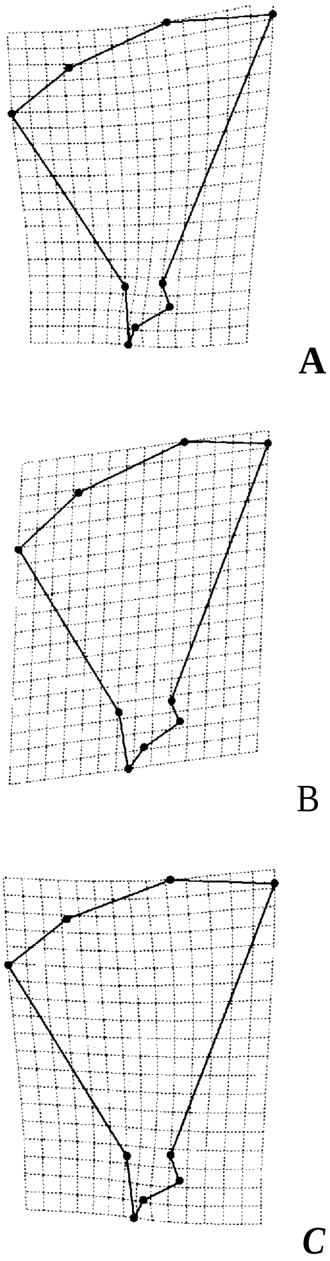

Figure 3. Multivariate regression results of shape on size for the *Dasypus* sample showing predicted shapes for large sizes (magnified 10 times for clarity) for: A) The entire tangent space (partial warps + uniform components). B) The uniform components (uniform subspace) only. C) The partial warps (localized subspace) only.

significant sexual dimorphism in scapular size in *Felis silvestris*. Because the scapula is a plastic structure (Kimes et al., 1981), any behavioral or size dimorphism may lead to a sexual dimorphism in large scale scapular shape.

There is large body of experimental evidence that the shape of certain bony structures can be altered by the atrophy or hypertrophy of attached muscles (Gans, 1972). Because the scapular blade lies in the center of a functionally important field of forces, its shape is largely dependent on the force exerted by muscles that insert and originate there. Kimes et al. (1981) induced changes in the scapular morphology of mice by behavioral modifications. Lehmann (1963) noticed that specialist species are distinguished from related generalists by the enlargement of certain specific muscle attachment sites on the scapula. Particularly. fossorial rodents can be distinguished from other rodent species by the enlarged teres major process.

The large development of the teres major process during development of the scapula in *Euphractus sexcinctus* and *Dasypus novemcinctus* is probably a function of the increased demand for digging (young individuals do not dig regularly). The global increase in the anteroposterior relative length and the uniform shearing increase the moment arm of this same muscle in both species during ontogeny. Although the shape of the scapular blade is largely modified during ontogeny, the small scale region composed by the coracoid process and the glenoid cavity changes very little (at least in the plane sampled by the landmarks). The uniform transformations do not imply large modifications to the coracoid, because the displacement of landmarks in a uniform shape change is dependent on the distance from the landmarks to the major axis of the configurations (Bookstein, 1996). In the case shown here, the landmarks in the localized small scale region of the coracoid are very close to the major axis of the landmark configurations, therefore, the uniform changes are not associated with modifications of this region as much as with the large scale region of the scapular blade.

The enlarged teres major process that characterizes the scapula of armadillos (Monteiro and Abe, 1999) is acquired during ontogeny. There are however, shape differences in the coracoid region that characterize the armadillos as a group, which are independent of the shape changes in the scapular blade (Monteiro and Abe, 1999). The reason for this conservativeness might probably be found in Walker and Liem's (1994) statement that the coracoid process was reduced in relative size and importance after the changes in limb position and movements during early mammal evolution. Due to the spatial nature of the methods of geometric morphoinetrics, and the possibility of decomposition of shape changes into components of varying scale levels, further research in the application of these methods to model systems might produce interesting results for the study of factors influencing the differentiation and integration of morphogenetic components during the development of complex morphological structures.

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