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No Directional Scapular Asymmetry among Tamarines of the Genus *Saguinus* (Primates: Callitrichidae)

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors designed the study, wrote the protocol, managed the literature searches and read and approved the final manuscript. Author PMPC performed the statistical analysis and managed the analyses of the study.

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ABSTRACT

Bilateral asymmetry is defined as a deviation of a whole organism or a part of it from a perfect symmetry, and different categories can be recognized. One is the fluctuating asymmetry, defined as the random developmental variation of a trait (or character) that is expected to be perfectly symmetrical on average, and the other one is directional asymmetry, which occurs when one of the sides shows stronger morphological structures or marks than the other. The aim of this study was to determine the kind of scapula asymmetry in *Saguinus* scapulae. On lateral surface of each right and left scapula, a set of 5 landmarks and 3 curves with semi-landmarks along the margins, on a sample of 16 pairs from different *Saguinus* species, were considered. Asymmetries (fluctuating and directional) on size and shape of the scapulae were analysed by means of geometric morphometric methods. Directional asymmetry was not detected, demonstrating no side scapular shape bias. The absence of significant directional asymmetry may indicate a similar contralateral pattern of employment of the shoulder, at least for one-arm vertical suspension, as it needs stronger forces

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than those for terrestrial locomotion and thus would cause more asymmetry in case side loadings were different. To our knowledge, this is the first investigation on the symmetrical/asymmetrical nature of scapulae in *Saguinus*. Our findings increase knowledge and understanding of humeral joint and arboreal locomotion in primates.

Keywords: Handedness; laterality; Neotropical primates; one-arm vertical suspension; shoulder joint.

1. INTRODUCTION

Geometric morphometrics methods (GMM) improve the morphometrics as it has the ability to measure displacements, deformations and rotations [1], enabling a more complete evaluation of shape than traditional linear and angle measurements [2]. In recent years, there have been a huge number of zoological studies carried out with the applications of GMM which between other research questions, have been applied to study symmetries [3] [4].

Bilateral asymmetry is defined as a deviation of a whole organism or a part of it from its perfect symmetry [5]. Two forms of bilateral symmetry are commonly distinguished: matching symmetry, where the two mirror images are considered separated parts of the structure (for instance paired long bones), and object symmetry, where the two mirror images are located at each side of a median (for instance skull) [6]. In both cases, different categories of asymmetry can be recognized. One is the fluctuating asymmetry (FA), defined as the random developmental variation of a trait (or character) that is expected to be perfectly symmetrical on average. The other one is directional asymmetry (DA), which occurs when one of the sides shows stronger morphological structures or marks than the other [7]. Since the mammal body is bilaterally symmetrical in most the body parts at least at birth [8], it is notable that most of the internal organs such as heart, lungs, kidneys and stomach as well as the brain present DA [9] [10].

Tamarins or long-tusked marmosets belong to genus *Saguinus*, platyrhine primates of the family Callitrichidae which are closely related to the Lyon tamarins of the genus *Leontopithecus* [11] [12]. They are predominantly arboreal and found in the forests of South and Central America -from the Amazon basin, Guianas to northern Colombia and Panama- [13] [14] [12]. They have quadrupedal locomotion and the displacement among the trees is mainly performed with jumps, however they suspend and walk on the branches with their four limbs into the branches of the trees [14].

Any study on this genus is important, since some of its species are included by the IUCN (International Union for Conservation of Nature and Natural Resources) on the list of endangered species [14]. The aim of this study was to determine the kind of scapula matching asymmetry in a sample of *Saguinus* scapulae. To our knowledge, there has not been a thorough investigation on the symmetrical/asymmetrical nature of this bone in these primates.

2. MATERIALS AND METHODS

A total of 16 pairs of adult dry scapulae of various species of the genus *Saguinus*, in good preservation state, were studied:

Saguinus imperator	1
Saguinus leucopus	8
Saguinus midas	2
Saguinus nigeur	1
Saguinus oedipus	1
Saguinus sp.	3

Bones that had evidence of trauma, malformations or other pathologies were excluded. Specimens are currently deposited in the collection of the *Museu de Zoologia de Barcelona* (Catalonia, Spain), and the Veterinary Anatomy Laboratory of the Faculty of Veterinary Medicine and Zootechnics of the *Universidad del Tolima* (Ibagué, Colombia).

The scapulae were fixed medially to make it easier for the lateral plane to be parallel to the camera's focal plane. A millimeter pattern was included in each image. A photograph of each pair on their lateral surface was obtained with a Nikon digital camera (D5100) equipped with an objective AF-S DX Micro Nikkor 40 mm f/1·2.8 G.

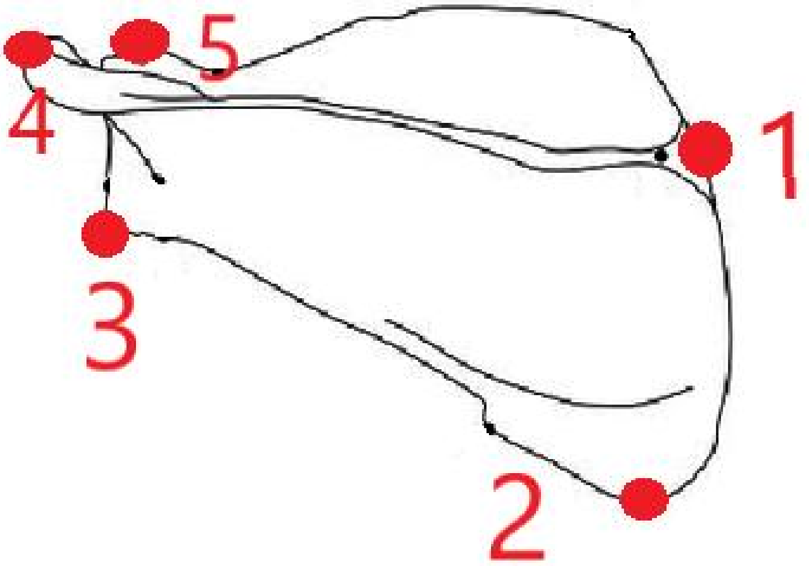

Fig. 1. The set of landmarks and semi-landmarks along the scapula of each side in *Saguinus*. A total of 5 landmarks were located on each scapula: point on the vertebral margin where the long axis of the scapular spine and the vertebral border meet (1), inferior angle (2), inferior-most point on glenoid fossa (3), distal-most point of the acromion (4) and coracoid prominence (5). A set of 3 curves with 7, 15 and 25 semi-landmarks along the dorsal, lateral and medial margins respectively was also considered to define these curves

A total of 5 landmarks were located on each scapula: inferior-most point on glenoid fossa, coracoid prominence, distal-most point of the acromion, inferior angle and point on the vertebral margin where the long axis of the scapular spine and the vertebral border meet (Fig. 1). As no reliable method exists to measure margins because of problems in defining the bony curved boundaries, a set of 3 curves with 7, 15 and 25 semi-landmarks along the dorsal, lateral and medial margins were also considered (Fig. 1). Landmarks and semi-landmarks were obtained in each scapula with the application of the software tpsDig2 v. 2.16 [15]. Semi-landmarks were transformed to landmarks with the program tpsUtility v. 1.70 [15].

Two replicas were obtained for each individual carried out by the first author. To assess whether the variation between the two spaces (Euclidean and tangent) was minimal, correlations between the tangent distances and the Procrustes distances spaces were also computed using the tpsSmall v. 1.33 application [16]. The result of this correlation (0.99998) confirmed that both spaces were almost identical. Anatomical landmarks were aligned using a Procrustes superimposition. This mathematical procedure estimates size as the square root of the sum of squared distances from the centroid of a landmark configuration. This is called centroid size. It should also be noted that with this type of test, highly significant individual variation can be found despite large measurement error. Therefore, we used the proportion of sum of squares accounted for by individual-by-side interaction.

Data was analysed in MorphoJ software v. 1.6.0c [17] and PAST v. 2.17c [18]. The statistical significance level was set at 95%.

3. RESULTS

3.1 Measurement Error

The ANOVA tested whether individual variation was significantly larger than error. Error was not a serious concern in this analysis as in both ANOVA tests for centroid size and shape, as the mean square value for the individual-by-side interaction was much larger as the variation between replicates images (Table 1).

3.2 Asymmetries

All pairs of scapulae were subjected to Procrustes superimposition (Fig. 2). The *p*-values in the shape analysis showed that FA was significant statistically, but individual effects and DA were not detected (Table 1).

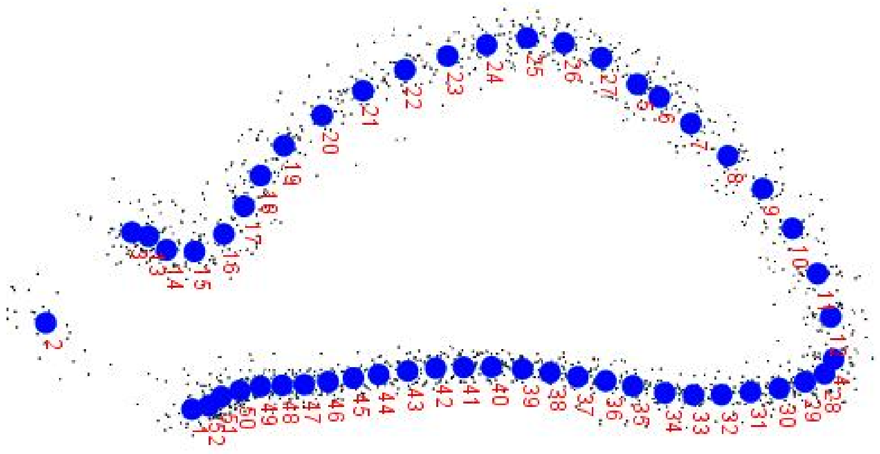

Fig. 2. Procrustes superimposition after semi-landmarks transformation for both right and left scapulae of *Saguinus*. Large filled dots are the average configuration

Table 1. ANOVA results for pure size and shape. The model allows simultaneous evaluation of the effect of side (directional asymmetry), individual*side interaction (fluctuating asymmetry) and the individual

Centroid size					
Effect	SS	MS	df	F	P
Individual	919223.969378	61281.597959	15	192.10	<.0001
Side	132.607734	132.607734	1	0.42	0.5288
Individual*side	4785.206300	319.013753	15	95825.88	<.0001
Error	0.106531	0.003329	32		
Shape					
Effect	SS	MS	df	F	P
Individual	0.35872141	0.0002391476	1500	1.04	0.2482
Side	0.02039580	0.0002039580	100	0.88	0.7855
Individual*side	0.34633655	0.0002308910	1500	569.78	<.0001
Error	0.00129674	0.0000004052	3200		

**side interaction (fluctuating asymmetry). SS: sum of squares; MS: mean squares; df: degrees of freedom; F: value of the statistics F; SS and MS are expressed in units of distances Procrustes (i.e. dimensionless). The mean square value for the individual; *side interaction was much larger as the variation between replicates for both size and shape*

4. DISCUSSION

Directional asymmetry corresponds to a pattern of asymmetry observed in a sample of individuals, where a statistically difference between sides, with the side that is larger being generally the same [19]. The Procrustes ANOVA for shape showed significant *p*-values only for individual-by-side interaction and for shape variation between individuals, which means that shape DA was not detected. FA can be explained by a random effect. The absence of DA may indicate a similar pattern of employment of the shoulder.

The scapulothoracic joint has no solid skeletal connection to the vertebrae, that is, the forelimb's attachment to the trunk is based on muscles [20], mainly the *m. serratus ventralis thoracis* and *cervicis* and *rhomboideus* muscles [21] [22]. These muscles would present similar biomechanical charges for right and left shoulder, at least during displacements other than quadrupedal walking, such as suspension and brachiation (arboreal arm swinging), as this advance requires stronger forces than phases in which hindlimbs are highly loaded [21]. Even to support the biomechanical charges, the scapula is complemented on its dorsal margin with a scapular cartilage where the rhomboideus muscles insert, as such it has been demonstrated in one species of the genus *Saguinus* [22]. On the other hand, the intrinsic shoulder muscles in the genus *Saguinus* are adapted to support the charges during quadrupedal locomotion to climb and walk on the branches of the trees [23] [24] [25].

In fact, among Primates, the shoulder complex includes more than 20 muscles (the exact number depending on the particular species) [26]. Furthermore, one might expect increased forces in forelimbs than in hindlimbs for these arboreal species, due to the need to interact with substrates arranged three-dimensionally around the body.

In the common chimpanzee (*Pan troglodytes*), most muscle groups from the left forelimb exhibit greater masses than right groups, but this group asymmetry is significant only for the manual digital muscles [27]. Manual laterality of cotton-top tamarins (*Saguinus oedipus*) has been observed for grasping for food but not for one-arm vertical suspension [28]. So symmetrical muscular loadings would be reflected as symmetrical contralateral shapes. Handedness has been described in cotton-top tamarins (*Saguinus oedipus*) [13] [29]. In *Saguinus* scapulae it appears no sidedness, considered as this sidedness would be expressed as a bilateral asymmetry of this bone. We argue that if muscular mechanical effects are the main responsible of bony asymmetries, in scapulae these muscular loads are not strong enough to determine different bony conformation and consequently, different contralateral bony shape via enthesis.

In conclusion, although it has been described that some *Saguinus* can show manual preferences [28] [20] [30] [31], this laterality would not be expressed for one-arm suspension, e.g. muscular forces would be evenly distributed between sides for work related to in that kind of arboreal displacement. But this hypothesis needs to be confirmed through further behavioural studies.

5. CONCLUSIONS

- Directional asymmetry was not detected in *Saguinus* scapula, demonstrating no side scapular shape bias.
- This absence may indicate a similar contralateral pattern of employment of the shoulder, at least for one-arm vertical suspension, as it needs stronger forces than those for terrestrial locomotion and thus would cause more asymmetry in case side loadings were different.
- In any case, our findings increase our knowledge and understanding of scapular joint in primates, which creates biomechanical considerations for shoulder assessment in Neotropical primates.

ETHICAL APPROVAL

This study was carried out on scapulas from existing osteological public collections, so an Ethics committee agreement was considered to be unnecessary.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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