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More Splanchnocranial than Neurocranial Differences in Two Species of *Sylvilagus* Gray, 1867 (Lagomorpha: Leporidae)

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Abstract

The aim of this study was to explore and compare patterns of morphological covariation of two basal skull osseous modules - splanchnocranium and neurocranium - in two different species of *Sylvilagus*, a leporid genus found in the New World. For this, digital pictures of the ventral aspect of skulls from 26 *S. brasiliensis* and 12 *S. floridanus* were studied by means of geometric morphometric methods, a multivariate, landmark-based approach to evaluate differences. A set of five landmarks was located on the horizontal plane of the splanchnocranial ventral bones (palatine process of the maxillary bone [*processus palatinus maxillae*] + palatine bone [*lamina horizontalis ossis palatini*]), and a set of seven landmarks was placed on the neurocranium (sphenoid [*os sphenoidale*] + basilar part of the occipital bone [*pars basilaris*] + *bulla tympanica*). From the obtained results, interspecific basal skull form (size and shape) differences are present. Shape differences between species are more marked on the splanchnocranial module than on the neurocranial one. Differences between *S. brasiliensis* and *S. floridanus* can be explained by feeding differences between both species.

Keywords: eastern cottontail; forest rabbit; palatine morphology; phylogeny; skull; tapiti

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1. Introduction

Evolutionary anatomical relationships among mammals are normally difficult to determine. Among the mammals with significant knowledge gaps are rabbits and hares (family Leporidae) [1]. In this family, there are different species of cottontail in the genus *Sylvilagus* [2]. Most of these species have stub tails with white undersides, which they show when they retreat, giving them their characteristic vernacular name. Cottontails are found in the New World [3,4], inhabiting a wide variety of habitats [5,6].

Speciation and subspeciation are prominent within this genus [7,8]. The Eastern cottontail (*Sylvilagus floridanus* Allen, 1890) is distributed over broad geographic areas from southern Canada to northwestern South America, including Cuba [4,9]. It inhabits arid and semiarid tropical regions, with an altitudinal range from sea level to approximately 1,000 meters above sea level, preferring dense and thorny thickets bordering open fields or savannas and scattered hedges and shrubs of scrub landscapes [10]. Another species of cottontail is the tapiti or forest rabbit (*Sylvilagus brasiliensis* Linnaeus, 1758), which is found from northern Mexico to western Guatemala [4,6]. It lives in tropical and temperate forests and in swamps, savannas, scrublands, and deserts, its presence being most evident in forest clearings and natural grasslands [10].

S. floridanus is large-sized, measuring 36–48 cm, with an average body weight of 1,300 g [4]. *S. brasiliensis* is small to medium-sized, with a head-body length of 320 mm and an average body weight of 934 g, and has been less studied than the former [8].

In South America, nine subspecies of *S. floridanus* and 22 subspecies of *S. brasiliensis* have been identified. Among these, the latter is the least studied.

The skull plays an important role in the study of evolutionary development of mammals. Anatomically, the cranium among vertebrates is divided into the brain case (neurocranium) and the pharyngeal arch skeleton (splanchnocranium) [11,12]. The ventral part of the neurocranium includes the ethmoid, the temporal, and the basilar part of the occipital bones [11]. The ventral part of the splanchnocranium includes, among others, the palatine process of the maxilla and the palatine bone [11], which constitute most of the hard palate and floor of the nasal cavity.

The ecomorphological adaptations of the genus *Sylvilagus* have not been investigated. In this research, the focus of the study is on the ventral skull osseous modules of the *Sylvilagus* skull using geometric morphometric methods, a multivariate, landmark-based approach, to evaluate whether splanchnocranial and neurocranial modules can discriminate *S. brasiliensis* and *S. floridanus*.

2. Materials and Methods

2.1 Sample Composition

Skulls examined in this study were from the mastological collection of the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia in Bogotá, Colombia. Specimens had been collected from different localities in Colombia and included a total of 38 *Sylvilagus* (26 *S. brasiliensis* – 9 ♀, 16 ♂, and one of unknown sex – and 12 *S. floridanus* – 4 ♀, 5 ♂, and 3 of unknown sex). No information on subspecies was available.

2.2 Imaging

Each skull was photographed at high resolution in a standardized ventral view with a Nikon® D70 digital camera (image resolution of 2,240 × 1,488 pixels) equipped with a Nikon AF Nikkor® 28–200 mm telephoto lens. Focal length, f-stop, and lighting conditions were adjusted for each image to avoid shadows and excessive grain. A scale in centimeters was included in each photo by placing a ruler parallel to the longitudinal axis of the skull. The images were subsequently stored in JPG format. For each specimen, the skull was leveled to obtain a parallel view.

2.3 Landmark Selection

A set of five landmarks (three sagittal and two bilateral) was located on the horizontal plane of the ventral splanchnocranial bones, and a set of seven landmarks (five sagittal and two bilateral) on the ventral neurocranium (Figure 1 and Table 1). The x and y coordinates of these landmarks were digitized from the images using TpsDig v. 1.40 [13]. Digitizations were performed twice to assess measurement error. Landmarks were superimposed using Generalized Least Squares Procrustes analysis, which removes information about location and orientation from the raw coordinates and scales each specimen to unit centroid size (CS). CS is defined as "the square root of the sum of squared distances of the set of landmarks from their centroid" [14]. The resulting Procrustes shape coordinates and CS were used for statistical analyses. A Mann–Whitney U test was applied to detect differences in CS for both modules between the two sexes.

2.4 Multivariate Analysis

Differences between replicates and sexes were tested with a two-way PERMANOVA, using Bray–Curtis distances and 9,999 permutations. A Mann–Whitney U procedure was applied to detect differences in CS for both modules between the two species. Then a multivariate regression of shape coordinates was used for the symmetric component on the logarithm of CS for each block to test for the potential influence of allometry, i.e., how differences in size can affect shape. To avoid bias resulting from asymmetries, the symmetric component was extracted (via reflection and averaging of bilateral landmarks).

These analyses were performed separately for the set of landmarks of the splanchnocranial bones (palatine process of the maxillary bone [*processus palatinus maxillae*] + palatine bone [*lamina horizontalis ossis palatini*]) and of the neurocranium (sphenoid [*os sphenoidale*] + basilar part of the occipital bone [*pars basilaris*] + *bulla tympanica*).

Multivariate methods were employed to investigate shape variation, specifically using Principal Component Analysis (PCA) to assess it. Because PCA considers shape variation across the entire sample, discriminant function analysis, Canonical Variate Analysis (CVA), and Discriminant Analysis (DA) were additionally used to emphasize differences between predefined groups.

Table 1: Landmarks used in this study; a set of five landmarks (1 to 3, 8 and 9) were located on the horizontal plane of the splanchnocranial bones (maxillary bone [*processus palatinus maxillae*] + palatine bone [*lamina horizontalis ossis palatini*]), and a set of 7 landmarks (4 to 7, and 10 to 12) on the neurocranium (*sphenoides* + *basioccipital*).

Landmark	Anatomical location	Module
1	Midsaggital ventral line between palatine fissuras (*fissura palatina*)	Splanchnocranium
2	Midsaggital ventral line on the suture between the maxillary bone (*processus palatinus maxillae*) and palatine bone (*lamina horizontalis ossis palatini*)	Splanchnocranium
3	Alveolon: midsaggital ventral line on the most caudal margin of palatine bone	Splanchnocranium
4	Hormion: midsaggital ventral line on the most rostral margin of presphenoides bone (*corpus ossis presphenoidalis*)	Splanchnocranium
5	Midsaggital ventral basilar (*os sphenooccipital*) suture.	Splanchnocranium
6	Midsaggital ventral line on the suture between pre and basisphenoides bones	Neurocranium
7	Basion: midsaggital ventral line on the most rostral margin of foramen magnum (*foramen [occipitale] magnum*)	Neurocranium
8, 9	Greater palatine foraminas (*foramen palatinum majus*)	Neurocranium
10	Midsaggital ventral line on the most caudal margin of foramen magnum (*foramen [occipitale] magnum*)	Neurocranium
11, 12	Holes in the bulla timpanica (*bulla tympanica*)	Neurocranium

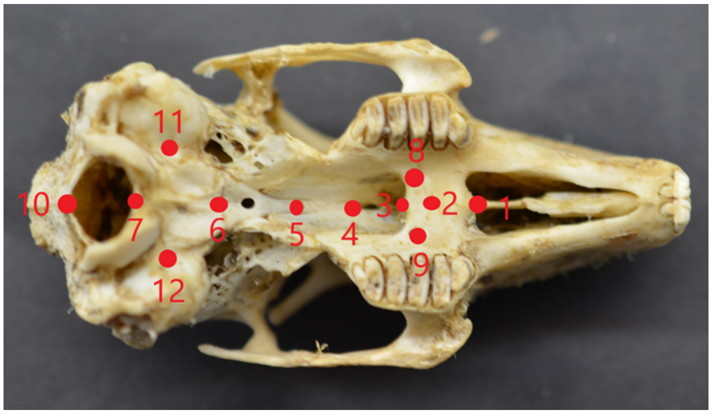

Figure 1: Ventral view of the skull showing the landmark locations used in this study.

The morphometric data were reduced using PCA, which allowed us to study the global variation of the landmark configurations and identify the most important trends in palatine shape. The shape trends, corresponding to the Principal Component axes (PC), were visualized using thin-plate spline reconstructions of the shapes. This method enables a thorough visualization of shape changes. CVA with 10,000 permutation rounds among groups was performed on the regression scores (representing size-corrected shape variables), and Mahalanobis distances (MhD) were obtained. CVA projects a multivariate dataset down to two or more dimensions in a way that maximizes separation between three or more given groups. DA was then used to verify whether the skull shapes of the two sampled groups were significantly different and diagnosable using a cross-validation classification test.

All analyses were performed using the MorphoJ v. 1.06c [15] and PAST v. 4.17c [16] packages. A p-value of < 0.05 was considered statistically significant. This probability was estimated by 9,999 random permutations.

2.5 Ethics Statement

No permits were required for this study, as the researcher worked with an existing public osteological collection.

3. Results

3.1 Differences Between Replicas

No significant difference was found between the repeated replicates, indicating that measurement error was small (Table 2). Sex differences were not statistically significant, so sexes were pooled for further analyses.

3.2 Size Differences Between Species

Skull CS was statistically different between species (Mann–Whitney U = 228; p << 0.0001), with the CS of *S. brasiliensis* being smaller than that of *S. floridanus*.

3.3 Allometric Trend

Allometric analysis showed allometric growth among individuals (p < 0.01), with 6.44% of the shape explained by size for the splanchnocranial bones (Figure 2) and 27.08% for the neurocranium (Figure 3). Allometries were similar for both species (p = 0.392).

3.4 Canonical Variate Analysis (CVA) and Discriminant Analysis (DA)

According to the results of the CVA on residual scores, significant differences were found in basal aspect shape for both modules analyzed separately (p < 0.0001). Inter-species differentiation was greater for the splanchnocranium than for the neurocranium (MhD = 1.930 and 1.584, respectively). In the DA for the neurocranium, 17.3% and 29.2% of *S. brasiliensis* and *S. floridanus*, respectively, were incorrectly classified. For the splanchnocranium, 15.4% and 8.3% of *S. brasiliensis* and *S. floridanus*, respectively, were incorrectly classified (Table 3).

3.5 Principal Component Analysis (PCA)

PCA for the neurocranium showed that the first two PCs explained 74.39% of the total observed variance (PC1 + PC2 = 53.44% + 20.95%) (Figure 4). The landmarks with the highest loadings were those on the most caudal margin of the foramen magnum, the hormion, and the openings in the bulla tympanica (Figure 5). The first two PCs explained 78.36% of the total observed variance in the splanchnocranium (PC1 + PC2 = 44.15% + 34.21%) (Figure 6). The landmark with the highest loading was that on the suture between the maxillary bone and the palatine bone (Figure 7).

Table 2: Two-way PERMANOVA between replicas and sexes for 26 *S. brasiliensis* (9 ♀, 16 ♂ and 1 of unknown sex) and 12 *S. floridanus* (4 ♀, 5 ♂ and 3 of unknown sex), using Bray-Curtis distances and 9,999 permutations.

Source	Sum of squares	Df	Mean square	F	p
Replica	1.22E+30	1	1.23E+30	3.094	0.448
Sex	3.92E+30	2	1.96E+30	4.945	0.399
Interaction	-3.78E+30	2	-1.89E+30	-4.779	0.744
Residual	2.77E+31	70	3.96E+29	-	-
Total	2.91E+31	75	-	-	-

Table 3. Discriminant analysis for neurocranium and splanchnocranium from 26 *S. brasiliensis* and 12 *S. floridanus* (two replicas/specimen).

Neurocranium	*S.brasiliensis*	*S.floridanus*	Total
S.brasiliensis	43 (82.7%)	9 (17.3%)	52
S.floridanus	7 (29.2%)	17 (70.8%)	24
Splanchnocranium			
S.brasiliensis	44 (84.6%)	8 (15.4%)	52
S.floridanus	2 (8.3%)	22 (91.6%)	24

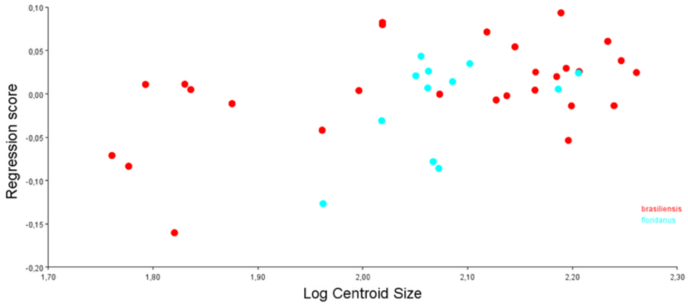

Figure 2: Allometric trend among individuals (p<0.005) for splanchnocranium from 26 *S. brasiliensis* and 12 *S. floridanus*; a 6.44 % of the shape was explained by size; regression scores represent size-corrected shape variables; regression was significative (p=0.0021).

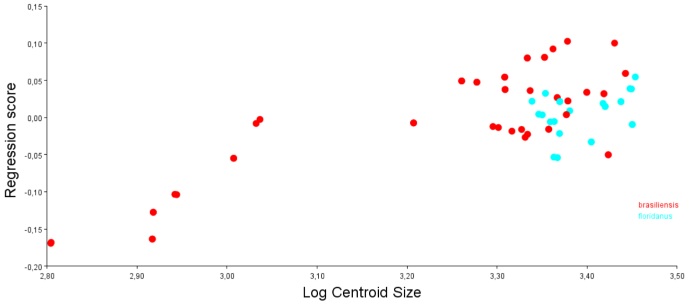

Figure 3: Allometric trend among individuals (p<0.005) for the neurocranium from 26 *S. brasiliensis* and 12 *S. floridanus*; 27.08% of the shape was explained by size; regression scores represent size-corrected shape variables; regression was significative (p<0.001).

4. Discussion

Skull morphology is crucial in the study of mammals. Environmental factors such as climate and subsistence strategies contribute to cranial form variation among related species. In this research, the aim is to assess the morphological interspecific skull differences between *S. brasiliensis* and *S. floridanus* by studying separately two ventral osseous modules: the splanchnocranium and the neurocranium. A geometric morphometrics approach was used,

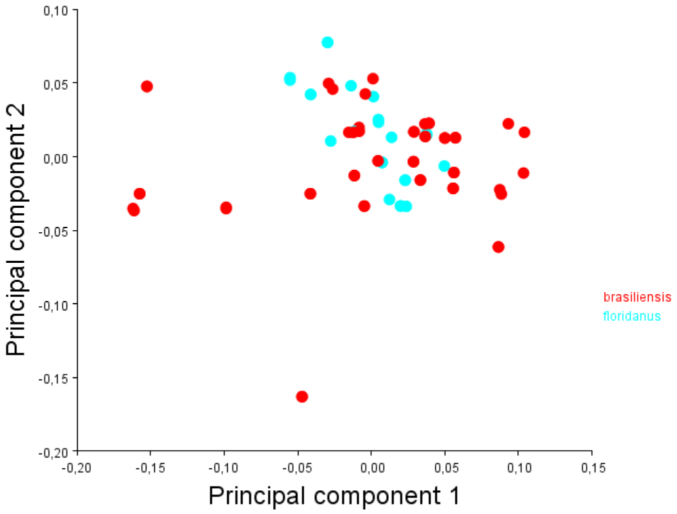

Figure 4: Principal component analysis for neurocranium from 26 *S. brasiliensis* and 12 *S. floridanus*; two first PCs explained 74.39% of total observed variance (PC1+PC2 = 53.44%+20.95%).

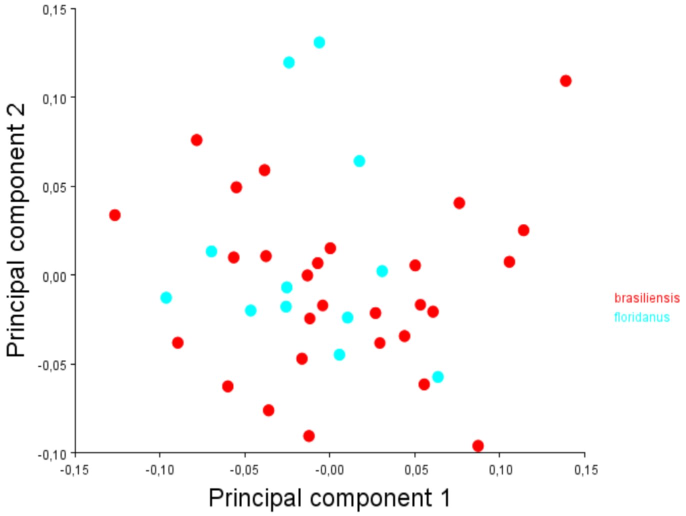

Figure 6: Principal component analysis for splanchnocranium from 26 *S. brasiliensis* and 12 *S. floridanus*; two first PCs explained 78.36% of total observed variance in splanchnocranium (PC1+PC2 = 44.15%+34.21%).

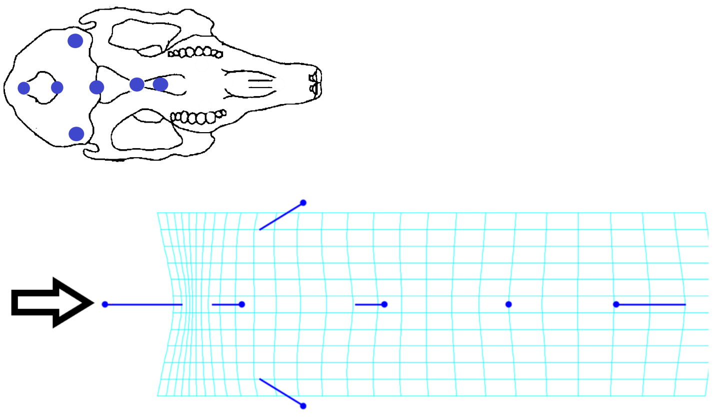

Figure 5: Thin plate spline representation of neurocranium on principal component 1; landmark with highest loading was that on the most caudal margin of foramen magnum (arrow) and hormion, which showed an elongation; holes in the bulla tympanica showed a widening.

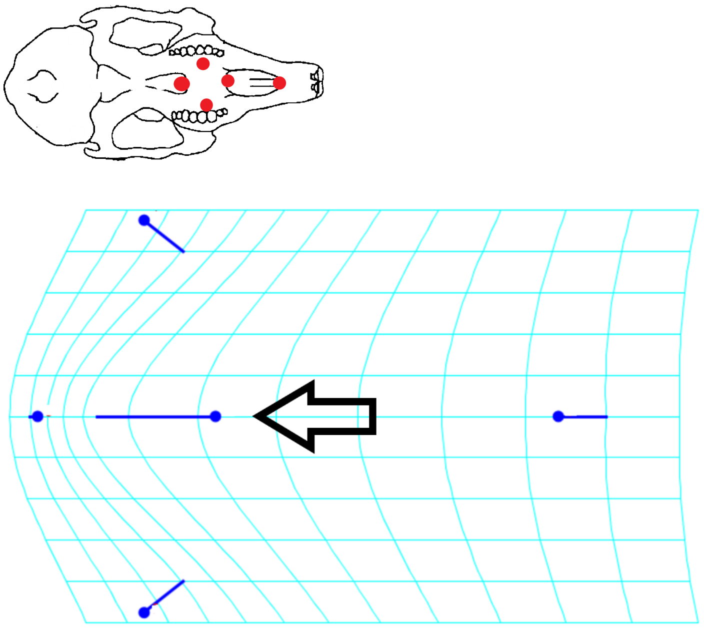

Figure 7: Thin plate spline representation of splanchnocranium on principal component; landmark with highest loadings was that on the suture between the maxillary bone and palatine bone (arrow), which tended to elongate.

which allowed the evaluation of shape patterns in skull structures by preserving the geometric or spatial relationships of landmarks throughout the analysis, something that traditional linear cephalometrics are poorly equipped to quantify [17].

Geometric morphometrics showed no association between differences in skull shape and sex. Species of *Sylvilagus* show varying levels of sexual dimorphism, with most species having females that are slightly larger than males (although there are exceptions and variation within the genus). This trend of females being larger in cottontails is associated with high female reproductive capacity and the fast growth of their offspring. Splanchnocranium and neurocranium do not increase proportionally with changes in skull size, but in *S. brasiliensis* and *S. floridanus*, existing sexual size differences do not seem to be sufficient to affect skull form between males and females [18].

A distinct difference in the geometric shape of the skull was observed between species, with length being the distinguishing feature. Biological traits are not independent variables [19]. Phylogeny can introduce morphological covariation indirectly through factors such as lifestyle and size [19]. The difference in shape is likely a response to differences in body size, but also to natural adaptations (in northwestern South America, habitats of tapitis and cottontails are mutually exclusive [10]). *Sylvilagus* rabbits are generalist plant-eating animals whose diet changes with the seasons and depending on the species. In warmer months, they mainly eat grasses, clover, leaves, and weeds, while in winter they consume woody materials like twigs, buds, and bark. They are opportunistic feeders, consuming a variety of plant parts including sprouts, fruits, and even garden vegetables, and they obtain water from their food and from dew. The subunits in this structure (mainly the oral structures) are related to trophic functions, but also to sensory functions, so they might have undergone directional selection as well.

In biological morphology, allometry is the study of how the size of a structure or organism relates to its shape. In general, a phylogenetic correlation with shape variance is difficult to establish for a diverse leporid group like *Sylvilagus*; they inhabit heterogeneous environments and adopt various lifestyles. From the results presented here, it can be inferred that natural selection may dilute this effect, but only to a certain extent, with developmental influences still being observed in this group. Allometry would have the power to direct the morphological changes in *Sylvilagus*. The large proportion of shape change in the oral structure could probably be attributed to the prominent oro-caudal elongation of the skull in the larger species, *S. brasiliensis*. The relatively lower proportion for the neural module is possibly evidence of its conservative nature. The different allometries between both species would also indicate that allometric changes have likely diverged greatly at different phylogenetic levels. The *Sylvilagus* skull might have evolved as a mosaic of characters composed of parts showing convergence mostly determined by size differences, with other parts showing less. Thus, the allometric effect cannot be underestimated. Determining the importance of allometry in the genus requires increased species sampling in further analyses.

From the obtained data, it can be concluded that the splanchnocranium showed more morphological differences between the two species than the neurocranium. Some studies outline that, among humans, changes in diet are linked to the gracilization of the masticatory apparatus [20]. There are dietary differences between species of *Sylvilagus* [21,22]. *S. brasiliensis* forages on green vegetation of grass and shrubs, while *S. floridanus* has a more varied diet, including trunks and branches. Thus, it would be logical to assume that, if there are differences in diet, splanchnocranium differences between *S. brasiliensis* and *S. floridanus* can be explained by those different feeding strategies.

The neurocranium is regarded as the rostral continuation of the vertebral column containing the central nervous system [12]. It ossifies early during craniofacial development [23] and, being centrally located in the skull, it is thought to act as a structural "nucleus" that organizes later growth of the skull skeleton [24]. Consequently, it is less subject to postnatal changes than the splanchnocranium and is therefore phylogenetically more conservative between species. The neurocranium can be more conservative and less prone to show differences between species. As it is not involved in feeding, it might be assumed that this structure is much more conservative and less influenced by lifestyle adaptations. The possible changes that may occur between species could likewise affect the splanchnocranium more than the neurocranium.

Moreover, morphological adaptive processes in the splanchnocranium rather than in the neurocranium are the main drivers of *Sylvilagus* diversity, with neurocranial traits perhaps being less useful to differentiate species of this genus. The researcher suggests focusing more on the visceral skull as an approach to morphometric phylogenetic studies in the genus *Sylvilagus*, as it can reflect ecomorphological adaptations. By integrating phylogenetic history with the geometric morphometric data, it would probably be shown that the *Sylvilagus* neurocranium exhibits a weaker phylogenetic signal and is more conservative than the splanchnocranium.

Nevertheless, it must be noted that this study employed unbalanced group sizes. With only 12 individuals, the form variation for *S. floridanus* may not be adequately captured, potentially leading to an over-optimistic or unreliable classification result. Another risk lies in the methodology of outcome measurement, as the study inferred variation in skull shape using only a small set of fixed landmarks, limiting the overall information about the full shape. In future studies, this limitation can be addressed by positioning sliding and surface semi-landmarks within the predefined boundary landmarks on curved surfaces. Furthermore, the intrinsic limitation of methods that rely on landmarks is that variations in areas of the shape farther from the landmarks are captured less effectively. Using both landmarks and semi-landmarks together will enable a more thorough measurement and analysis of the overall form, providing better insights for profiling individuals. Ideally, it is preferable to have landmark coordinates in three dimensions (x, y, and z) rather than just two dimensions (x and y).

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Conflict of Interest Statement

The author declares no conflict of interest.

Author Contributions

The author confirms sole responsibility for the following: study conception and design, analysis and interpretation of results, and manuscript preparation. The author has approved the final version of this manuscript.

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