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# Skull Isometry in Two Species of the Genus *Sylvilagus* Gray, 1867 (Lagomorpha: Leporidae)

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**Abstract**

A comparison in skull size and shape was done in two species of the genus *Sylvilagus* (31 *S. brasiliensis* Linnaeus, 1758, and 16 *S. floridanus* Allen, 1890) from Colombia using geometric morphometrics. In each specimen, 12 landmarks were fixed in digital images from dorsal aspect, and we tested if there were interspecific differences for allometric size variations. Skull shape variation was clearly allometric for both species, with no significant differences between species. Since the area of the skull to which the masticatory muscles are attached is closely linked to the functional aspects of food acquisition and processing, the allometric similitudes detected between these species may suggest no differences in food habit, a logical conclusion as both species are allopatric.

***Keywords:*** *Allometry, Cottontail rabbit, Forest rabbit, Neotropics, Tapiti*



## 1. Introduction

Allometry is the statistical association between size and shape, and it is an important component of species variation because it accounts for most of the variation within species or most of the divergence between species (Swiderski, 2003). Decomposition of raw data into those independent size and shape variables can be done by means of geometric morphometric techniques. Not only geometric morphometrics partitions the form of an object into components of size and shape, but, using landmarks as form descriptors, allows making comparisons homologous. Geometric morphometric analyses of allometry have been done in many taxa of animals, but, at least at our knowledge, there has been no survey of allometry in American lagomorphs.

According to (Klingenberg, 2016), static allometry reflects variation among individuals within homogeneous age groups at the population level. Ontogenetic allometry (growth allometry) is the consequence of covariation among traits during growth. Both types of allometry can be used for various comparisons across different populations of the same species that have different histories, live in different environments, and are subjected to different environmental constraints.

Cottontail rabbits, genus *Sylvilagus*, Order Lagomorpha, Family, Leporidae, Subfamily Leporinae (Davis and Roth, 2008), are found in the New World (Cervantes and Lorenzo, 1997; Chapman *et al*., 1990), inhabiting a wide variety of habitats (Diersing and Wilson, 2017). Most species have stub tails with white undersides that show when they retreat, giving them their characteristic name. Speciation and subspeciation is high among this genus (Diersing and Wilson, 1980; Durant and Guevara 2001). A revision of South American cottontail rabbits recognized two main species: *S. floridanus* and *S. brasiliensis* (Hershkovitz, 1950; Bonvicino *et al*., 2015).

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Eastern cottontail (*Sylvilagus floridanus*) (Allen, 1890) is distributed over broad geographic areas from southern Canada to northwestern South America (Chapman *et al.,* 1990; Mancina *et al.,* 2015). It inhabits arid and semiarid tropical regions, never in virgin or fully reestablished forests, with an altitudinal range from sea level to approximately 1,000 meters above (Hershkovitz 1950). Eastern cottontails prefer to hide in dense and thorny thickets bordering open fields or savannas and under scattered hedges and shrubs of scrub country (Hershkovitz, 1950). Tapiti or forest rabbit (*Sylvilagus brasiliensis* Linnaeus, 1758) is found in north as southern Tamaulipas, Mexico, southward along the eastern coast of Mexico and the Yucatan Peninsula to western Guatemala (Chapman *et al.,* 1990; Diersing and Wilson, 2017). Tapitis live in Tropical and temperate zone forests and in swamps, savannas, scrublands, and deserts, and their presence is most evident in forest clearings and natural grasslands (Hershkovitz, 1950), nesting in brush heaps, in hollow trunks of trees, at the base of trees, and amid tangled roots (Hershkovitz, 1950). In northwestern South America, habitats of tapitis and cottontails are mutually exclusive (Hershkovitz, 1950). Eastern cottontail is large-sized, measuring 36–48 cm, with an average body weight of 1,300 g (Chapman *et al.,* 1990). Tapiti is a small to medium-sized rabbit, with a head-body length of 320 mm and an average body weight of 934 g, and less known than the former (Durant and Guevara, 2001).

The recognition of South American *Sylvilagus* taxa has been based normally on the external characteristics (Hoffmeister and Zimmerman, 1967; Diersing and Wilson, 1980) (Cervantes and Lorenzo, 1997; Durant and Guevara, 2001; Bond *et al.,* 2004; Castañeda *et al*., 2015) and karyotypic and phylogenetic data (Bonvicino *et al.*, 2015). Allometric comparisons are important in clarifying interspecific cranial shape differences that are dependent on size variation, even among adults (Suzuki *et al.,* 2011). To better understand the allometry patterns in populations of some cottontail rabbits, we investigated static allometry from skulls by means of geometric morphometrics to address the following subjects:

1. To analyse the relationship between size and shape in two species of the genus *Sylvilagus*: *S. brasiliensis*, and *S. floridanus*.
2. The visualization of their allometric patterns, and
3. The comparison of these patterns of allometry.

Geometric morphometric approach allows to characterize the complex geometry (shape) of the cranium and understand how it relates to function (Kraatz and Sherratt, 2016).

The present work is part of a more ambitious project that attempts to find change patterns in cranial skeletal morphology in wild and domestic lagomorphs.

## 2. Materials and Methods

### *2.1. Sample Composition*

All specimens examined in this study are from the mastological collection of the *Instituto de Ciencias Naturales* of the *Universidad Nacional de Colombia* in Bogotá. The specimens had been collected from different localities in Colombia, and they included 47 skulls of *Sylvilagus* (31 *S. brasiliensis* -16 males, 13 females and 2 of unknown sex-, and 16 *S. floridanus* -6 males, 7 females and 3 of unknown sex-). No information of subspecies was available.

### *2.2. Data Collection*

Digital images of skulls were taken with a Nikon D1500 digital camera equipped with a 40 mm 1:2.8G MicroNikkor lens in a standardized manner: the camera was placed with the camera lens parallel to the ground, while the skulls were placed in the centre of the optical field, with dorsal face of the skull oriented parallel to the image plane. To eliminate distortions of the relative positions of the corners of the angular process due to parallax effects, all images were taken with the camera positioned at a sufficient distance to ensure that the specimen occupied only the part of the field known to be free of this distortion. A scale bar was included in all the photographs.

Images were then saved in jpg in 9.3 Mb format and transferred to a computer. In each photograph, 12 two-dimensional (2D) landmarks, covering all most important aspects of the dorsal view of the cranium (Figure 1). The digitized landmarks are described as follows:

1. Most oral part of the skull
2. Most caudal part of the skull
3. Left side of maxilla-incisive suture
4. Right side of maxilla-incisive suture
5. Left side of zygomatic notch

6. Right side of zygomatic notch
7. Lacrimal notch of left orbital socket
8. Lacrimal notch of right orbital socket
9. Most lateral left side of zygomatic arch
10. Most lateral right side of zygomatic arch
11. Left temporo-parietal suture
12. Right temporo-parietal suture.

The landmarks chosen were present on all specimens and were considered to sufficiently summarize the morphology of all dorsal aspect of skull -neurocranium and splanchnocranium-. Landmarks were digitized using tpsDig v. 2.26 software (Rohlf, 2010). A generalized Procrustes analysis conducted separately for each species using package MorphoJ (Klingenberg, 2011) in order to obtain Procrustes coordinates (shape variables) and centroid sizes. This is an iterative procedure that scales, rotates and translates landmarks to reduce the sum of squared distances of specimen landmarks to an average shape (Adams *et al*., 2013). These shape variables were used for interspecific comparisons.

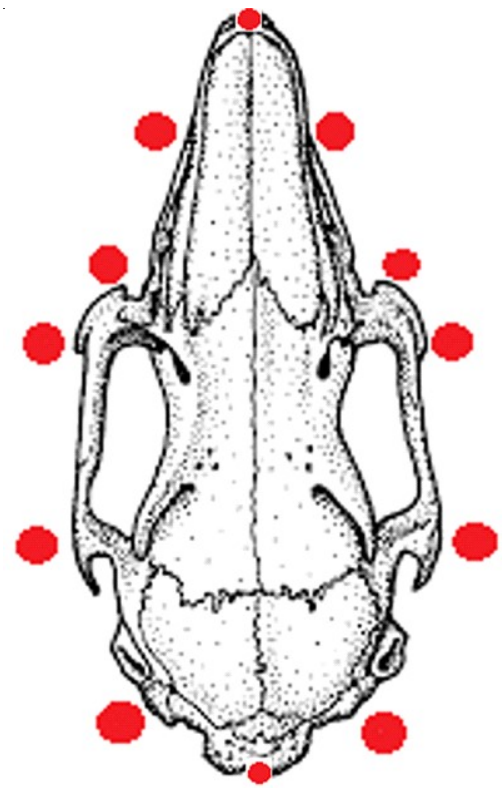

**Figure 1: Outline Drawing of Dorsal Surface of Skull With Locations of Landmarks Digitized on Each Specimen of *Sylvilagus*. See Text for Anatomical Descriptions of Landmarks**

### *2.3. Correlation Between Shape and Tangent Space*

Correlation between the Procrustes and tangent-shape distances were calculated using tpsSmall v. 1.33 software (Rohlf, 2015).

### *2.4. Size and Shape*

Centroid size (CS) is an isometric measure of size in geometric morphometrics (Adams *et al*., 2013), and it is defined as the square root of the summed squared distances of each landmark from the median shape of the landmark configuration (Swiderski, 2003). In the absence of allometry it is the only size measurement that is uncorrelated with shape variation. Differences between sexes and species were assessed by the non-parametric Mann-Whitney *U* test.

### *2.5. Relationship Between Size and Shape and Comparison Among Patterns*

We regressed shape on log-CS to obtain individual allometric relationships for both species. CS is commonly used to investigate allometry in morphometric studies. The percent of shape variation accounted for by regression with log-CS was used as an indicator of the relative strength of the relationships. Finally, an Analysis of covariance (ANCOVA) test for equality of means for two univariate groups, adjusted for covariance with another variate, was done. Analyses were performed by using MorphoJ v.1.06d (Klingenberg, 2011) and PAST v.2.17c (Hammer *et al*., 2001) softwares.

## 3. Results

From preliminary analysis in our sample there appeared no statistical sex differences neither for *S. brasiliensis* ($U$=98, $p$=0.809) nor for *S. floridanus* ($U$=19, $p$=0.830), so genders were clustered for analysis. *S. brasiliensis* skulls were significatively larger than those form *S. floridanus* ($U$=141; $p$=0.016).

Variation of the specimens in shape space was perfectly correlated ($r$=0.999) with tangent space, so the projection of three-dimensional skull landmarks into a two-dimensional plane involves a low dimensionality reduction error and allowed the use of the plane approximation in future statistical analyses and interpretation of results.

Prior to allometric correction, PCA of the landmark configurations taken from radiographs yielded results that were generally similar to those from the analysis of linear measurements. For *S. brasiliensis*, three components summarized in total 84.30% of the variance in the landmark coordinates following Procrustes superimposition, with PC1, PC2, and PC3 summarizing 56.5, 18.4, and 9.3% of that variance, respectively. The remaining components each indexed 7% or less of total variance. Despite the removal of variation because of scaling, translation, and rotation during the Procrustes fit, only first component correlated significatively with log CS (Pearson product-moment correlations of 0.819, -0.030 and -0.283, for PC1 to 3, respectively). For *S. floridanus*, three components summarized in total 79.52% of the variance in the landmark coordinates following Procrustes superimposition, with PC1, PC2, and PC3 summarizing 45.7, 18.8 and 14.9% of that variance, respectively. The remaining components each indexed 9% or less of total variance. Again, only first component correlated significatively with log CS (Pearson product-moment correlations of 0.622, -0.365 and 0.147, for PC1 to 3, respectively). Those values indicate that for both species the allometric shape change is confined to a single axis rather than being distributed across multiple axes. This effect is apparent in a scatterplot of PC1 *versus* CS, which, reflecting an overlap amongst groups, the line of allometry running obliquely from lower left to upper right and is aligned with CS (Figure 2).

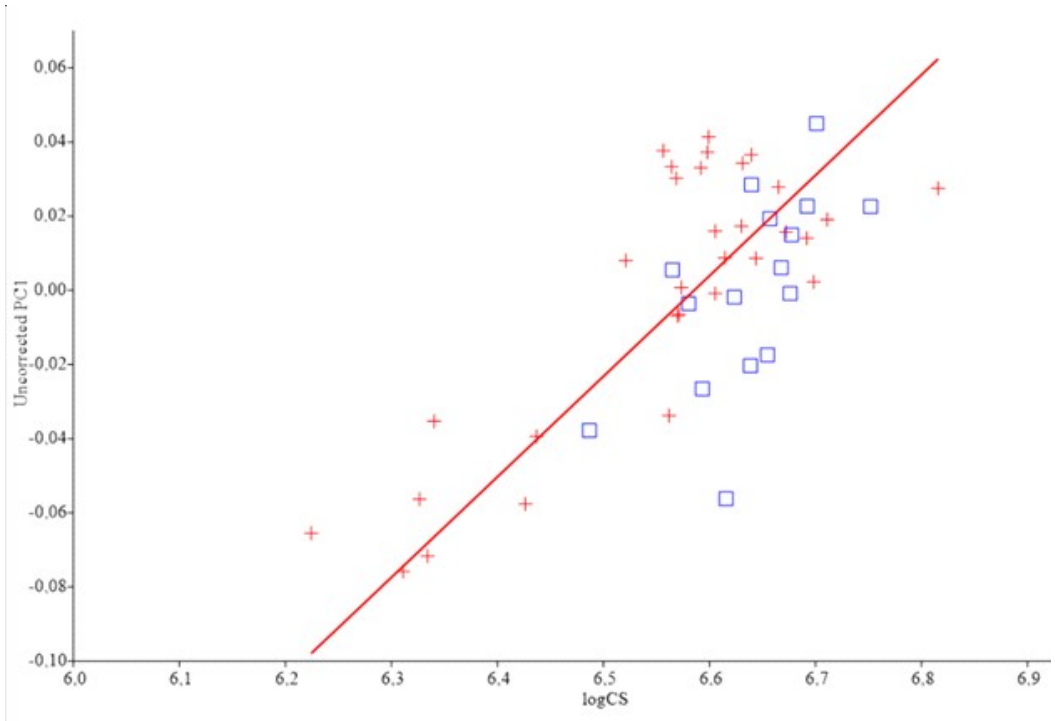


**Figure 2: Reduced Major Axis Regression of Principal Component One (Pc1) Scores on Log Centroid Size (Log Cs) for Skulls of 31 *Sylvilagus brasiliensis* and 16 *S. floridanus*. Trendline Represents A Universal Regression that Does Not Take Species Membership Into Account.**

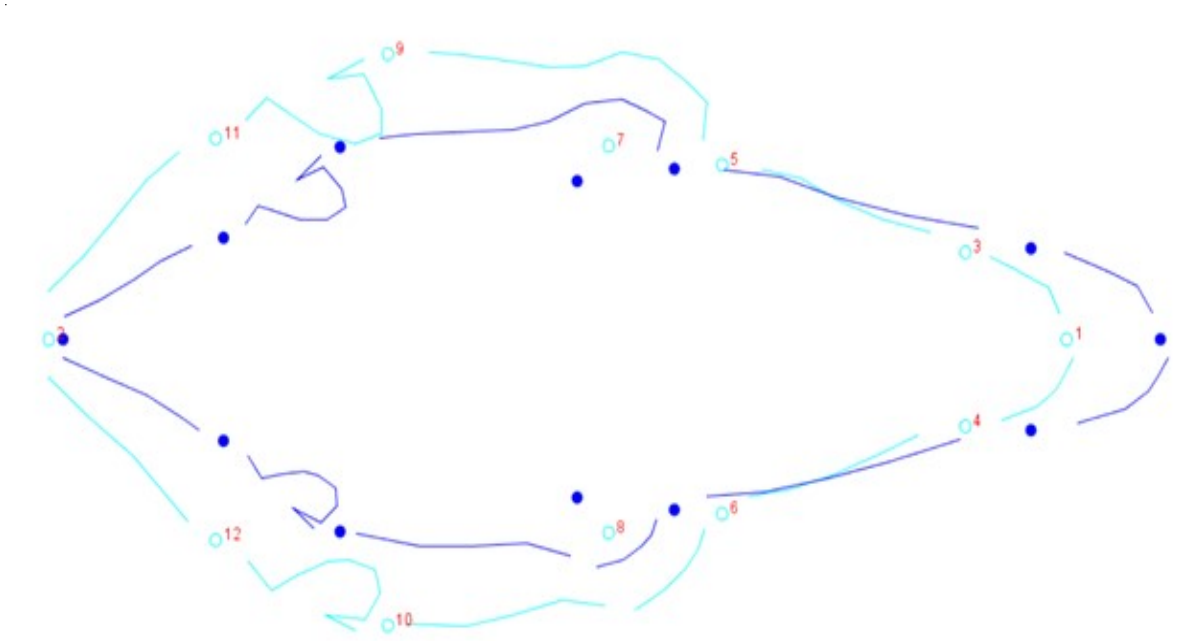


**Figure 3: Wireframe Visualization of Allometric Shape Change Along the Least Squares Regression Line of Procrustes Coordinates on Log Centroid Size for *S. brasiliensis*. Grey Landmarks Represent the Average Configuration Amongst all Specimens, Whereas Black Landmarks Represent the Approximate Extreme of Variation in the Direction of the Smallest Specimens, Which Presented Wide Heads**

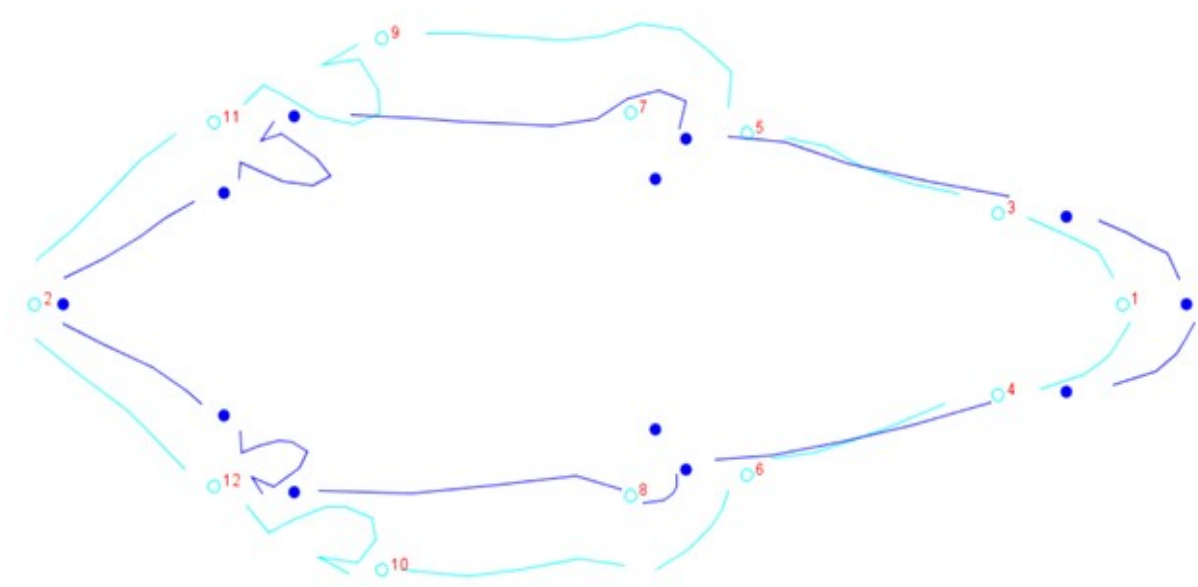


**Figure 4: Wireframe Visualization of Allometric Shape Change Along the Least Squares Regression Line of Procrustes Coordinates on Log Centroid size for *S. floridanus*. Grey Landmarks Represent the Average Configuration Amongst all Specimens, Whereas Black Landmarks Represent the Approximate Extreme of Variation in the Direction of the Smallest Specimens, Which Presented Shorter Snouts**

There appeared strong allometric signals in the geometric data for both species ($p<0.01$), meaning that size variations affect shape. The scale-dependent (allometric) shape variation described by the regression line primarily indexes variation in the relative size for two species, as visualized by the wireframe diagram, appear in Figures 3 and 4. The ANCOVA for the respective allometric model showed non-significant differences between species ($F=0.239$; $p=0.626$) (Figure 5).

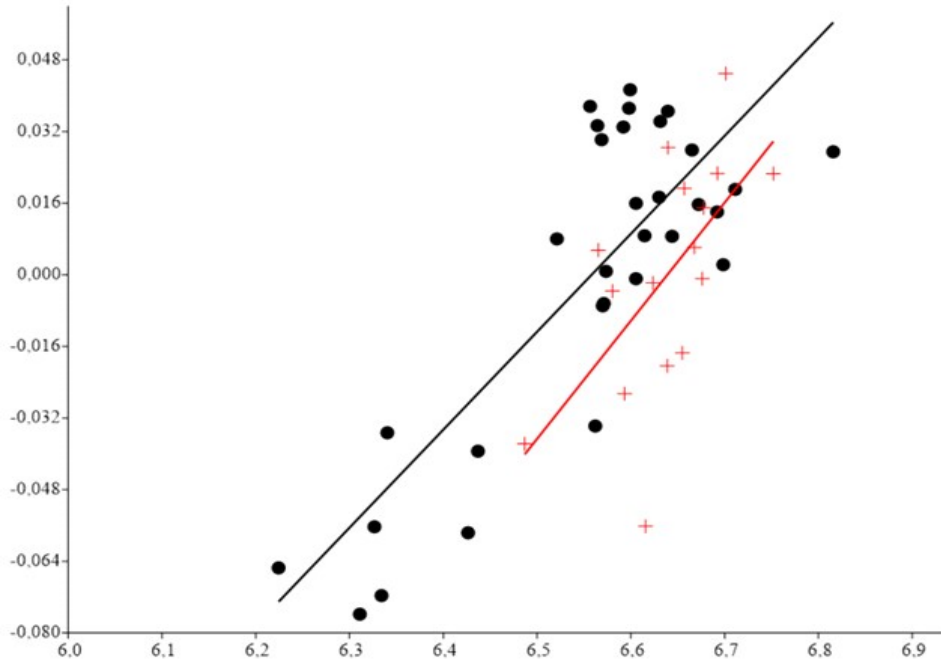


**Figure 5: Scatter Plot and Linear Regression Lines for Skulls of 31 *Sylvilagus brasiliensis* and 16 *S. floridanus*. The ANCOVA for the Respective Allometric Model Showed Non-Significant Differences Between Species ($F$ = 0.239, $p$ = 0.626).**

## 4. Discussion

Many morphological studies between species made between adults using non-allometric comparisons can be not adequate, since size and shape differences occur not only in ontogeny, but also in static intraspecific and interspecific series (Suzuki, Abe, and Motokawa 2011). In the present study, we investigated static allometric differences between the skulls of two closely related, but differently body sized species of the genus *Sylvilagus*: *S. brasiliensis* and *S. floridanus.* The null hypothesis of isometry was rejected in *S. brasiliensis* and *S. floridanus,* e.g. skull shape variation was clearly allometric for both species. Moreover, differences of slopes could not be rejected for both species. Since the area of the skull to which the masticatory muscles are attached is closely linked to the functional aspects of food acquisition and processing (Suzuki, Abe, and Motokawa 2011), the allometric similitudes detected between these species may suggest no differences in food habit, a logical conclusions as both species are allopatric. In fact, tapitis cling to dwindling forests and the clearings therein and to natural savannas of the Andean crests, while cottontails are replacing them in artificial savannas cutting through the original forests. No doubt introduction of the larger, more prolific, and more aggressive cottontail, together with the train of predators following it, is the most important factor contributing to the exclusion of tapitis from the continuously expanding artificial savannas and scrublands of northwestern South America (Hershkovitz 1950).

Results hold only for the specimens examined, since the species in question have a very broad geographic distribution and are likely to vary in size in relation to latitude or possibly competition.

## 5. Conclusion

The relationship between skull size and shape in two allopatric species of the genus *Sylvilagus* -*S. brasiliensis* and *S. floridanus*- is not isometric, presenting a similar allometric pattern. The allometric similitudes detected between these species may suggest no differences in food habit.

## 6. Acknowledgment

I thank Catalina Cárdenas and Hugo Fernando López for the access to scientific collection of the *Instituto de Ciencias Naturales* of the *Universidad Nacional de Colombia* collection, in Bogotá. My wishes also to anonymous reviewers for their comments and suggestions.

## 7. Competing Interests

The author declares no competing interests regarding the publication of this paper. There were no funders in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

## 8. Availability of Data and Materials

The datasets generated and analysed during the current study are available from the author upon on reasonable request. List of voucher specimens is available upon request to author, too.

## 9. Ethic Approval Consent to Participate

Not applicable.

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