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Research Article

A Reassessment of the Cranial Diversity of the West African Giraffe

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The West African giraffe *Giraffa camelopardalis peralta*, the rarest giraffe subspecies, is one of the least studied taxa of the African megafauna in terms of anatomy, physiology, and taxonomy due to the limited material hosted in museum collections. Here, we discuss specific morphological features of the holotype of this subspecies, re-evaluate its diagnostic characteristics and expand our knowledge of the morphology of the taxon with the addition of specimens collected in the wild. Our results show that *G. c. peralta* is not a subspecies of 'gigantic' proportions, as indicated in previous studies. This misunderstanding arose from the misidentification of the holotype specimen (NHMUK-ZD-1898.2.19.1) as a female instead of a male. The only other *G. c. peralta* specimen, which is hosted in the same collections in the Natural History Museum of London (NHMUK-ZD-1904.11.2.2), is a male of morphology and size much closer to that of an average *G. camelopardalis* male. Our findings show that in comparison to other giraffe subspecies the dimensions of *G. c. peralta* are as metrically expected and reveal preliminary evidence of the strongest sexual size dimorphism in the genus *Giraffa*. We further suggest that the holotype should be relabeled as a male. The evolutionary history and the phylogenetic position of *G. c. peralta* are discussed, favoring the mixing-isolation-mixing pattern with the Kordofan giraffe (*G. c. antiquorum*).

Keywords: evolution; *Giraffa camelopardalis peralta*; holotype; morphometrics; skull; taxonomy

1. Introduction

The West African giraffe (*Giraffa camelopardalis peralta* [1]) is the rarest giraffe subspecies with a current estimate of less than 700 individuals remaining in the wild, an increase from a low of 49 individuals in the 1990s [2–7]. The only remaining natural free-living population occurs exclusively in Niger and is genetically isolated from its closest living relative the Kordofan giraffe (*Giraffa camelopardalis antiquorum* [8–14]). Its type locality is in Nigeria, southeast of the junction of Benue and Niger Rivers (near Lokoja, Kogi), but the subspecies has been extirpated from the area. The type specimens, a skull and a mandible with associated metacarpals published by Thomas [1], are hosted in the collections of the Natural History Museum of the United Kingdom (NHMUK) in London (NHMUK-ZD-1898.2.19.1) (Figure 1). The only other verified cranial specimen of this subspecies is hosted in the same collection (NHMUK-ZD-1904.11.2.2) and originated from east of Sharu (Plateau), Nigeria. Therefore, only two cranial specimens of this form (from the wild) are hosted in museum collections worldwide, making it one of the rarest mammalian taxa available for comparative studies.

Thomas [1] concluded that the holotype specimen belonged to a female because of its lightness, fragility, and the narrow and short parietal ossicones (Figure 1). Lydekker [15, 16] and Seymour [17] both followed this assessment and also considered this specimen a female. However, Thomas [1] noted that the parietal ossicones are, in fact, diverging and not parallel, the medial ossicone is considerably developed, and the overall size of the skull far exceeds the known dimensions of females. Nevertheless, all these authors noted that if this specimen was indeed a female, it is extremely large. Thus, they considered that *G. c. peralta* was a much larger form in relation to the other giraffe subspecies. In the absence of additional data, aside from the second skull in NHMUK (NHMUK-ZD-1904.11.2.2), the sex of the holotype was never questioned in the literature, leading to the gigantic proportions of *G. c. peralta* being considered as one of its defining features.

Here, we re-evaluate the distinguishing cranial characteristics of *G. c. peralta* by reviewing the sex and age of the holotype specimen and by reporting on additional morphological data collected from specimens found in the wild in Niger. Remarks on the taxonomy and evolution of *G. c. peralta* are made based on a wider comparison with *Giraffa* skulls Africa-wide.

2. Materials and Methods

The studied cranial material of *G. c. peralta* consists of 11 skulls. Two of these specimens are stored in the collections of NHMUK (NHMUK-ZD-1898.2.19.1 and NHMUK-ZD-1904.11.2.2; both are males as argued in the discussion), whereas new material was collected in the Kouré Region, Niger, in 2023. The Niger samples were CT-scanned in the Polyclinique Magori (Niamey, Niger) and are now stored at the field base of the Association for the Safeguarding of Giraffes in Kouré, Niger (13.326042N, 2.593746E). The Niger samples showed various degrees of damage and dental wear. The NHMUK specimens were 3D-scanned using an EinScan Pro HD handheld surface scanner (https://www.einscan.com/handheld-3d-scanner/einscan-pro-hd/). In total, 11 specimens were scanned: five male skulls, four female, and two juveniles of unknown sex.

The 3D Geometric Morphometrics data and results, as well as the attribution to age classes follow Kargopoulos et al. [18]. Sex identification of the specimens was based on the labels in the collections. Considering the occasional misattributions, as discussed in the following paragraphs, we believe that genetic acquisition would be a valuable future perspective to solidify the information on this sample. Measurements of the skulls were taken using 3D Slicer [19], following the protocol explained in Supporting Table 1 (based on [17]). Statistical analysis was conducted in PAST 4.16 [20].

Institutional Abbreviations: HNHM—Hungarian Natural History Museum, Budapest (Hungary); NHMUK—Natural History Museum of the United Kingdom, London (United Kingdom); NMW—Naturhistorisches Museum Wien (Austria); SNM—Slovak National Museum, Bratislava (Slovakia).

3. Results and Discussion

3.1. Defining the Sex of the Holotype. Even though the identification of the holotype skull as female [1, 15–17] has merit based on specific morphological traits, there are other features that support its attribution as male. Concerning the female characteristics, the attribution by Thomas [1] was based on two traits: “lightness and fragility” and “slender horns.”

The specimen is of a relatively young giraffe, based on the suture closure and dental wear stages, since the distal infundibulum of M1 is still separate from the metastyle and hosts a small cuspule [18, 21]. In addition, Thomas [1] mentioned the presence of “anterior cannon-bones” (meaning metacarpals) stating that their epiphyses were still unfused. The unfused epiphyses verify that this is indeed a subadult individual [22].

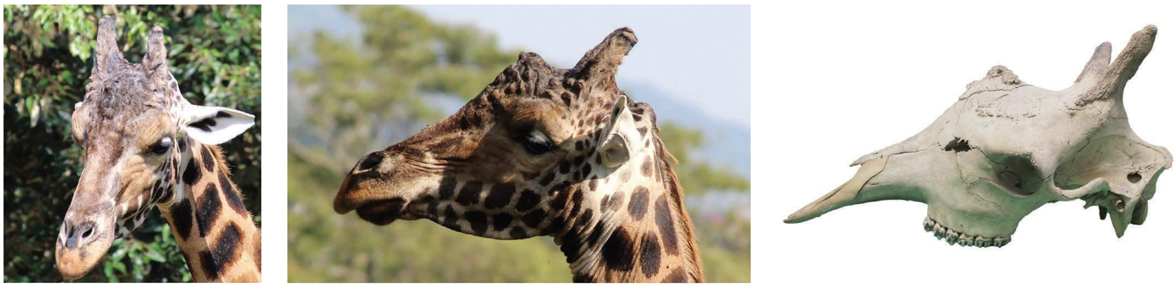
Despite the parietal ossicones of the holotype being short and slender, Thomas [1] noted that not only are they significantly divergent, which is unusual for a female, the median ossicone is also well developed, with distinct secondary ossification that would be highly exceptional for a female. Therefore, some indication was made by Thomas [1] on the possible attribution of the skull to a male. It is true that the parietal ossicones of the holotype are narrow and short in comparison to the average morphology of male *Giraffa* [18]. However, there are other verified male specimens in our comparative *Giraffa* dataset [18] that exhibit similarly narrow and short parietal ossicones, such as those seen in Figure 2.

In addition, the relatively short and narrow ossicones have been observed in numerous living individuals (J & S. Fennessy, N. Kargopoulos, S. Ferguson pers. obs.). An example of this is the Nubian giraffe (*Giraffa camelopardalis camelopardalis* [23] in the Giraffe Center (Nairobi, Kenya) (Figure 3). While the degree of secondary ossification on the dorsal surface of this male’s skull (like that of HNHM-83.65.1 or SNM-C-1968 in Figure 2) suggests an advanced age, the parietal ossicones are short and slender, similar to those of the *G. c. peralta* holotype. In the NHMUK-ZD-1904.11.2.2 specimen from Nigeria, secondary ossification is present on the sides of the parietal ossicones and on the median ossicone, suggesting that with increasing age, it could have developed a similar profile to the *G. c. camelopardalis* male in Kenya (Figure 3).

Thomas [1] highlighted that the dimensions of the holotype specimen are far larger than those of any other female. Principal component analysis using the variance–covariance matrix based on all cranial and dental measurements except

Figure 1: The holotype skull of West African giraffe (*Giraffa camelopardalis peralta*) in the Natural History Museum of the United Kingdom in London (NHMUK-ZD-1898.2.19.1). (a) Left view; (b) right view; (c) ventral view; (d) dorsal view; (e) proximal view; and (f) distal view.

Figure 2: Male *Giraffa* specimens with similarly short and narrow parietal ossicones as the holotype of *G. c. peralta*: NMW-B-5432 (*Giraffa camelopardalis antiquorum*), NMW-5552 (*Giraffa camelopardalis* subsp.), HNHM-83.65.1 (*Giraffa* sp.), and SNM-C-1968 (*Giraffa* sp.). Scale bars equal 5 cm.



(a) (b) (c)

Figure 3: Comparison of the holotype skull of *Giraffa camelopardalis peralta* at the Natural History Museum of the United Kingdom in London (NHMUK-ZD-1898.2.19.1) to the head of a male *Giraffa camelopardalis camelopardalis* in the Giraffe Center (Nairobi, Kenya; photographs' N. Kargopoulos), showing the similarly developed ossicones. (a) Male *G. c. camelopardalis* in the Giraffe Center in proximal view; (b) male *G. c. camelopardalis* in the Giraffe Centre in lateral view; and (c) *G. c. peralta* holotype (NHMUK-ZD-1898.2.19.1) in lateral view.

that of the parietal ossicones showed that there is a clear distinction between the new wild *G. c. peralta* males (blue) and females (orange), and the *G. c. peralta* holotype (black star) falls neatly within the cloud of males (Figure 4(a)). PC1 corresponds to 67.0% of variance and PC2 corresponds to 14.5%, whereas the percentages of all the other *P*Cs are below 10%. PC1 mainly reflects positive loadings of the measurements POL (premaxillae to occipital ridge), MMH (distal end of the M3 to the tip of the median ossicone), PCL (premaxillae to occipital condyles), and NCL (nasals to occipital condyles). PC2 includes loadings in MMH (negative), BPH (braincase height; negative), POL (positive), PCL (positive), and NCL (positive). Therefore, the changes include cranial length (POL, PCL, and NCL), braincase height (BPH), and the height of the median ossicone (MMH).

The premaxilla to occipital condyle (PCL) measurement was used as a proxy for quantifying total cranial size in a boxplot between males (blue) and females (orange) (Figure 4(b)). In this plot, the value for the *G. c. peralta* holotype far exceeds any other female value and it is also higher than most males. It should be added that the specimen was obtained from a hunter [1]; it is, therefore, possible that it was chosen based on its relatively large size. The size of trophies should, therefore, be taken with a dose of skepticism when they are chosen as holotypes. The same plot was made using the centroid size of the adult skulls (Figure 4(c)). Also here, the value of the West African giraffe holotype fits into the range of the male specimens instead of the female ones; however, the difference is less notable since the centroid size incorporates (as a measure of skull size) the lengths of the short ossicones.

It is noted that the other specimen housed in London (NHMUK-ZD-1904.11.2.2) is a male of more standard morphology and dimensions. The term "standard morphology" is defined in reference to the average ossicone shape seen in the other two subspecies of the species *Giraffa camelopardalis*. On the PCA plot (Figure 4), this specimen is represented by the black dot closest to the holotype (black star). The two male specimens collected in Kouré are in bad preservation. However, NER-KOU-5 retains its ossicones which are also of normal size and morphology. Therefore, the morphology of the holotype deviates from the typical phenotype of male *G. c. peralta* and should not be considered as characteristic for the subspecies. As seen in Figure 2, such variations have been recorded in other taxa and are expected in large sample sizes. The fact that the first published specimen of *G. c. peralta* has these variant/atypical traits does not deprive it from its holotype status, but it should be noted that it does not represent an average morphology of the subspecies.

Based on our analysis, we conclude that the *G. c. peralta* holotype is a relatively young male with short and slender parietal ossicones. Therefore, the argument about the 'gigantic' size of this taxon [1, 15–17], or the possible attribution of the holotype to a different taxon than the other known specimens, should be disregarded since it is evident that there is a certain amount of plasticity of these dimensions among the males. The holotype specimen should, therefore, be relabeled as a male to avoid further confusion regarding the morphology of the subspecies. Acquisition of genetic material from the skull would be ideal to certify whether our sex attribution is indeed valid.

3.2. Cranial Size of G. c. peralta. The addition of the wild skulls from Kouré, Niger, provided more critical information on the actual size range of *G. c. peralta*. The males showed more extensive skull damage from limited field management in contrast to the female skulls which were better preserved, allowing for a better size comparison between the sexes in the different subspecies using PCL as a proxy of total skull size (Figure 5). Male *G. c. peralta* are the largest of all *Giraffa* taxa in terms of average skull length, even though others exhibited higher extreme values. On the contrary, the females are relatively small compared with other *Giraffa* taxa. Figure 5 shows the range of cranial size of all four *Giraffa* species and their subspecies, also quantifying sexual size dimorphism through skull length and the ratio of the average PCL values for males and females. The average sexual size dimorphism ratio is 11.1% for the eight taxa, with the lowest observed at 7.98% for the reticulated giraffe (*Giraffa reticulata* [24]) and the highest at 18.3% for *G. c.*

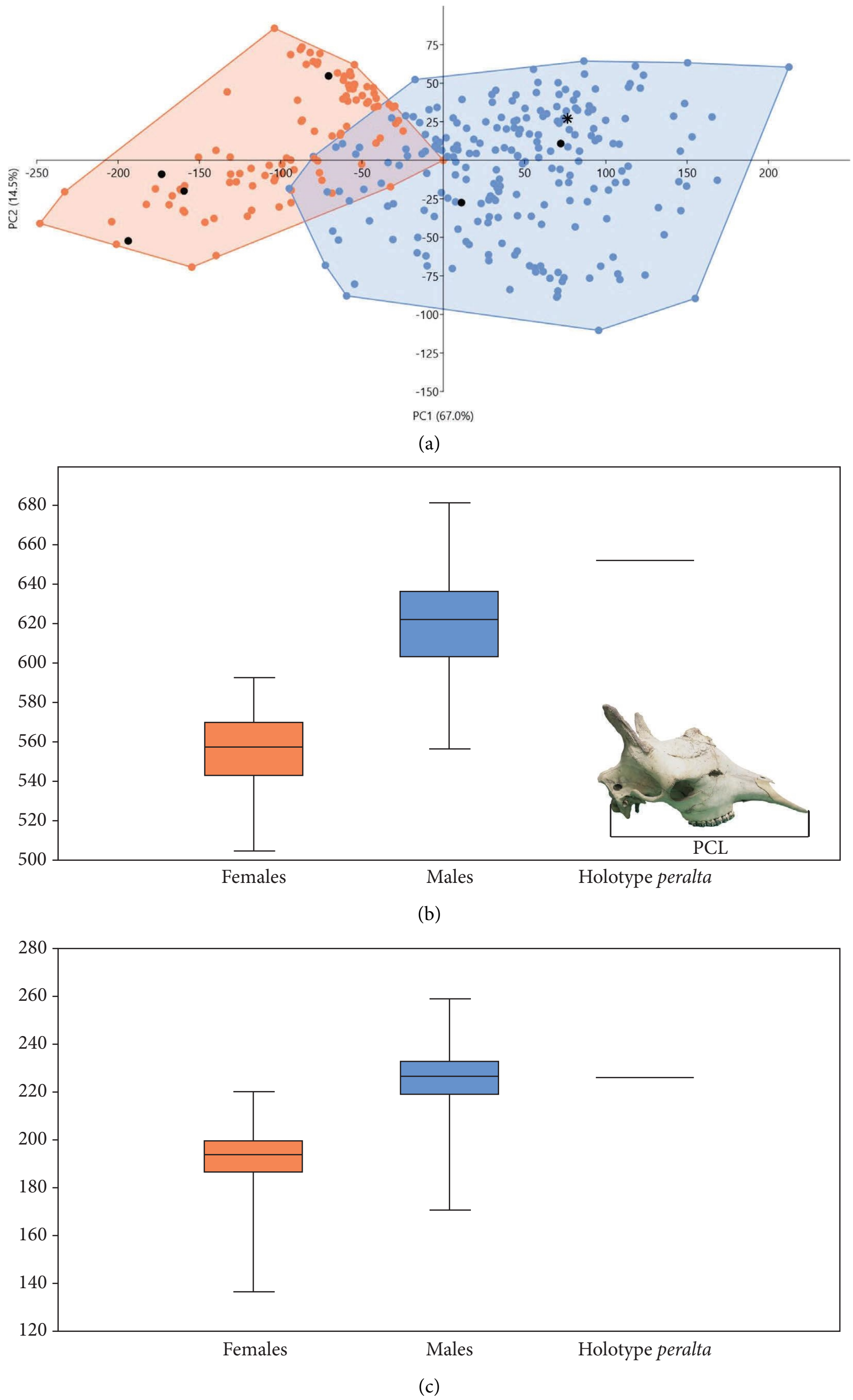


FIGURE 4: (a) Principal components analysis based on the cranial and dental measurements excluding that of the parietal ossicones with the *Giraffa camelopardalis peralta* specimens marked in black, showing the attribution of the *G. c. peralta* holotype (black star) to the cloud of males (blue) instead of the females (orange); (b) boxplot of the measurement premaxilla to occipital condyle (PCL) of males and females showing the large size of the *G. c. peralta* holotype; (c) boxplot of the centroid size (CS) of males and females showing the high value of the *G. c. peralta* holotype.

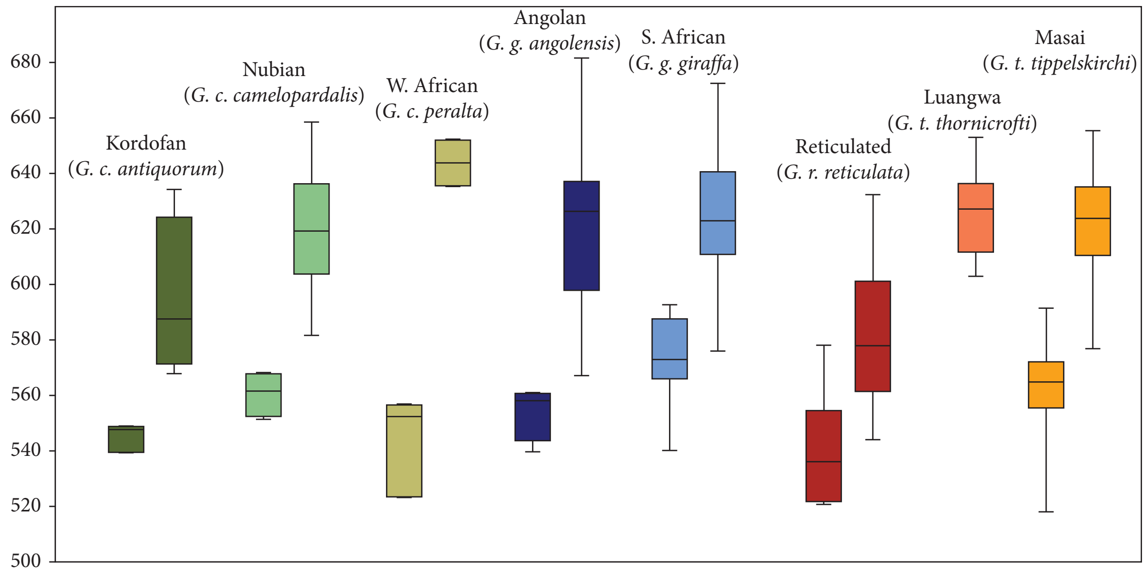


FIGURE 5: Boxplot comparison of the premaxilla to occipital condyle (PCL) values for the females and males of each *Giraffa* taxon. In each case, the females are shown on the left column, whereas the males are shown on the right column.

peralta. Whether this extreme value is indeed indicative of the sexual dimorphism of *G. c. peralta* remains to be further interrogated since the male specimens were from the last century in Nigeria and the females are modern from Niger. Centroid size was also used as a proxy of cranial size in order to assess sexual dimorphism across adult specimens (age class $\geq D$). Accordingly, the West African giraffe shows the highest degree of sexual size dimorphism (20.3%) slightly higher than the Angolan giraffe (20.2%), whereas the smallest was the reticulated giraffe (13.3%). When only the Niger specimens are considered, this value slightly drops down from 20.3% to 19.7%, retaining a preliminary result that is noteworthy, leaving plenty of room for further research in the future. The addition of more specimens in the future will help us understand even more about the range of cranial diversity of the West African giraffe and to establish a powerful comparative dataset that will be useful for more detailed studies. More specimens of the rare taxonomic groups will also provide the opportunity to conduct statistical analysis that will validate the degrees of sexual dimorphism in the different species and subspecies.

3.3. Evolution of G. c. peralta. The evolution of *G. c. peralta* is interesting, as genomic evidence clearly shows it as a subspecies of the northern giraffe (*G. camelopardalis*), but over the years, several assumptions were made about its closest affinities. In previous works, it was suggested that *G. c. peralta* was a sister taxon to *G. c. antiquorum* [14, 25] and *G. c. camelopardalis* [10] or that it was an outgroup inside *G. camelopardalis* [12, 25]. However, the most recent studies based on updated genetic data support its distinction as a separate subspecies, with *G. c. antiquorum* being its most closely related subspecies [14, 25]. With respect to skull shape, Kargopoulos et al. [18] (Figure 4) showed that the distributions of *G. c. antiquorum* and *G. c. peralta* are indeed closely aligned, and statistical evaluation showed that there is no significant difference between them [18]. Therefore, cranial shape analysis aligns with the results of genetic analysis conducted by Coimbra et al. [25] and Bertola et al. [14], suggesting that *G. c. antiquorum* and *G. c. peralta* are closely related in terms of both genetics and cranial morphology.

Even though the *G. c. peralta* samples are relatively limited, they are the largest dataset to date, and our results highlight the close evolution of the three subspecies of *G. camelopardalis* across northern Africa. Based on the results of Brown et al. [26], Bertola et al. [14], and Kargopoulos et al. [18], *G. c. antiquorum* is more closely related to *G. c. peralta* than *G. c. camelopardalis*, aligning with the mixing-isolation-mixing pattern. It is likely that the dispersal from East to West Africa historically occurred when the distribution of vegetation was conducive and natural or anthropogenic barriers limited. The greatest modern natural barriers in northern Africa are the Sahara Desert, which today limits the distribution of *Giraffa*in the north, and the Nile River, which separates the current distribution of *G. c. camelopardalis* and *G. c. antiquorum* (e.g., [27] and references therein). Such large barriers are not present between the ranges of *G. c. antiquorum* and *G. c. peralta*, suggesting that ancestral mixing or direct population ancestry between these two subspecies is plausible. However, such complex evolutionary mechanisms on such a large scale cannot be deciphered on the basis of a few skulls. The comments above are an attempt to interpret the accumulated data and to offer promising hypotheses for future studies.

4. Conclusion

Based on the abovementioned, we conclude that the holotype skull of *G. c. peralta* (NHMUK-ZD-1898.2.19.1) housed in the NHMUK should be relabeled as a male, pointing out that it is relatively young and has irregularly short and narrow parietal ossicones, whereas the other specimen in the same collections (NHMUK-ZD-1904.11.2.2) is a male with more standard morphology. In addition, we conclude that *G. c. peralta* has relatively normal cranial dimensions in comparison to those of other *Giraffa*. Cranial shape supports their phylogenetic affinities with *G. c. antiquorum* and supports their evolutionary relationship through the mixing-isolation-mixing model.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Conceptualization was made by N.K.; methodology was developed by N.K., J.M.-L., A.C., J.F., and S.F.; data sampling was conducted by N.K., S.F., M.B., A.P., S.W., and A.R.M.Z.; N.K. and J.F. led the writing of the manuscript; J.F., S.F., J.M.-L., and A.C. offered academic supervision; N.K. created and edited the figures. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. *(Supporting Information)*

Supporting Table 1: Protocol for the cranial measurements taken of *G. c. peralta* skulls and the comparative sample based on Seymour [17].

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