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Fossil rarities from the Bolt's Farm Palaeokarst System, Gauteng, South Africa

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Certain skeletal elements of mammals are rare in both modern and fossil collections. These include clavicle, baculum, haemal arches; basically, skeletal elements with little or no articulation with the rest of the skeleton. The reason for this is complex. In cases of the modern specimens the above-mentioned elements could be easily disposed together with the muscle mass prior to skeletonisation, while in cases of fossilised specimens this phenomenon might be due to misidentification or the lack of preservation. Whatever the reason, here we have recovered multiple haemal arches and two clavicles from two Plio-Pleistocene fossil deposits at the Bolt's Farm Palaeokarst System, South Africa. All the preserved material appears to be that of *Panthera Oken*, 1816. Keywords: *Panthera*, Clavicle, Haemal Arch, Plio-Pleistocene.

INTRODUCTION

For various reasons, from preservation to simply being overlooked or misidentified, certain anatomical structures are rare in the fossil record. These include clavicles (in particular non-primate) (Hartstone-Rose et al., 2012) and haemal arches (to date no references have been found regarding mammalian haemal arches in the Plio-Pleistocene fossil record). Even in modern anatomical collections in some of the largest museums around the world these bones are rare (pers. obs.). The major exception is the Rancho La Brea Tar Pit collections at the George C. Page Museum in Los Angeles, California (Hartstone-Rose et al., 2012). Hartstone-Rose et al. suggest the reason why modern collections lack clavicles is that the bone was simply tossed aside with the muscle mass during skeletonisation. The morphology of haemal arches are widely published in species of fish, reptiles and dinosaurs, but aside from veterinary texts and some comparative anatomy texts, little is published from the mammalian groups, and even less in the fossil literature (Kardong, 2019; Otero et al., 2012; Evans and de Lahunta, 2013; Gatesy, 1990; Romer, 1956 and references therein). In reptiles and sauropods, the haemal arches start at the 2nd or 3rd caudal vertebrae and continue down the tail, with distinct morphological changes as the tail thins (Otero et al., 2012). In mammals the haemal arch is located on the ventral surface of some of the caudal vertebrae and slopes caudally. In dogs it is only found in association with the fourth, fifth and sixth caudal vertebrae (Evans and de Lahunta, 2013). One consistency between these elements in various groups of vertebrates is that they do not maintain a strong articulation with the rest of the skeleton (Evans and de Lahunta, 2013). For whatever reason, these skeletal elements are rarely recovered, or are misidentified in the fossil record.

Recent excavations at the site of Bolt's Farm, South Africa (Fig. 1), have yielded three examples of haemal arches and two non-primate clavicles. These rare elements come from two different fossil deposits within the Bolt's Farm Palaeokarst System (Fig. 2). The haemal arches and one clavicle were all recovered from the site known as Bridge Cave (BC) and the second clavicle was recovered from Aves Cave I (AC). Bolt's Farm has a long history of exploration and excavations. Dr Broom and Mr Bolt did their initial reconnaissance of the area back in 1936 (Cooke, 1991) and subsequent descriptions of a few specimens were completed by Broom (1937, 1939, 1948). The University of California African Expedition run by Dr Charles Camp excavated numerous localities at Bolt's Farm in April of 1948 (Camp, 1948). Sporadic publications have trickled out from this expedition over the years, for instance Peabody's report on Taung (1954), and specific fauna descriptions by Cooke (1985, 1991, 1993a,b). 51 bulk of specimens from the expedition remain unpublished at the University of California Berkeley Museum of Paleontology. In 2001 the combined team of the DITSONG: National Museum of Natural History (formerly the Transvaal Museum) Pretoria, South Africa, the CNRS in France, HOPE (Human Origins and Past Environments) and HRU (HOPE Research Unit) began to relook the Bolt's Farm complex (Gommery et al., 2016; Gommery et al., 2008; Thackeray et al., 2008). Of the approximately 30 loci excavated by Camp and Peabody, the latest excavations have recovered over 2000 fossils from 16 distinct fossil deposits (Fig. 2). Five rare fossils were recovered from two of the aforementioned fossil localities, clavicles and haemal arches. Here we discuss the morphology and species identification of these elements. In addition, we illustrate that through careful excavations and identification processes even these rare skeletal elements can be recovered.

MATERIAL AND METHODS

All specimens were recovered from decalcified breccia. Bridge Cave specimens BC 255 and BC 276 were excavated in 2014. Aves Cave I specimen AC 384 and Bridge Cave specimen BC 369 were excavated in 2015. BC 512 was excavated in 2016. AC 384 is a partial clavicle recovered from Aves Cave I. BC 255, BC 276 and BC 369 are all haemal arches recovered from Bridge Cave. BC512 is a partial clavicle recovered from Bridge Cave. All measurements were taken with PROFiTEXX digital calipers to the nearest 0.01 mm. All of the fossils are curated in the Plio-Pleistocene Palaeontology Section, Vertebrate Department, DITSONG: National Museum of Natural History, Pretoria, South Africa. Digital photos were taken with a Pentax K 20 D digital SLR camera. Modern leopard (*Panthera pardus* Linnaeus, 1758) clavicle is part of the University of the Witwatersrand comparative lab. In addition, fossil comparative material from *Machairodus* is housed at the Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). Additional comparative material from *Panthera spelaea* at Château (Château, France) and *Panthera spelaea* and *Homotherium crenatidens* material at Université Claude Bernard Lyon 1 (Villeurbanne, France) were also used during this study. Additional comparisons were made with a pair of modern *Panthera leo* clavicles (see Fig. 3) and published results of Hartstone-Rose et al. (2012: 985).

RESULTS

AC 384 and BC 512 are partial left clavicles recovered from Aves Cave I and Bridge Cave, respectively (Fig. 3). Both specimens are missing the sternal ends, thus measurements A, D, E, F and G (from Hartstone-Rose et al., 2012) were unattainable. For AC 384 measurement B (acromial width) is 9.03 mm and measurement C (acromial thickness) is 3.18 mm. Visually AC 384 is distinct from the two modern lion (*Panthera leo* Linnaeus, 1758) clavicles used for comparative purposes and most resembles LACM HC 30082 ('C'), *Panthera atrox* (Leidy, 1853) from Hartstone-Rose et al., (2012: 983). In a comparison of measurements (Table. 1) AC 384 has an acromial width much less than *P. atrox* (Leidy, 1853) and noticeably less than *P. leo*.

(Linnaeus, 1758). The acromial width of AC 384 falls between *P. tigris* (Linnaeus, 1758) and *P. onca* (Linnaeus, 1758). The acromial thickness of AC 384 is slightly greater than those reported for both *P. leo* and *P. tigris* and less than that recorded for *P. atrox* – the large morph from Rancho La Brea (see Hartstone-Rose et al., 2012). BC 512 has an acromial width (B) of 8.94 mm and acromial thickness (C) of 2.86 mm. The acromial width is less than the measured width of AC 384, as well as the reported widths for lion and tiger and the left lion clavicle measured here. The acromial thickness falls within the range of measured and reported lion and tiger and is noticeably less than AC 384.

All three haemal arches come from the Bridge Cave deposits, and in particular are directly associated with fossils of an extremely large Pantherinae (Kuhn et al., in prep.). Two of the three specimens are complete (Fig. 4). Aside from some sauropod descriptions (Otero et al., 2012) there is little in the way of published descriptive analyses for mammalian haemal arches. We have chosen to measure the breadth of the specimen (A), the height of the specimen (B) and the length of the haemal spine (C) (Fig. 4, Table. 2). Unlike the aforementioned sauropod descriptions which illustrate morphological change as one examines the length of the tail, these three specimens appear to have similar morphology. That being said, one can observe differences between the three specimens, suggesting that they could come from different caudal vertebrae.

BC276, while damaged, is more robust than the other two specimens and has a distinctly broader convex shape than the other two specimens. In addition, BC276 has a groove where the other specimens have a ridge running down the ventral midline. While BC255 and BC369 appear more alike than BC276, there are subtle differences between them as well. BC369 has a more gracile, slender appearance when compared to BC255. These differences suggest that BC276 is more cranial in anatomical position, BC255 would follow with BC369 being the most caudal of the three vertebrae.

DISCUSSION AND CONCLUSION

When examining the clavicle referred here as AC 384 the initial identification pointed towards *Dinofelis* (Zdansky, 1924). After reviewing the work of Hartstone-Rose et al. (2012), it was concluded that this specimen is that of a large *Panthera* (Oken, 1816), and not *Machairodont*. Size alone eliminates *P. pardus* as a possibility (see Table. 2). Considering the variation reported by Hartstone-Rose et al. (2012), and the visual difference in the pair of clavicles taken from an individual male lion, to go beyond *Panthera* (Oken, 1816) is difficult. While *P. atrox* is not a likely fit, the records for fossil pantherine cats in Africa are sparse, with likely candidates being *P. leo*, or a potentially new species (Kuhn et al., in prep.). BC 512 is morphologically indistinct from modern lion clavicles that have been reported or examined. This specimen is definitively *Panthera*, and due to association with other pantherine fossils we are confident in identifying it as a new species of *Panthera* (Kuhn et al., in prep.).

Of note is the identification of two suid species from Aves Cave, *Potamochoeroides hypsodon* (Dale, 1948) and *Notochoerus capensis* (Broom, 1925), which date the locality to c. 3.0–2.6 Ma (Pickford and Gommery, 2016, 2020). Bridge Cave has also yielded suid remains, *Phacochoerus modestus* (Van Hoepen and Van Hoepen, 1932) and *Metridiochoerus andrewsi* (Hopwood, 1926), both of which give an approximate age of 1.8 Ma (Pickford and Gommery, 2020). With a sparse published literature regarding haemal arches we have little in the way of comparative, documented, material with which to draw conclusions. We can conclude with confidence that we have seen haemal arches in two separate fossil collections, one of *Machairodus* (Kaup, 1832) specimens and the other from an extensive collection of *P. spelaea* (Goldfuss, 1810). The three specimens from Bridge Cave are morphologically indistinguishable from either *Machairodus* (Kaup, 1832) or *P. spelaea* (Goldfuss, 1810). This comes as no

surprise given Machairodontinae (Gill, 1872) and Felidae (G. Fisher, 1817) are sister taxa (Christiansen, 2008, 2013) and share many similarities in their postcranial anatomy (pers. obs). Here we have identified five specimens of two skeletal elements (BC 255, BC 276, BC 369, BC 512 and AC 384) which are known to be rare in both modern and fossil collections around the world, clavicle (non-primate) and haemal arch. Worth noting is that both of these elements come from one of the rarer genera identified in the South African fossil record, that being *Panthera* (Oken, 1816). Of note is that when combined with the identified Suidae (Gray, 1821), we can say with confidence that Pantherinae (Pocock, 1917) existed at Bolt's Farm as far back as 2.6–3.0 Ma.

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Fig. 1
Map showing location of Bolt's Farm.

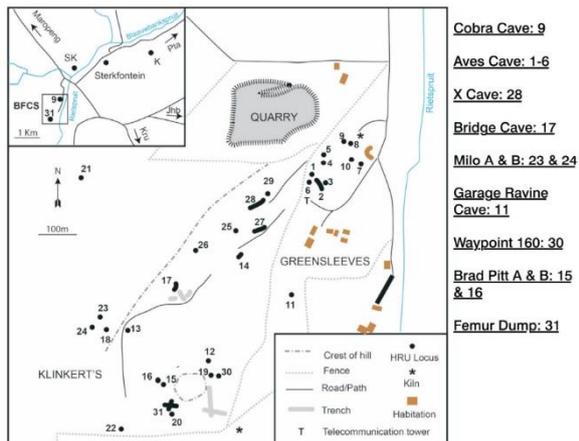


Fig. 2
Map showing fossil localities within Bolt's Farm Palaeokarst System (adapted from Kuhn et al., 2018).



Fig. 3
Clavicles from *Panthera*, BC512 and AC384.

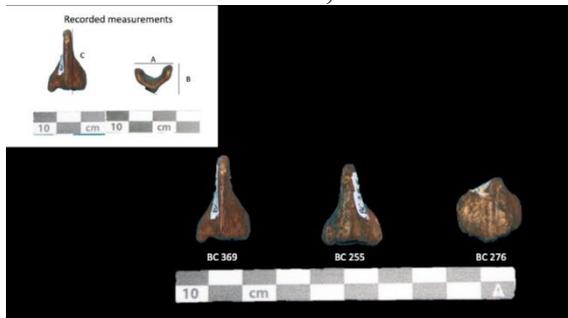


Table 1

Acromial width and thickness of AC 384 compared to reported large *Panthera* species and modern specimens. All measurements are in mm.

Species Acromial	Acromial width (B)	Acromial thickness (C)
AC 384	9.03	3.18
<i>Panthera leo</i> *	11.6	2.9
<i>Panthera onca</i> *	8.1	1.7
<i>Panthera tigris</i> *	10.1	2.6
Rancho La Brea large morph (<i>P. atrox</i>)*	15.1	3.9
<i>Panthera pardus</i> BPI 12/75	4.81	1.55
<i>Panthera leo</i> (R)	6.52	2.41
<i>Panthera leo</i> (L)	9.18	2.49

*Hartstone-Rose et al., 2012

Table 2

Measurements of haemal arches BC255, BC276 and BC369; A is the width of the cranial aspect, B is the height dorsal–ventral and C is the length of the spine.

Specimen	A	B	C
BC255	17.81 mm	11.41 mm	25.11 mm
BC276	18.86 mm	10.01 mm	Damaged
BC369	16.12 mm	11.35 mm	25.06 mm