

Is there evidence for a Congo peafowl (*Afropavo congensis*) in the Middle Stone Age of South Africa? – Comments on Stidham (2008)

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Recently, a fossil Congo peafowl (*Afropavo congensis*) was described from Middle Stone Age Plovers Lake Cave, South Africa.¹ Because this species is now restricted to rainforests in the Congo Basin, it was concluded that the fossil indicates forested, or even rainforest, habitats in the vicinity of Plovers Lake Cave during the Pleistocene.¹ The correct identification of the fossil specimen is, however, questionable, and the hypothesis of densely forested areas in this area 71 000 years ago is at odds with manifold evidence that grasslands and open woodlands predominated the palaeoenvironment in Pleistocene southern Africa.

Key words: *Afropavo*, Plovers Lake, Middle Stone Age, Pleistocene, rainforest, climate change

Recently, Stidham¹ assigned a fossilised proximal end of a right humerus to the Congo peafowl (*Afropavo congensis*). Today, this species is restricted to the Democratic Republic of Congo where it inhabits undisturbed equatorial primary rainforests with dense undergrowth.² The fossil, however, was found in the deposits of the South African Middle Stone Age cave site, Plovers Lake, which has an estimated age of approximately 71 000 years.³ Although other vertebrate fossils found at the same locality indicate a predominance of grassland- and woodland-inhabiting species,³ Stidham¹ proposed that fossil evidence for a Congo peafowl indicates the 'presence of forested or even rainforest habitats near Plovers Lake' and 'represents a significant expansion of its [*Afropavo congensis*] known geographic range'.

Stidham's¹ conclusions are, however, unconvincing for several reasons. First of all, the fossil specimen is almost completely covered with flowstone, making detailed morphological comparisons with fossil and extant galliforms impossible. The majority of the fossil specimens collected at the same site as the putative *Afropavo* humerus are also heavily coated with such a layer of

calcium carbonate,³ though this layer could be removed, for example, with acetic acid.³

It is indeed possible to distinguish *Afropavo* from other galliforms based on distinct features of the proximal humerus, such as the shapes of the fossa pneumotricipitalis and the crista deltopectoralis.^{4,5} In the fossil specimen from Plovers Lake, however, these features are entirely concealed by a calcite crust as mentioned above. Stidham's¹ comparisons are therefore limited to the few exposed areas of the humerus, but it is questionable if the discernible features allow any taxonomic conclusions. Stidham¹ gave two characteristics for distinguishing the fossil from guineafowl (Numididae) – 'rounded ventral expansion' of the bicipital crest and the lack of a 'raised area adjacent to the capital incisure'. When a large set of guineafowl specimens representing all modern species as well as *Afropavo congensis* is considered, both characters turn out to be highly variable within species, and thus unsuitable for identifying the fossil. Hence, the Plovers Lake specimen cannot be distinguished from that of Numididae based on its few discernible morphological features.

The assignment of the fossil to modern Congo peafowl would then rely on size, but not on discrete characters. We found that the proximal end of the humerus of helmeted guineafowl (*Numida meleagris*) and vulturine guineafowl (*Acryllium vulturinum*) is similar in size to that of the fossil specimen as well as of the Congo peafowl (Table 1). Stidham¹ himself vaguely stated that the fossil is 'in the size range of a guineafowl or a peacock' without mentioning which guineafowl species were considered. Furthermore, in comparisons with our own measurements, the dimensions given for the thickness of the humeral head by Stidham¹ appear to be too large relative to the proximal width of the humerus.⁴ Thickness of the humeral head was obviously measured in different ways and comparisons of these measurements are elusive. Therefore, we rely on the proximal width of the humerus only.

The identification of the fossil specimen with *Afropavo* is not convincing, and it is unwarranted to assume the existence of a 'more closed forest or even rain forest [sic]¹ in the vicinity of Plovers Lake area during the Middle Stone Age on the basis of this specimen alone. In fact, the faunal list presented for the very same site³ comprises species that are characteristic either of vast grasslands, e.g. zebra (*Equus burchelli*) and several alcelaphine antelope species, or of open woodlands, e.g. vervet monkey (*Chlorocebus aethiops*), baboon (*Papio ursinus*) and Cape buffalo (*Syncerus caffer*), but not a single species unequivocally indicates the presence of dense forest, let alone rainforest. These observations are in agreement with those at other southern African fossil sites from the Plio-Pleistocene, especially those in the Sterkfontein Valley, less than 10 km southwest of Plovers Lake. The faunal composition at these sites indicates the predominance of grasslands and open woodlands during the past two million years.⁶⁻⁸ During the same period subtropical to tropical woodlands, as well as forests, were evidently replaced by savanna and grasslands in the interior of southern Africa as well as other parts

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Table 1. Measurements (mm) of modern guineafowl species and Congo peafowl in comparison to dimensions of the Plovers Lake specimen.¹ Measurements of the thickness of the humerus head provided by different authors appear to be not comparable (see text). Specimens measured are listed in Table 2.

Humerus	<i>Agelastes niger</i>	<i>Agelastes meleagrides</i>	<i>Guttera plumifera</i>	<i>Guttera pucherani</i>	<i>Numida meleagris</i>	<i>Acryllium vulturinum</i>	Plovers Lake fossil	<i>Afropavo congensis</i>	
								This study	Stidham ^{1,†}
Proximal width	18.1–18.7 (n = 2)	19.7 (n = 1)	17.9–18.7 (n = 2)	18.3–21.4 (n = 5)	19.2–22.0 (n = 8)	21.4–24.0 (n = 4)	21.8	20.6–23.0 (n = 4)	22.4–26.0 (n = 8)
Thickness of head	7.6–7.7 (n = 2)	–	7.8 (n = 1)	7.5–8.8 (n = 4)	8.3–8.9 (n = 2)	8.9–9.4 (n = 3)	9.6	8.4–9.1 (n = 4)	9.6–11.0 (n = 8)

[†]Stidham¹ measured dimensions of left and right humeri of four male *Afropavo congensis*.

Table 2. List of the modern specimens measured.

Species	Specimen numbers
<i>Agelastes meleagrides</i>	LAC 1882.137
<i>Agelastes niger</i>	BMNH S/1961.3.1; IRSN 41605
<i>Guttera plumifera</i>	FMNH 313049; RMCA (QA01)-86337
<i>Guttera pucherani</i>	BMNH S/1971.4.5; CAS 86157; LAC 1888.187; MCZ 342098; RMCA 83364
<i>Numida meleagris</i>	BMNH S/1999.43.66; LAC A 4374; LAC 1835.103; LAC 1880.213; LAC 1885.332; LAC 1909.7; LAC 1921.60; RMCA A2 014 A01
<i>Acryllium vulturinum</i>	LAC 1880.1985; RMCA 98025 A12; RMCA 98025 A07; RMCA 89049 A08
<i>Afropavo congensis</i>	BMNH S/1989.19.16; BMNH S/1977.20.1; BMNH S/1975.16.1; UCBL 1988.1

Acronyms: BMNH, Natural History Museum (Bird Group), Tring, U.K.; CAS, California Academy of Sciences, San Francisco, U.S.A.; FMNH, Field Museum of Natural History, Chicago, U.S.A.; IRSN, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LAC, Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris, France; MCZ, Museum of Comparative Zoology, Peabody Museum, Harvard University, U.S.A.; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; UCBL, Université Claude Bernard Lyon 1, Villeurbanne, France.

of the continent.^{9–11} These environmental changes were triggered by a decrease in both temperature and annual precipitation, a situation also reflected by the dramatically low levels of Lake Malawi, Lake Tanganyika and Lake Bosumtwi.¹² Contemporary African rainforests require an annual precipitation of at least 1 500 mm to exist.¹³ During the Pleistocene, which was generally drier and cooler than today, only a few regions in western and central Africa would have received this level of precipitation.^{13,14} If one accepts current estimates of the distribution of African rainforests during glacial maxima,¹⁴ Plovers Lake would have been about 2 500 km from the nearest rainforest patch in the Congo basin. The restricted distribution of African rainforests obviously prevented the dispersal of folivore colobine monkeys into southern Africa during the Pleistocene.¹⁵ The lack of suitable habitats should also have affected the southward dispersal of other typical rainforest species such as *Afropavo congensis*.

Avery^{7,8} estimated that annual precipitation did not exceed 550 mm during the Plio-Pleistocene at the fossiliferous sites at Sterkfontein, Swartkrans and Kromdraai, just less than 10 km southwest of Plovers Lake. This is obviously far below the threshold for modern rainforests. Rainfall—100 000 years ago—might even have been as low as 330 mm at one particular Middle Stone Age site at Sterkfontein (post Member 6 infill).^{7,8} It seems unlikely that rainfall would have quintupled during the subsequent 30 000 years in this part of southern Africa, which would have been essential for the establishment of a connection to the Pleistocene equatorial rainforest refugia, several thousand kilometres to the north.

Finally, Stidham's speculations on the taphonomy of the fossil specimen are unfounded. Stidham¹ noted that 'bite marks on the specimen likely indicate that the specimen was brought into the cave by mammalian predators...'. These 'bite marks' are two pits discernible in the bone-covering flowstone. Without the removal of this flowstone, it remains unclear as to whether the crust is contouring the relief of actual bite marks on the bone's

surface, or whether the pits are caused by some other, post-depositional taphonomic process.

In conclusion, Stidham's¹ evidence for a Congo peafowl at the Middle Stone Age site, Plovers Lake, is insufficient and probably erroneous. Until the encrusting calcite is removed from the specimen, it would be impossible to rule out its identification as a guineafowl. Any conclusions on the palaeoenvironment and the distribution of rainforests in southern Africa during the late Pleistocene are at this point unjustified and not in accordance with other information, such as composition of mammal faunas, pollen analyses and isotope studies.^{3,7–9}

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- Stidham T.A. (2008). The first fossil evidence of the Congo peafowl (*Galliformes: Afropavo*). *S. Afr. J. Sci.* **104**, 511–512.
- Urban E.K., Fry C.H. and Keith S. (eds) (1986). *The Birds of Africa*, vol. II. Academic Press, London.
- De Ruiter D.J., Brophy J.K., Lewis P.J., Churchill S.E. and Berger L.R. (2008). Faunal assemblage composition and palaeoenvironment of Plovers Lake, a Middle Stone Age locality in Gauteng Province, South Africa. *J. Hum. Evol.* **55**, 1102–1117.
- Louchart A. (2003). A true peafowl in Africa. *S. Afr. J. Sci.* **99**, 368–371.
- Ksepka D.T. (2009). Broken gears in the avian molecular clock: new phylogenetic analyses support stem galliform status for *Gallinuloides wyomingensis* and rallid affinities for *Amitabha urbsinterdictensis*. *Cladistics* **25**, 173–197.
- Vrba E.S. (1976). The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Mus. Mem.* **21**, 1–166.
- Avery D.M. (1995). Southern savannas and Pleistocene hominid adaptations: the micromammalian perspective. In *Paleoclimate and Evolution with Emphasis on Human Origins*, eds E. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 459–478. Yale University Press, New Haven and London.
- Avery D.M. (2001). The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *J. Hum. Evol.* **41**, 113–132.
- Scott L. (1995). Pollen evidence for vegetational and climatic change in southern Africa during the Neogene and Quaternary. In *Paleoclimate and Evolution with Emphasis on Human Origins*, eds E. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 65–76. Yale University Press, New Haven and London.
- Bobé R. and Behrensmeyer A.K. (2004). The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Paleogeogr. Paleoclimatol. Paleocol.* **207**, 399–420.
- McCarthy T. and Rubidge B. (2005). *The Story of Earth and Life – A Southern African Perspective on a 4.6-Billion-Year Journey*. Struik Publishers, Cape Town.
- Cohen A.S., Stone J.R., Beuning K.R.M., Park L.E., Reinthal P.M., Dettman D., Scholz C.A., Johnson T.C., King J.W., Talbot M.R., Brown E.T. and Ivory S.J. (2007). Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. *Proc. Natl. Acad. Sci. USA* **104**, 16422–16427.
- Tchouto M.G.P., de Wilde J.J.E.E., de Boer W.F., van der Maesen L.J.G. and Cleef A.M. (2008). Bio-indicator species and Central African rain forest refuges in the Campo-Ma'an area, Cameroon *Syst. Biodivers.* **7**, 21–31.
- Plana V. (2004). Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. *Phil. Trans. Roy. Soc. Lond. B* **359**, 1585–1594.
- Benefit B.R. (1999). Biogeography, dietary specialization, and the diversification of African Plio-Pleistocene monkeys. In *African Biogeography, Climate Change, and Human Evolution*, eds T.G. Bromage and F. Schrenk, pp. 172–188. Oxford University Press, New York and Oxford.