IBIS
BOU international journal of avian science
*Ibis* (2021), **163**, 714–720
doi: 10.1111/ibi.12907

Short Communication

# Bucerotidae from the early Miocene of Napak, Uganda (East Africa): the earliest hornbill with a modern-type beak

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Hornbills (Bucorvidae and Bucerotidae) are among the most recognizable groups of birds. Their large, curved beak topped by a casque is their most obvious feature. Here, we describe the earliest fossil of a hornbill, and more precisely a Bucerotidae, from the early Miocene of Napak, Uganda. This fossil is a proximal part of a maxilla that can be tentatively assigned to the genus *Tockus* and which attests to an ancient evolutionary origin of this particular beak shape. The new fossil, as well as several postcranial bones, represents the earliest record of the Bucerotidae dated to about 19 million years ago, and can serve as a calibration point in future molecular phylogenies.

**Keywords:** Bucerotiformes, casque, evolution, fossil, *Tockus*.

The family Bucerotidae (hornbills) includes 62 extant species represented by medium to very large birds with large, curved bills, topped by a hollow casque, a dorsal outgrowth of their maxilla composed of bone covered by rhamphotheca (Gamble 2014, Winkler *et al.* 2020). There is considerable variation in the size and shape of these casques. In many hornbill species it is developed as a large, imposing and elaborate structure, but some species possess only a vestigial casque, reduced to a ridge (Mayr 2018). Casques are present in both sexes, being usually larger in the males. The Bucerotidae are palaeotropical birds with a distribution that extends from sub-Saharan Africa to southeast Asia and northern Australasia (Gonzalez *et al.* 2013, Winkler *et al.* 2020).

The fossil record of hornbills is sparse and relatively controversial (Olson 1985). The oldest valid hornbill specimens belong to *Bucorvus brailloni* (Brunet 1971) from the middle Miocene (14–13 Ma) of Beni-Mellal, north of the Atlas Mountains in Morocco, and cf. *Tockus* sp. from the middle Miocene (15–14 Ma) of Kenya (Mayr 2014). The only other pre-Pleistocene records are from the late Miocene (8–7 Ma) of Bulgaria and the early Pliocene (4.4 Ma) of Ethiopia (Boev & Kovachev 2007, Louchart *et al.* 2009). Herein we describe a fossil hornbill from the early Miocene (20–18 Ma) of East Africa discovered at Napak (Uganda), which represents the earliest record of the Bucerotidae.

## METHODS

Our adopted systematic arrangement conforms to that in the International Ornithological Congress World Bird List (Gill *et al.* 2020). In particular, the genus *Bucorvus* (ground hornbills) belongs to the family Bucorvidae, separated from the family Bucerotidae (all other hornbills).

### Fossil material

The fossil (NAP XII 8'10) was collected during the 2010 field season of the Uganda Palaeontology Expedition (a Franco-Ugandan cooperative project in Palaeontology). The fossil is a fragment of the proximal part of the maxilla. It is composed of a sedimentary infilling forming an internal mould which is partially covered with bone (Fig. 1). The bone cortex is very thin in some Bucerotidae, particularly the cranial parts, which explains why bone does not cover all of the natural internal mould of the Napak maxilla. All the Napak fossil specimens are curated at the Uganda Museum, Kampala.

### Comparative materials

The Napak fossil was compared with 13 extant species of Bucerotidae, as well as at least one species each of other Bucerotiformes (Upupidae, Phoeniculidae) and of most other bird families, in particular those comprising species that exhibit a rather wide and high proximal maxilla of comparable dimensions and/or shape, such as the Ramphastidae (Piciformes), Psittacidae (Psittaciformes), and most other non-passerine families and large-beaked passerines (see Supporting Information Appendix S1).

### Geological context and age

Fossil NAP XII 8'10 was collected from the Napak fossil deposits, located in the Karamoja region in northeastern

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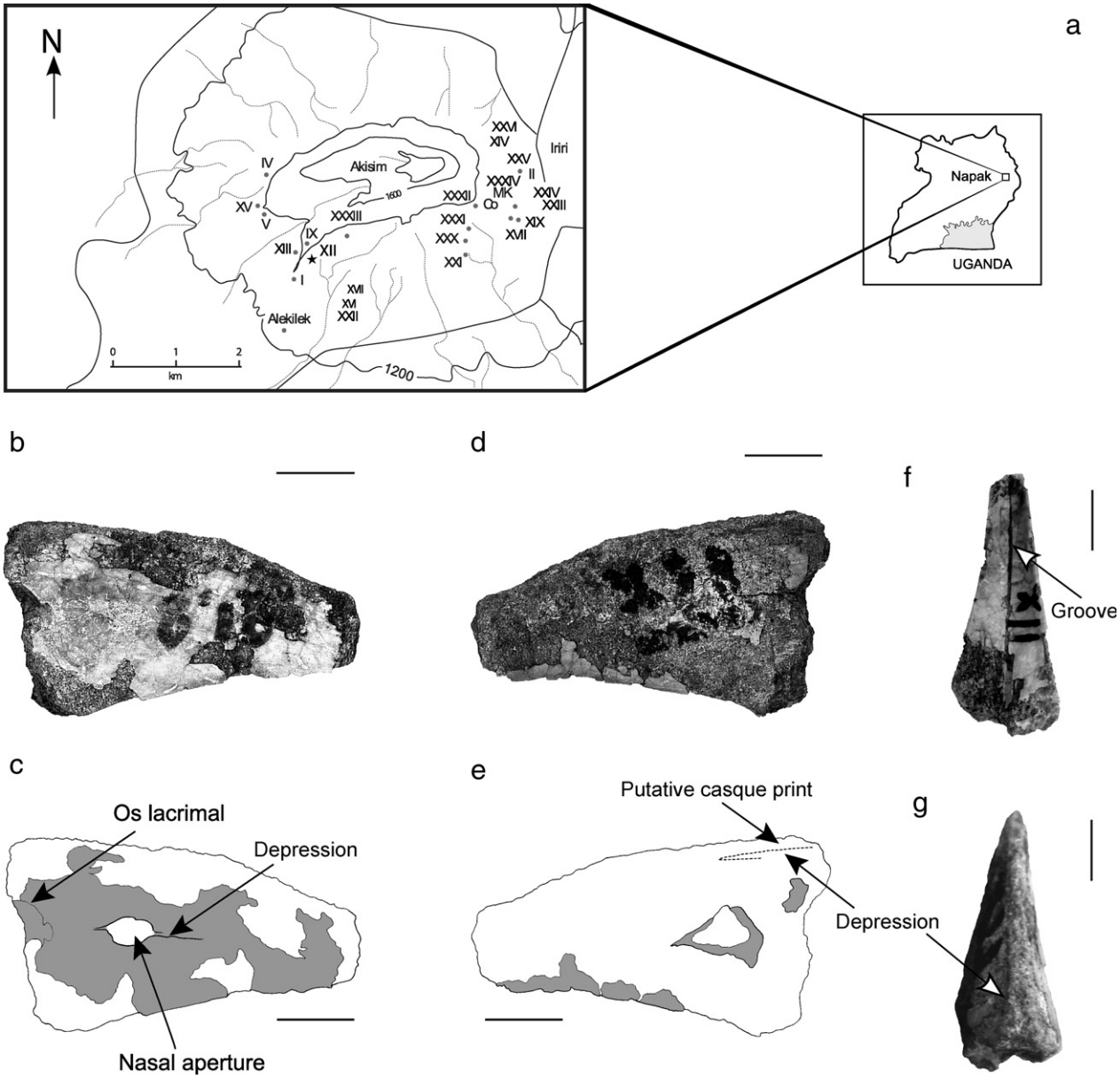


**Figure 1.** Map of the Napak Volcano, Karamoja, and different views of the Napak fossil. (a) Position of the fossiliferous localities at Napak from Pickford *et al.* (2019). The star symbol corresponds to the site where the fossil was collected. (b,d,f,g) Fossil proximal maxilla NAP XII 8'10. (b,d) Lateral view. (f) Ventral view. (g) Dorsal view. In the photos, the bone is a lighter colour than the background matrix. (c,e) Interpretative line drawing with the areas in grey corresponding to the bone. Scale bars: 10 mm.

Uganda. This geological formation consists of volcano-sedimentary strata, which accumulated on the slopes of the Napak volcano. Ash deposition resulted in rapid burial and played a role in fossil mineralization. Tuffs (volcano-sedimentary rocks formed by consolidation of millimetric volcanic projections, under the action of water) often enhance the preservation of fossils (Hay 1986). Two stratigraphic units have been identified in the deposits; the locality NAP XII is situated in the upper unit, the Napak Member, which consists of palaeosols developed on subaerial tuffs (Pickford *et al.* 1986). The Napak strata were dated to the Lower Miocene, 20–18 Ma (Bishop *et al.* 1969, Pickford 2002, Y. Sawad, B. Senut, M. Pickford, M. Hyodo, unpubl. data). Napak fossil sites have yielded many fossils, including Hominoidea and a high diversity of other Mammalia

and Mollusca (Bishop *et al.* 1969, Senut *et al.* 2000, Gommery *et al.* 2002, Pickford 2002, 2004, Musalizi *et al.* 2009, Bento Da Costa *et al.* 2019). Site NAP XII is located on the southern side of the volcano, near a ridge line (Fig. 1).

## RESULTS

### Systematic palaeontology

Order Bucerotiformes Fürbringer, 1888
Family Bucerotidae Rafinesque, 1815
Genus *Tockus* Lesson, 1830
cf. *Tockus* sp.

### Description and comparisons

The Napak fossil was compared with birds with imposing beaks (toucans, parrots and hornbills) and a number of other species in almost all non-passerine families (and large-beaked passerines such as corvids). The position and size of the nasal aperture and the general morphology of the fossil are very different from those of toucans and parrots; and the maxillae of all other birds (except hornbills) differ strongly in morphology from the fossil, too. In contrast, the fossil maxilla matches that of hornbills, especially the Bucerotidae, in particular exhibiting: (1) relatively imposing size, height and width (Mayr 2018); (2) some evidence of a rudimentary ridge-like casque (see below); (3) a downcurved shape (see Winkler *et al.* 2020); and (4) small nasal apertures located at the base of the casque (Figs 1 and 2). In view of the morphology of the maxilla, the Napak bird seems to have possessed a rather small beak surmounted by a ridge-like casque. In extant hornbills, the casque can be imposing and elaborate or of small size and reduced to a ridge. In all species with a well-developed casque, the beak – and in particular the base of the casque – is wider than in ridge-like, simple casqued species. The casque of the Napak hornbill is obviously narrow, is of very small size and appears to have corresponded to a ridge, and there is no indication of a missing or broken part dorsal to the proximal maxilla (Fig. 1). In addition, the beak of extant hornbills with a casque reduced to a ridge shows a slight depression at the base of the casque and the Napak fossil exhibits this depression (Fig. 1). These characters are present in the genera *Lophoceros*, *Tockus*, *Horizocerus* and *Ocyceros* (Gamble 2014). However, the male and female of the Indian Grey Hornbill *Ocyceros birostris* and Crowned Hornbill *Lophoceros alboterminatus* possess a better developed and more elaborate casque compared with that of the fossil (Fig. 2). Like the extant Bucerotidae with a casque reduced to a ridge, the maxilla of the Napak bird has a very thin bone cortex (Fig. 1, Supporting Information Fig. S1). In ventral view, the fossil maxilla shows a sagittal groove extending over the length of the preserved maxilla (Fig. 3), similarly visible in most extant Bucerotidae, separating the right and left parts of the premaxillary.

In lateral view, the fossil maxilla shows a depression in line with the nasal aperture, rostrally (Fig. 3). This morphology is found on the maxilla of the Bucerotidae with greater curvature. This characteristic, combined with the size of the fragmentary maxilla, indicates some resemblance between the fossil and extant species such as African Pied Hornbill *Lophoceros fasciatus* and Von der Decken's Hornbill *Tockus deckeni*. The tomial ridges are low. The maxilla is relatively narrow dorso-ventrally and has a narrow culmen. The only extant species compared that possesses all these characters is Von der Decken's Hornbill (Fig. 3). However, in lateral view and even when taking account of the expanded tomial edges and tip of the maxilla rhamphotheca beyond those of the underlying bone, the fossil maxilla probably corresponds to a shorter beak that is less down-curved than in a male Von der Decken's Hornbill (Fig. 3), but is otherwise equivalent in size. The distance between the nasal aperture and the lacrimal, as well as the width of the maxilla, are similar in the fossil and in Von der Decken's Hornbill. A smaller, female specimen of the latter species exhibits closer similarity in all shape criteria with the fossil, including in lateral view with profile and curvature as in the fossil and is only smaller in size (Fig. 3).

Extant hornbill species other than *T. deckeni* and the closely related and morphologically similar Jackson's Hornbill *Tockus jacksoni* (Kemp 1976, Winkler *et al.* 2020) appear morphologically more distant from the fossil and, among them, the Bucorvidae (genus *Bucorvus*) are distinctly different in size (much larger) and shape (e.g. shape of casque, beak much less curved, nostril more distal and the proportions of the maxilla in transverse section are different; Fig. 2).

## DISCUSSION

The part of the maxilla of the Napak bird exhibits a narrow culmen (Fig. 1), unlike all hornbills with a developed casque, which have a wide culmen. The beak of hornbills with a casque reduced to a ridge shows a slight depression at the base of the casque, as does the fossil (Fig. 1). The upper part of the fossil maxilla is only preserved as an internal mould and the distal part of the putative casque appears not to be preserved. However, we feel the available evidence suggests that the casque of the Napak bird is reduced to a narrow and undeveloped ridge.

The fossil maxilla from Napak is rather similar to that of male Von der Decken's Hornbill, but it seems slightly less curved and exhibits a less domed culmen; the whole

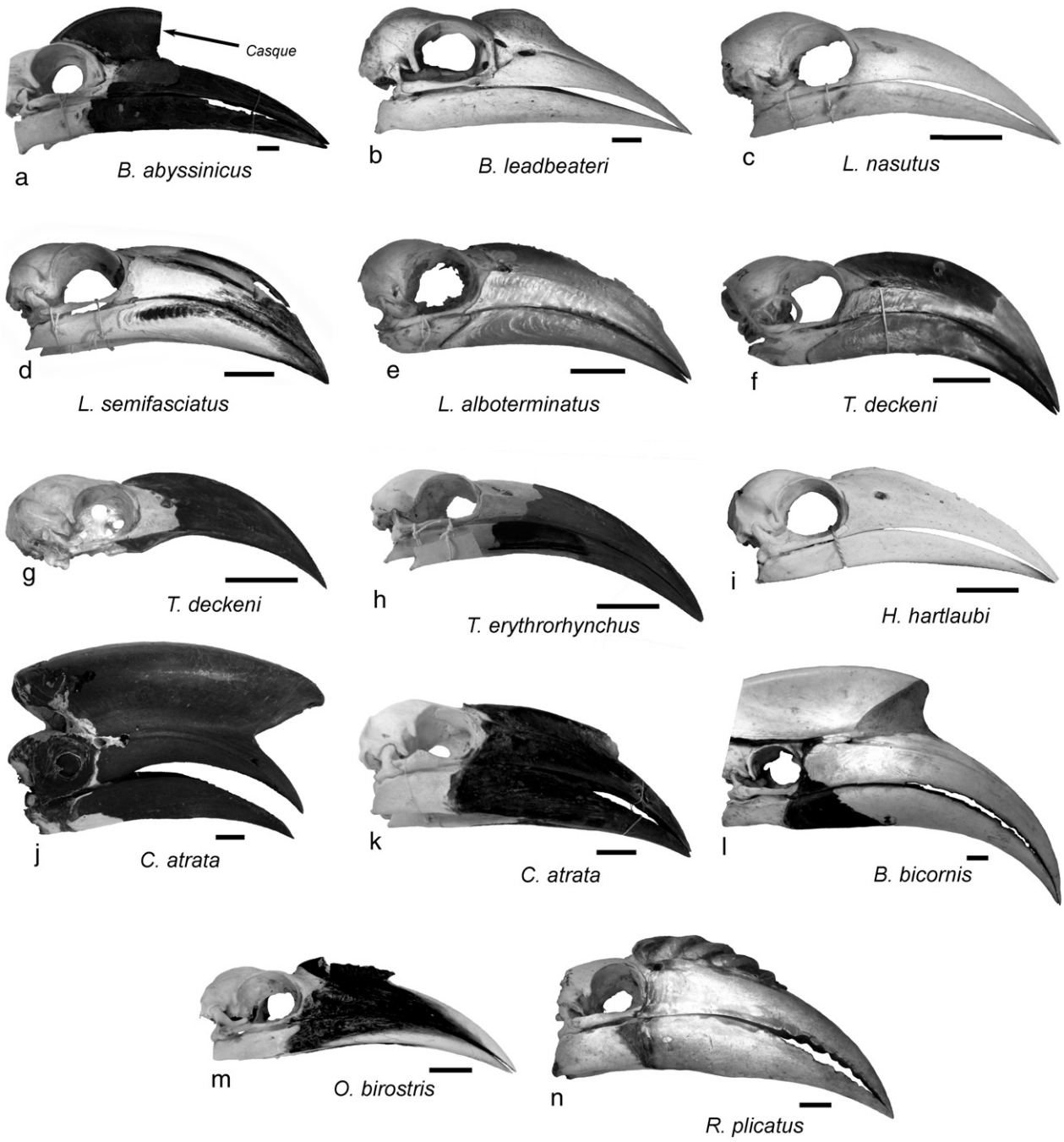


**Figure 2.** Skulls of extant Bucorvidae and Bucerotidae compared with the Napak fossil. All individuals are adults. (a) Abyssinian Ground Hornbill *Bucorvus abyssinicus*. (b) Southern Ground Hornbill *Bucorvus leadbeateri*; absence of the rhamphotheca. (c) African Grey Hornbill *Lophoceros nasutus*; absence of the rhamphotheca. (d) *Lophoceros fasciatus*; the distal part of the casque is broken. (e) *Lophoceros alboterminatus*; the top of the beak is broken. (f) *Tockus deckeni* (male). (g) *Tockus deckeni* (female). (h) Northern Red-billed Hornbill *Tockus erythrorhynchus*; absence of the rhamphotheca on the proximal part of the beak. (i) Black Dwarf Hornbill *Horizocerus hartlaubi*; absence of the rhamphotheca. (j) Black-casqued Hornbill *Ceratogymna atrata* (male). (k) *Ceratogymna atrata* (female); the tip of the casque is broken. (l) Great Hornbill *Buceros bicornis*. (m) *Ocyceros birostris*; the top of the casque is missing. (n) Blyth's Hornbill *Rhyticeros plicatus*. (a,b,j–n) Hornbills with an imposing and elaborate casque. (c–i) Hornbills with a vestigial casque, reduced to a ridge. All right lateral views. The sex of each individual compared is specified in Appendix S1, when known. Scale bars: 20 mm.

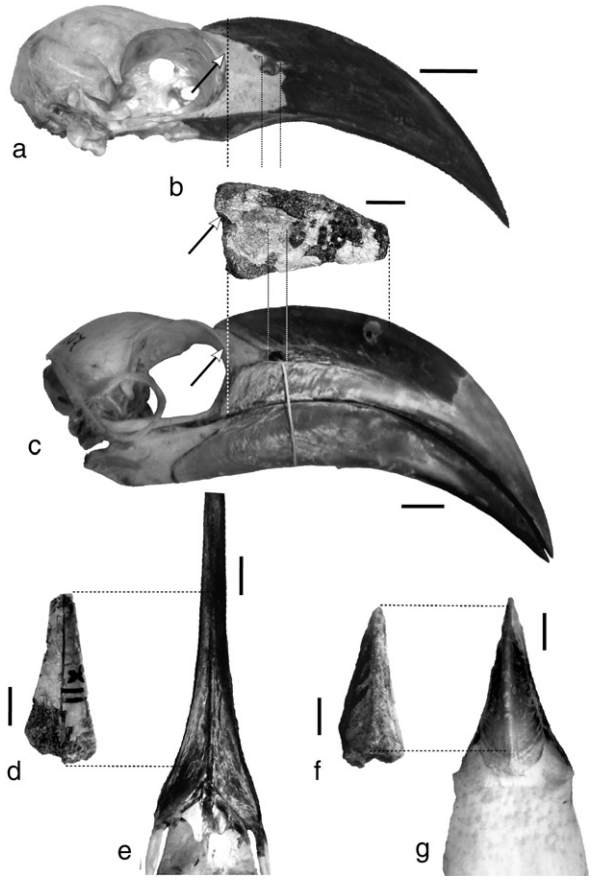


**Figure 3.** Comparisons between the Napak fossil and Von der Decken's Hornbill. (a) Von der Decken's Hornbill (with large part of the rhamphotheca), female. (b,d,f) NAP XII 8'10. (c,e,g) Von der Decken's Hornbill (with rhamphotheca), male. (a–c) Right lateral views. (d,e) Ventral views. (f,g) Dorsal views. In ventral view the fossil shows the sagittal line separating the right and left parts of the premaxillary as in the modern hornbill. The Napak fossil and Von der Decken's Hornbill have similar beak sizes and proportions. The thick dotted lines indicate the position of the fossil maxilla relative to that of Von der Decken's Hornbill. The thin dotted lines indicate a similar size and location of the nasal aperture of the Napak fossil with those of Von der Decken's Hornbill. Arrows show the lacrimal. Only the lateral profile differs between the fossil and the modern specimen (especially the male), and this is partly due to the latero-ventral expanded tomia and tip of the maxilla rhamphotheca, beyond the tomial edges of underlying bone, and unlike other parts of the maxilla, where the rhamphotheca is regularly thin. The smaller female specimen (a) better matches the fossil in shape, being smaller and less domed than the male. Scale bars: 10 mm.

maxilla was probably shorter. The casque of hornbills comprises the keratinous rhamphotheca, which covers the bony core. In most species, the casques have spongy bone limited to the caudal part of the casque. The shape of the casque is therefore not reflected entirely by the bony parts of the beak. In small hornbill species such as *Tockus*, the bony portions of the beak are almost unmodified by the rhamphotheca covering, which is thin (Mayr 2018) (Fig. S1), except on the tomial regions. Therefore, the rhamphotheca does not explain (except, partly, towards the tomia and tip of the maxilla) the differences between the fossil beak morphology and that of the beak of male Von der Decken's Hornbill.

However, in Von der Decken's Hornbill, sexual dimorphism is clearly expressed in the beak. The female is smaller than the male and possesses a smaller beak. The female beak also has a slightly less developed casque (Fig. 2), resulting in a less domed culmen (Winkler *et al.* 2020). The Napak hornbill fossil maxilla appears to be larger than that of a female Von der Decken's Hornbill, but is close in shape, including in lateral view, being similarly less domed and shorter than in a male (Fig. 3). The fossil maxilla is therefore considered compatible with a representative of the genus *Tockus*, even though we prefer to make this generic assignment tentatively here, given the fragmentary nature of the fossil. It probably represents an extinct species that we refrain from naming here for the same reason as above.

Being compatible with *Tockus*, different from other Bucerotidae and even more distant morphologically from *Bucorvus* (Bucorvidae), the Napak fossil is *a minima* assignable to the Bucerotidae (exclusive of the Bucorvidae).

Interestingly, Napak localities have provided a number of bird fossils of different families, including five post-cranial fragments belonging to the Bucerotidae (Supporting Information Fig. S2). Postcranials in the Bucorvidae are very different from the present fossils and much lighter with a thinner bone cortex. The Napak postcranials (and of all represented bird families from Napak) will be described separately. However, they are morphologically similar to a representative of the genus *Tockus* and slightly smaller than in a female Von der Decken's Hornbill (Fig. S2). Therefore, these five postcranials, even though not of a single individual, can potentially represent the same hornbill species as the maxilla, all tentatively assigned to the genus *Tockus*. This species would have had a large beak relative to the postcranials when compared with a female Von der Decken's Hornbill. Alternatively, more than one species tentatively assignable to *Tockus* was represented in the early Miocene of Napak.

The fossil record of hornbills is extremely poor and consists of only four other published pre-Pleistocene occurrences, presumably in part due to the particularly thin bone cortex of hornbills (maximally in the Bucorvidae). One is the distal tarsometatarsus of *Bucorvus brailloni* (Bucorvidae) from the middle Miocene (14–13 Ma) of Morocco (Brunet 1971). Another is a right coracoid, from the middle Miocene (15–14 Ma) of Maboko,

Kenya, assigned to cf. *Tockus*, and tentatively a distal humerus (Mayr 2014) (Bucerotidae). Two other specimens are a fragmentary scapula and femur of *Euroceros bulgaricus* (Bucorvidae) from the late Miocene (8–7 Ma) of Bulgaria (Boev & Kovachev 2007). In addition, two bones (distal ulna and distal radius) of a species of *Bucorvus* (Bucorvidae) were identified in the Pliocene (4.4 Ma) of Ethiopia (Louchart *et al.*2009). The Napak fossils (maxilla and postcranials), at 20–18 Ma, are thus the oldest known representatives of a hornbill and of the Bucerotidae in the world. They increase the age of differentiation of the crown hornbills (earlier than 20–18 Ma) and furthermore of the Bucerotidae. This age is consistent with the latest phylogenetic studies, which indicate a divergence age between Bucorvidae and Bucerotidae (at least between Bucorvidae and *Tockus* hornbills) in the late Oligocene (22.5 Ma, with a large 95% confidence interval between 39 and 7.5 Ma; Prum *et al.* 2015). Given this large confidence interval for the lower limit of Bucerotidae, the Napak fossil Bucerotidae cf. *Tockus* sp. will be useful for calibrating future phylogenies. Other recent analyses noticeably place the Bucorvidae as sister to *Tockus* hornbills (divergence at 25.8 Ma, with crown *Tockus* hornbills age at 19.1 Ma), forming together a clade sister to all other hornbills (see OneZoom Tree of Life explorer online; Jetz *et al.* 2012, Rosindell & Harmon 2012). Under this framework, the new fossil similarly has the potential to help add precision to calibrating phylogenies. In addition, the existence of hornbills of large and very small sizes, of the two families, slightly later in the middle Miocene of Africa (15–14 Ma, Mayr 2014; 14–13 Ma, Brunet 1971) indicates that the hornbills were already morphologically diversified by that time and that the origin of the stem group lies substantially earlier (possibly as early as the middle or late Eocene according to recent molecular studies; Prum *et al.* 2015). Finally, the Napak bucerotid hornbill is interesting in that, being the oldest representative of this characteristic family, it already possessed a modern-type beak morphology, revealing limited subsequent morphological change (albeit with later important diversification), although bird beaks generally show significant scalability. This recalls (even though less markedly) the example of 'evolutionary stasis' illustrated by an Oligocene pelican beak (Louchart *et al.* 2011).

We thank the following curators and institutions for providing extant comparative specimens and photographs: Emmanuel Robert (UCBL-FSL, Villeurbanne, France), Christine Lefèvre (MNHN, Paris, France), Alain Reygel (RMCA, Africamuseum, Tervuren, Belgium) and Gerald Mayr (Senckenberg, Frankfurt, Germany). We thank the Uganda Museum (Rose Nkaale Mwanja, Ezra Musiime and Sarah Musalizi) for arranging access to the Ugandan fossils. Authorization to carry out research in the country since 1985 was obtained from the UNCST and to excavate from the Commissioner for Antiquities. The research was funded by the Commission des Fouilles Archéologiques à l'étranger (MEAE) and the CNRS (GDRI 193, PICS 1048, UMR 7207). Support of the French Embassy in Kampala is greatly appreciated. Thanks are due to the field team in Napak and the local leaders. We thank two anonymous reviewers, Gary Voelker and Rauri Bowie for comments on an earlier draft of the manuscript that helped to improve it.

## AUTHOR CONTRIBUTION

**Ségolène Riamon:** Formal analysis (equal); Investigation (equal); Validation (supporting); Visualization (lead); Writing-original draft (equal). **Martin Pickford:** Data curation (lead); Funding acquisition (lead); Methodology (supporting); Resources (supporting); Supervision (supporting); Validation (supporting); Writing-review & editing (supporting). **Brigitte Senut:** Data curation (equal); Funding acquisition (lead); Methodology (supporting); Resources (lead); Supervision (supporting); Validation (supporting); Writing-review & editing (supporting). **Antoine Louchart:** Conceptualization (lead); Formal analysis (supporting); Investigation (supporting); Methodology (lead); Supervision (lead); Validation (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (lead).

## Data Availability Statement

All the data supporting the present study are included within the article itself and the online supporting information.

## REFERENCES

**Bishop, W.W., Miller, J.A. & Fitch, F.J.** 1969. New potassium–argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Am. J. Sci.* **267**: 669–699.

**Boev, Z. & Kovachev, D.** 2007. *Euroceros bulgaricus* gen. nov., sp. nov. from Hadzhidimovo (SW Bulgaria) (late Miocene) the first European record of hornbills (Aves: Coraciiformes). *Geobios* **40**: 39–49.

**Brunet, J.** 1971. Oiseaux miocènes de Beni-Mellal (Maroc); un complément à leur étude. *Notes Mém. Serv. Géol. Maroc.* **31**: 109–111.

**Da Costa, L.B., Senut, B., Gommery, D. & Pickford, M.** 2019. Dental remains of Lower Miocene small rodents from Napak (Uganda): Afrocricetodontidae, Myophiomyidae, Kenyamyidae and Sciuridae. *Ann. Paléont.* **105**: 155–167.

**Gamble, K.C.** 2014. Coraciiformes (Kingfishers, Motmots, Bee-Eaters, Hoopoes, Hornbills). *Fowler's Zoo and Wild Animal Medicine*. Volume 8-E-Book **8**: 225.

**Gill, F., Donsker, D. & Rasmussen, P. (eds).** 2020. *IOC World Bird List*. (v10.2). https://doi.org/10.14344/IOC.ML.10.2

**Gommery, D., Senut, B., Pickford, M. & Musiime, E.** 2002. Les nouveaux restes du squelette d'*Ugandapithecus major* (Miocène inférieur de Napak, Ouganda). *Ann. Paléont.* **88**: 167–186.

**Gonzalez, J.C.T., Sheldon, B.C., Collar, N.J. & Tobias, J.A.** 2013. A comprehensive molecular phylogeny for the hornbills (Aves: Bucerotidae). *Mol. Phylogenet. Evol.* **67**: 468–483.

**Hay, R.L.** 1986. Role of tephra in the preservation of fossils in Cenozoic deposits of East Africa. *Geol. Soc. Lond. Spec. Publ.* **25**: 339–344.

**Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O.** 2012. The global diversity of birds in space and time. *Nature* **491**: 444–448.

**Kemp, A.C.** 1976. Radiation in the behaviour and external morphology of the members of the genus *Tockus*. *Transvaal Mus. Mem.* **20**: 35–46.

**Louchart, A., Tourment, N. & Carrier, J.** 2011. The earliest known pelican reveals 30 million years of evolutionary stasis in beak morphology. *J. Ornithol.* **152**: 15–20.

**Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, J.K., Black, M.T., Asnake, M. & White, T.D.** 2009. Taphonomic avian and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science* **326**: 66: 66e1-66e4.

**Mayr, G.** 2014. On the middle Miocene avifauna of Maboko Island, Kenya. *Geobios* **47**: 133–146.

**Mayr, G.** 2018. A survey of casques, frontal humps, and other extravagant bony cranial protuberances in birds. *Zoomorphology* **137**: 457–472.

**Musalizi, S., Senut, B., Pickford, M. & Musiime, E.** 2009. Geological and palaeontological archives relating to early Miocene localities of Uganda, 1957–1969. *Geo-Pal. Uganda* **1**: 2–96.

**Olson, S.L.**1985. The fossil record of birds. In: Farner, D.S., King, J.R. & Parkes, K.C. (eds). *Avian Biology*, Vol. **8**; 79–238. New York: Academic Press.

**Pickford, M.** 2002. Ruminants from the early Miocene of Napak, Uganda. *Ann. Paléont.* **88**: 85–113.

**Pickford, M.** 2004. Palaeoenvironments of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Ann. Paléont.* **90**: 1–12.

**Pickford, M., Senut, B., Hadoto, D., Musisi, J. & Kariira, C.** 1986. Nouvelles découvertes dans le Miocène inférieur de Napak, Ouganda Oriental. *C. R. Acad. Sci. Paris Sér* **2** (302): 47–52.

**Pickford, M., Senut, B., Musalizi, S., Gommery, D. & Ssebuyungo, C.** 2019. Early Miocene Victoriapithecid Monkey from Napak, Uganda. *Geo-Pal. Uganda* **12**: 1–17.

**Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M. & Lemmon, A.R.** 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**: 569–573.

**Rosindell, J. & Harmon, L.J.** 2012. OneZoom: A Fractal Explorer for the Tree of Life. *PLoS Biol.* **10**: e1001406. https://doi.org/10.1371/journal.pbio.1001406. Website: http://www.onezoom.org/OZtree/static/OZLegacy/EDGE_birds.htm (accessed 29 October 2020).

**Senut, B., Pickford, M., Gommery, D. & Kunimatsu, Y.** 2000. A new genus of Early Miocene hominoid from East Africa: *Ugandapithecus major* (Le Gros Clark & Leakey, 1950). *C. R. Acad. Sci. Paris Sér IIa* **331**: 227–233.

**Winkler, D.W., Billerman, S.M. & Lovette, I.J.** 2020. Hornbills (Bucerotidae), version 1.0. In Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (eds) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.bucero1.01

Received 7 April 2020;
Revision 26 September 2020;
revision accepted 24 November 2020.
Associate Editor: Gary Voelker

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of comparative skull specimens of extant species that were examined.

Figure S1. Skulls of extant Bucerotidae, with a casque reduced to a ridge, showing a thin rhamphotheca that exactly parallels the shape of the underlying beak bone.

Figure S2. Napak post-cranial fossil fragments of Bucerotidae (cf. *Tockus* sp.) compared with the same elements in an extant Bucerotidae (*Tockus deckeni*, SMF 19366, female).