Using Mitogenomes to Explore the Social and Ecological Contexts of Crocodile Mummification in Ancient Egypt

Evon R. Hekkala[1], Roger Colten[2], Seth W. Cunningham[3], Oliver Smith[4], and Salima Ikram[5]

[1]*Corresponding author*: Department of Biological Sciences, Fordham University, Bronx, NY 10458 USA
—*email*: EHekkala@Fordham.edu

[2]Division of Anthropology, Peabody Museum of Natural History, Yale University, New Haven, CT 06520–8118 USA

[3]Department of Biological Sciences, Fordham University, Bronx, NY 10458 USA

[4]Micropathology, Ltd., University of Warwick Science Park, Coventry, CV4 7EZ, United Kingdom

[5]Department of Sociology, Egyptology, and Anthropology, The American University in Cairo, Cairo, Egypt

ABSTRACT

We used isotopic and genomic data to explore the ecological and social context of cultural practices associated with the mummification of crocodiles in ancient Egypt. Ancient DNA was recovered from four mummified crocodile hatchlings held in the collections of the Peabody Museum of Natural History, Yale University. Previous genetic analyses of crocodile mummies have indicated that most mummies represent the newly resurrected taxon, *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807. However, mitogenomic data for the Yale Peabody Museum mummies indicates that these specimens represent the first genomically authenticated representatives of the Nile crocodile (*Crocodylus niloticus* Laurenti, 1768) in museum collections. We explore these findings within the broader context of modern and historical distributions of both crocodile species and the potential implications for our understanding of funerary practices involving crocodiles in ancient Egypt.

KEYWORDS

Ancient DNA, *Crocodylus*, Nile crocodile, Egyptian animal mummies, religion

Introduction

Communities living in close proximity to, and exploiting, local wildlife populations gather knowledge via direct observations of natural history or through the cultural transmission of such knowledge. Cosmologies and cultural practices involving animals usually entail highly developed taxonomies and belief systems regarding the relationships of animals to both the natural and divine world. By examining the prevalence of a specific species from bioarchaeological settings over time and space we may be able to detect evidence for shifts in species distributions attributable to environmental conditions, overexploitation, or directly due to changing cultural preferences. Here, we contribute to the broader understanding of cultural and ecological contexts for crocodile mummification in ancient Egypt by adding isotopic and genomic data for a set of mummies from the collections at the Yale Peabody Museum of Natural History.

The ancient Egyptians mummified crocodiles within two main contexts: sacred animals and votive offerings (Ikram 2015:1–16). In the case of the former, the Egyptians believed that part of the soul of the god Sobek (the crocodile headed god responsible for fertility) entered the body of a crocodile that could be identified as special by its markings. During its lifetime the crocodile would be revered as if it were a god and consulted as an oracle. Priests would feed it with delicacies, care for it, and adorn it with gold jewelry, as described by 5th and 1st century BC visitors to these cult centers (Herodotus, bk 2, 69; Strabo, bk 17, 38). On its death the crocodile would be mummified and buried in a tomb or within a larger catacomb, and the god's soul would then pass into the body

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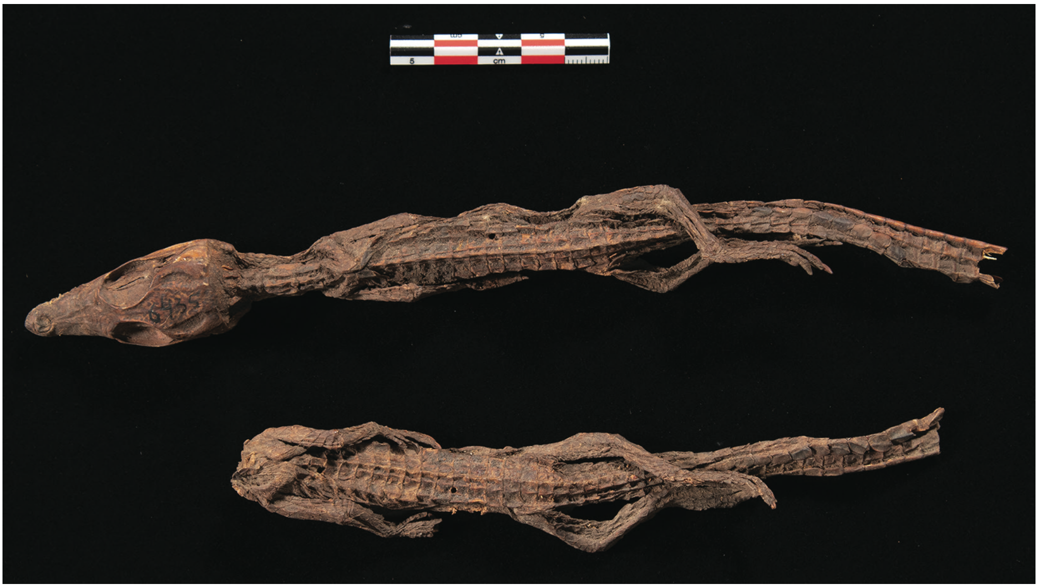

Figure 1. Two hatchling crocodile mummies from the Barringer Egyptian Collection, Division of Anthropology, Yale Peabody Museum of Natural History. *Top*: YPM ANT 006435.004 (2070 ± 30 BP), for which we recovered mitochondrial genomic fragments. *Bottom*: YPM ANT 006435.007 (2010 ± 30 BP), for which we recovered a nearly complete mitochondrial genome. Scale bar is in centimeters.

of another crocodile; this idea is similar to the concept of the soul of the Dalai Lama migrating from body to body (Bresciani 2005; Ikram 2005, 2015). Occasionally, large temple crocodiles were mummified with sets of hatchling crocodiles attached along the dorsal surface, in the mouth, or distributed elsewhere within the wrappings (e.g., Egyptian Museum, Cairo, Egypt, CG 29628; British Museum, London, United Kingdom, EA38562; Phoebe A. Hearst Museum of Anthropology, Berkeley, Californai, USA, 55–12, 55–13, 55–14). The specific meaning of the association is unclear, but several hypotheses have emerged. The relationship of the adult to the hatchlings could be the purely symbolic representation of Sobek's fertility (any adult crocodile could be mummified with multiple unrelated hatchlings attached) or could represent the true biological relationship of the adult to its own offspring (likely an adult female crocodile with hatchlings from her nest attached).

Votive crocodile mummies, in contrast, were given as offerings to Sobek. As living animals deliberately sacrificed in order to be mummified, perhaps they represented more potent offerings than statues or stelae (Ikram 2005, 2015). These votive animals were usually hatchlings or subadults (Figure 1) and were so abundant in tombs that they were used as ballast, fertilizer, and fuel during the height of Egyptomania (Ikram 2015; Lewis 2017; Baber 2019; Nicholson 2021). Examples of votive crocodiles have been found throughout Egypt, notably at sites in the Fayum, Ma'abda, and Kom Ombo, and in the environs of ancient Thebes (modern Luxor).

The identity of Egyptian crocodiles (both ancient and modern) was long thought to be the Nile crocodile (*Crocodylus niloticus* Laurenti, 1768). However, in recent years fragmentary genetic data from sets of hatchling crocodile mummies from Thebes and the grottes de Samoun (Ma'abda) indicated that the genetic identity of these mummies was entirely distinct from the Nile crocodile (*C. niloticus*) and suggested that the Egyptians preferentially mummified a cryptic lineage of crocodiles for use as votive offerings (Hekkala et al. 2011). These findings were consistent with early writings describing two crocodile species in Egypt. Citing Herodotus, the French naturalist Geoffroy

Saint-Hilaire referred to historical accounts of ancient Egyptian priests recognizing two forms of crocodile in the Nile in his description of a new species, *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807, or the "sacred" crocodile (Geoffrey Saint-Hilaire 1807; Hekkala et al. 2011). In 2020, the first complete mitogenome from an adult temple crocodile mummy was sequenced (Hekkala et al. 2020). The molecular results for this large specimen, purportedly from Kom Ombo and held in the collections of the Natural History Museum of the Salzkammergut, Bad Ebensee, Austria (NMSG-A), conformed to the previously recovered fragmentary genomic data from crocodile hatchlings and suggested that *C. suchus* might have been preferred for the Egyptian crocodile cults dedicated to Sobek (Hekkala et al. 2020). Geoffroy Saint-Hilaire (1807) refers to Strabo (bk 17, 38) noting that the sacred crocodiles that were tamed, anointed, and ornamented by the Egyptians were called Suchus. Modern accounts of behavioral differences between extant populations of *C. suchus* in western African localities, which are said to be more docile and less aggressive than *C. niloticus* (Shine et al. 2001; Brito et al. 2011; Campos et al. 2016; Eniang et al. 2020), suggest that behavior might have been a factor in the Egyptians' preference for *C. suchus*.

To broaden our understanding of the changing cultural and ecological contexts of animal worship and use in ancient Egypt and the wider region over time we analyzed isotopic and genomic data for a set of mummified crocodiles from the Barringer Egyptian Collection, Division of Anthropology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM ANT; Scott 1986). Our aims were to add to the growing body of work exploring whether Egyptians consistently used *Crocodylus suchus* throughout the period during which crocodile cults were flourishing (c. 600 BCE–300 CE) and to determine whether clutches of hatchling crocodiles found in association with adult crocodile mummies are related to one another.

Victor Clay Barringer's collection was made during his 20 years as Justice on the International Court of Appeals in Alexandria, Egypt (1874–1894), and the Barringer Egyptian Collection comprises some 700 objects, including nine mummified crocodiles (Table 1). In notes regarding the transfer of the collection there are separate entries for two crocodile mummies of medium size, with another note indicating the transfer of a set of small crocodile hatchlings (Figure 1). It is thought that these might have been attached to the back of one of the crocodiles, as has been noted in several examples of crocodile mummies, such as ones in the British Museum (EA38562), the Phoebe A. Hearst Museum of Anthropology (55-13), and the Sharm el-Sheikh Museum (no number, probably from Saqqara). However, in the case of the Yale Peabody Museum's material, there is no specific description of such a relationship between the crocodile mummies in the original documents.

Materials and Methods

Sample Dating

Samples from two specimens (YPM ANT 006435.004 and YPM ANT 006435.007) were sent to Beta Analytic (Miami, Florida, USA; http://www.radiocarbon.com/) for accelerator mass spectrometry radiocarbon dating. The samples consisted of skin removed from the underside (belly) of the crocodiles. Conventional radiocarbon ages and sigmas are rounded to the nearest 10 years per the conventions of the 1977 International Radiocarbon Conference. All work was performed under strict chain of custody and quality control under ISO/IEC 17025:2005 Testing Accreditation PJLA No. 59423 accreditation protocols.

Genomic Sample Preparation

Small tissue samples were collected from both hatchling and adult crocodile mummies from the Yale Peabody Museum (Table 1). Using sterile collecting tools, we removed 1–2 mm bits of tissue from areas where the specimen was damaged and tissue was exposed. The samples were shipped to and processed in a clean lab facility at the Globe Institute, University of Copenhagen, Copenhagen, Denmark.

To remove the initial surface contamination, all samples were immersed in a 5% bleach solution and rinsed three times in ultrapure water, purified using a MilliporeSigma system (Merck, https://www.sigmaaldrich.com/).

TABLE 1. Crocodilian mummy specimens included in this and prior genomic analyses. Archival samples are from museum collections represented by acronyms as follows: MNHN, Muséum national d'Histoire naturelle, Paris, France; NMSG-A, Natural History Museum of the Salzkammergut, Austria; YPM ANT, Division of Anthropology, Yale Peabody Museum of Natural History. Radiocarbon ages reported by Beta Analytic, Miami, Florida, USA. Ages and sigmas are rounded to the nearest 10 years according to the conventions of the 1977 International Radiocarbon Conference. NA, None attempted; NR, None recovered.

Catalog number	Specimen	Site	^{14}C age	Calibrated date (probability)	Gene ID
YPM ANT 021829[a]	Medium	Egypt (Barringer Collection)	NA		NR
YPM ANT 006435.001[a]	Medium	Egypt (Barringer Collection)	NA		NR
YPM ANT 006435.002[a]	Hatchling	Egypt (Barringer Collection)	NA		*Crocodylus niloticus*
YPM ANT 006435.003[a]	Hatchling	Egypt (Barringer Collection)	NA		NR
YPM ANT 006435.004[a]	Hatchling	Egypt (Barringer Collection)	2070 ± 30 BP	169 cal BCE (p=.095) −8 cal CE	*C. niloticus*
YPM ANT 006435.005[a]	Hatchling	Egypt (Barringer Collection)	NA		NR
YPM ANT 006435.006[a]	Hatchling	Egypt (Barringer Collection)	NA		*C. niloticus*
YPM ANT 006435.007[a]	Hatchling	Egypt (Barringer Collection)	2010 ± 30 BP	54 cal BCE (p=.092) −82 cal CE	*C. niloticus*
YPM ANT 006435.008[a]	Hatchling	Egypt (Barringer Collection)	NA		NR
NMSG-A[b]	Adult	Kom Ombo	1400 BP		*C. suchus*
MNHN-RA-1886.445[c]	Juvenile	Haute Egypte (Schoelcher)	NA		*C. suchus*
MNHN-RA-1986.1471[c]	Hatchling	Thebes (Cailloud, collected 1820s)	NA		*C. suchus*
MNHN-RA-1986.1473[c]	Hatchling	Thebes (Cailloud, collected 1820s)	NA		*C. suchus*
MNHN-RA-1986.1475[c]	Hatchling	Grottes de Samoun (Ma'abda) Gervais	NA		*C. suchus*
MNHN-RA-1986.1478[c]	Hatchling	Grottes de Samoun (Ma'abda) Gervias	NA		*C. suchus*
MNHN-RA-1986.1479[c]	Hatchling	Thebes (Cailloud, collected 1820s)	NA		*C. suchus*
MNHN-RA-1986.148[c]	Hatchling	Grottes de Samoun (Ma'abda) Pariset	NA		*C. suchus*

[a] This paper.
[b] Hekkala et al. 2020.
[c] Hekkala and Shirley et al. 2011.

Between 100 and 300 mg of each sample was digested in ethylenediaminetetraacetic acid and proteinase K overnight. The extraction then followed Dabney et al. (2013), with digests transferred to 15 ml of binding buffer and then into Zymo reservoirs (Zymo Research, https://www.zymoresearch.com/) attached to MinElute spin columns (QIAGEN, https://www.qiagen.com/). Each sample was eluted twice with 40 µL of elution buffer (Buffer EB, QIAGEN) for a final volume of 80 µL.

Library Preparation

Mummy DNA extractions and negative controls were shipped to Daicel Arbor Biosciences in Minneapolis, Minnesota, USA. Archival specimen extracts were prepared as Illumina Truseq libraries (Illumina, https://www.illumina.com/) before enrichment with either crocodilian derived RNA baits, or with synthetic mitobaits derived from genomic sequence data. Libraries were created using 25 µL of each archival DNA extract in two duplicate Illumina library preparations and index-amplified using unique P5 and P7 indexing primers (Meyer and Kircher 2010) in 40 µL reactions using 10 µL of each library according to standard protocols. Amplifications were performed in real time with a CFX96 Real-time PCR platform (BioRad, https://www.bio-rad.com/). Indexed libraries were purified with MinElute PCR Purficiation Kit (QIAGEN, https://www.qiagen.com/) to 15 µL TEB.

Enrichment and Re-amplification

Daicel Arbor Biosciences (https://arborbiosci.com/) used the myBaits MYcroarray kit protocol for enrichment at 2 µM each per capture (Enk et al. 2014). Each capture reaction used 1 µg each of crocodilian mitobaits and RNA baits and 9 µL indexed library, which ranged from 0.5 to 5.3 ng/µL as estimated with total library quantification. Hybridizations were done at 48 °C for 48 hr. Following bead cleanup and MinElute purification to 15 µL TEB, enriched eluates were amplified for 10 cycles and then purified with MinElute to 13 µL TEB. Then 9 µL of these re-amplified enriched eluates were used in another round of capture using conditions identical to the first round except incubated at 55 °C for 39 hr. These were cleaned and then purified with MinElute to 13 µL TEB, which we then re-amplified for five cycles. These final re-amplified doubly enriched libraries were then purified to 13 µL TEB.

Sequencing

Enriched myBaits Mito and myBaits Expert Whole Genome Enriched (WGE; Daicel Arbor Biosciences, https://arborbiosci.com/) libraries were combined in pools in a 75-to-25 ratio and paired-end sequenced on one lane of an Illumina HiSeq 2500 flowcell (Illumina, https://www.illumina.com/).

Analytical Methods

Using the python script TQSfastq.py (Warren et al. 2007), reads from each sample were demultiplexed and trimmed and those with a quality (q) value of 20 and a minimum read length of 30 were retained. Reads for each sample were mapped to our bait sequences using the BWA-MEM algorithm with default settings (Xin et al. 2013; Xu et al. 2021) and read duplicates were identified and marked using the tool MarkDuplicates from Picard Version 1.77 (http://broadinstitute.github.io/picard/). Using BCFtools (Danecek et al. 2021) to call divergent sites with the mpileup and call commands, we generated a consensus of each sample's mitochondrial genome. This was followed by indel realignment using IndelRealigner from the Genome Analysis Toolkit (GATK Version 3.8; McKenna et al. 2010). Next, for each sample we used the program BCFtools (Version 1.9; Li 2011) to call divergent sites with the mpileup and call commands. With mpileup the maximum read depth was set to 1,000. For the call command, we used the multiallelic-caller with ploidy set to haploid. For both commands, we included nonvariant sites grouped into blocks by minimum depth. We then generated a consensus of each sample's mitochondrial genome incorporating divergent sites. Sites that had mapping quality less than 20, a base quality less than 20, and a read depth less than 10 were masked and nucleotides were replaced with Ns in the resulting FASTA file.

Sequences were aligned to mitochondrial reference sequences of *Crocodylus niloticus* (GenBank JF502243.1) and *C. suchus* (GenBank JF502244.1; Meredith et al. 2011) using

Bowtie2 (Langmead and Salzberg 2012). Consensus sequences of alignments of portions of the mitochondrial (mt) genome from GenBank (Sayers et al. 2021), the National Center for Biotechnology Information (NCBI) nucleotide (nt) database, for both *Crocodylus niloticus* and *C. suchus* (COX1, 12S, and D-loop) were used to identify the most likely origin of recovered sequences according to sequence identity and average coverage depth. Subsequently more complete mitochondrial sequences were compared with full mitogenomes of African *Crocodylus* species.

Phylogenetic Analysis

We aligned one nearly complete mitogenome from the Yale Peabody Museum samples with published mitogenomes of *Crocodylus niloticus* and *C. suchus* (Hekkala et al. 2020) using Clustal Omega (Larkin et al. 2007). After alignment, we trimmed both ends of the sequence to match the sequence length of the newly recovered genome and used RAxML Version 8.2.12 (Stamatakis 2006, 2014) to generate 1,000 bootstrap replicate phylogenies to assess the phylogenetic relationship of the mummy sample to published contemporary and archival crocodile samples.

Results

Carbon Dating

The conventional radiocarbon dates for the two specimens are YPM ANT 006435.004, 2070 ± 30 BP (Beta-602771; tissue; δ^{13}C: −20.2‰), and YPM ANT 006435.007, 2010 ± 30 BP (Beta-602772; tissue; δ^{13}C: −17.2‰).

Genomic Results

Of the nine Yale Peabody Museum crocodile mummies sampled (two adults and seven hatchlings), only four mummies (44%) yielded results of high enough quality to definitively assign the mummy to one species or the other. The quality of the data varied greatly across those four samples, with most samples yielding only small fragments from diagnostic mitochondrial gene regions (Hekkala et al. 2011). Because of low endogenous content, we were unable to recover nuclear data from any WGE enriched sample libraries. BLAST analysis (NCBI n.d.) of COX1, 12S, and D-loop regions showed that in all cases, the closest database hits by percent identity to the consensus sequences derived from *Crocodylus niloticus*. Despite the limitations of the data, all four hatchlings' mummies were found to definitively match *C. niloticus* mitochondrial sequences to the exclusion of *C. suchus*. Of these, one specimen (YPM ANT 006435.007) yielded a nearly complete *C. niloticus* mitogenome with 99.9% identity to the reference (GenBank JF502243.1).

To better understand phylogeographic variation within the Nile crocodile's distribution we used RaxML analysis of an aligned set of historical and contemporary *Crocodylus niloticus* mitogenomes to examine the phylogeographic position of the recovered haplotype of specimen YPM ANT 006435.007 relative to haplotypes representing existing populations of *C. niloticus* throughout Africa (Meredith et al. 2011; Hekkala et al. 2020). Our phylogeographic analysis places the ancient sample haplotype within the same subclade as extant representatives of *C. niloticus* from northern Lake Nasser (Figure 2).

Discussion

Prior to molecular work on crocodiles in the Nile River basin, it had been assumed that all Egyptian crocodiles, extant or mummified, were *Crocodylus niloticus*, the only crocodile species identified in the Nile today (Shirley and Salem 2008). Molecular results for other crocodile mummies previously confirmed Geoffroy Saint-Hilaire's (1807) identification of *C. suchus* as distinct (Hekkala et al. 2011) and supported the idea that the ancient Egyptians consistently and possibly deliberately chose *C. suchus* to be venerated (Hekkala et al. 2020). The identification of *C. niloticus* in the Yale Peabody Museum holdings is the first genetic identification of true Nile crocodiles (*C. niloticus*) from ancient Egyptian mummified animal remains. The identification of *C. niloticus* mummies suggests that we must once again revisit previous interpretations of ancient Egyptian vernacular taxonomies and funerary practices with respect to crocodiles. Further, this finding affirms the historical, social, and biological value of natural history museum holdings in contemporary research.

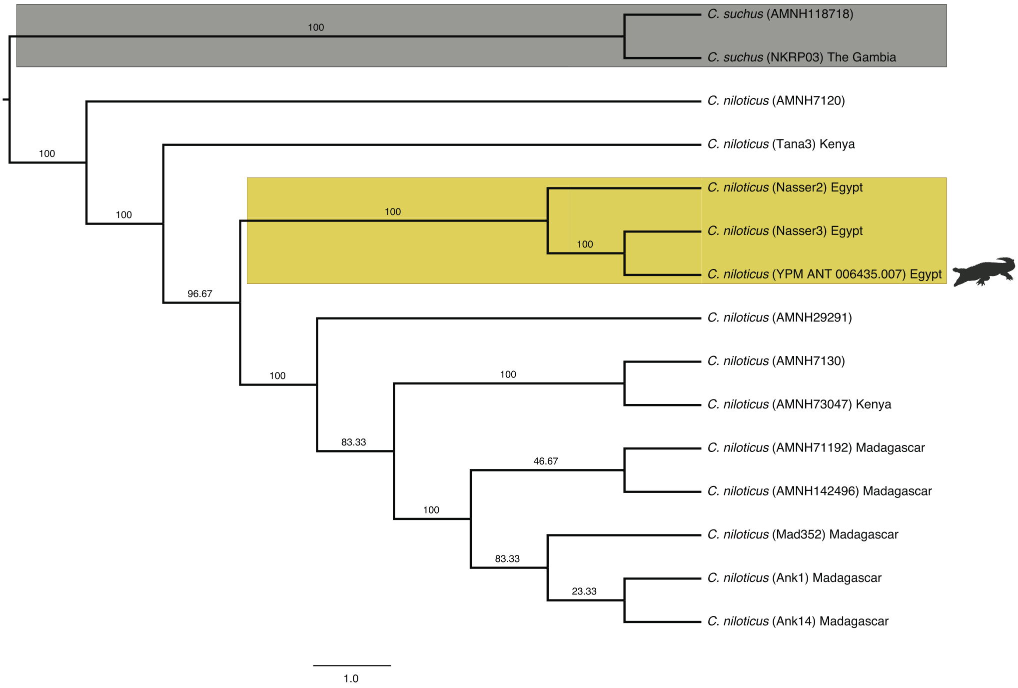

Figure 2. Maximum likelihood (RAxML) cladogram representing the phylogenetic placement of the mitochondrial genome recovered from a hatchling crocodile mummy specimen (YPM ANT 006435.007) from the Barringer Egyptian Collection, Division of Anthropology, Yale Peabody Museum of Natural History. Branch values are Maximum Likelihood bootstrap support. The results confirm the mummy haplotype as representing *Crocodylus niloticus* and a placement within a subclade (bounded by yellow box) of modern sequences recovered for crocodile samples from Lake Nasser, Egypt. Other sample sources include museum specimens from AMNH (American Museum of Natural History, New York) and modern samples Ank1 and Ank14 (Ankarana National Park, Madagascar), Mad352 (LacBemaba, Madagascar), Tana3 (Tana River, Kenya), and NKRP03 (The Gambia)(Hekkala et al. 2020).

Our dates for the two molecularly identified *Crocodylus niloticus* mummies, 2070 ± 30 and 2010 ± 30 BP (Beta Analytic), indicate that they were harvested during the height of the period of the crocodile cults (c. 600 BCE–300 CE). Although it is possible that Egyptians were less adept at identifying two distinct crocodilian taxa than previously hypothesized (Hekkala et al. 2011, 2020), it is also possible that shifting access to a particular species for a particular practice may have driven these cultural choices. It may be that, as increasing numbers of *C. suchus* were harvested to make mummies, the population of that species declined and the ancient Egyptians then switched opportunistically to *C. niloticus*, at least for votive offerings, targeting them when young and easier to hunt and collect.

Alternatively, our identification of the first authenticated *Crocodylus niloticus* mummies may indicate that, while as an adult *C. suchus* would hypothetically be less of a danger to its carers and devotees in the context of temples dedicated to Sobek (Behangana et al. 2020; Pooley et al. 2020), *C. niloticus* hatchlings would have been easy to handle and plentiful (Pooley 1969) and thus could be used as the raw material primarily for votive mummies that were generally sacrificed when young and small (Richardin et al. 2017). However, the molecular identification of additional mummies to confirm which crocodile species was used for each type of mummification and the associated ^{14}C dates for these mummies over the breadth of the period of the crocodile cults would greatly improve our understanding of these cultural and ecological trajectories.

While our new evidence confirms that both species were present in ancient Egyptian ritual practices, the specific timing and driver(s) of the decline and extirpation of *Crocodylus suchus* from the Nile during the recent past remains unclear. Despite dramatic climate shifts in northern Africa (Jolly et al. 1998; Drake et al. 2011; Vale and Brito 2015; Liz et al. 2021) and the Egyptian Nile (Zalat and Vildary 2007; Pennington et al. 2017; Beck et al. 2019) during the Holocene, distribution models for both crocodile species suggest that some degree of suitable habitat would have remained in the Nile River drainage (Cunningham 2015). More broadly, these models suggest that climatic factors may have played a more important role in distribution for *C. suchus* than for *C. niloticus* over time (Cunningham 2015), and thus the continued presence of the latter species in the Nile River system today.

The combination of climatic and anthropogenic stressors, including changing agricultural practices, during the past two millennia may have driven more recent patterns of wetland desiccation (Touzeau, Lécuyer, and Amiot 2017; Huebner 2020). Studies of other animal mummy species have suggested that a shift in available wetland habitat or moisture along the Nile River may have resulted in the overall decline in Egyptian biodiversity over time. Detailed examinations of both avian (ibis; Wasef et al. 2019) and insectivoran (shrew; Woodman 2015; Woodman and Ikram 2021) mummies indicate that species once present in ancient Egypt have either shifted in their present distributions or are simply no longer there.

Although we were unable to recover data sufficient for genotyping individuals and thus to test for relatedness between mummies specifically, it is notable that the Yale Peabody Museum hatchling specimens for which data were recovered were all *Crocodylus niloticus* and seem to be of the same stage of development, suggesting they may represent one clutch of eggs. In each of the two sets of associated hatchlings analyzed so far (Hekkala et al. 2011 and the present work) only a single species has been found, perhaps indicating that, in each case, the source population contained only one species, whether harvested directly from the wild (Porcier et al. 2019) or from a controlled context.

The Egyptian crocodile-headed god Sobek is always identified as a male and yet in nature, with the exception of the Indian gharial (Lang and Kumar 2013) and the caiman (Murray, Crother, and Doody 2020), a relative of the American alligator, among crocodilians, it is primarily females that have been observed to carry and protect hatchlings that have emerged from their nests (Garrick and Lang 1977; Pooley 1977; Alcala, Ross, and Alcala 1987; Brazaitis and Watanabe 2011; Chabert et al. 2015). Therefore, the attachment of hatchling crocodiles to the back (or in some cases placement in the mouth; Ikram 2005; Richardin et al. 2017) of adult mummies is intriguing in terms of its cultural significance. The presence of hatchlings associated with a male animal are simply symbolic of Sobek's fertility and fecundity. Although there is no genomic data yet available for either of the larger individuals to determine relatedness, it would be helpful to know whether they represent males or females. Because crocodiles exhibit temperature dependent sex determination, they cannot yet be sexed using molecular methods. However, a computed tomography examination of the large mummies might help to determine whether these were male or female and thus give insight into the meaning of the association.

Human cultural practices have long affected animal populations either directly via exploitation for religious, nutritional, or agricultural use, or indirectly through modifications of the landscapes and habitats where species are found (Rubin et al. 2012; Boivin et al. 2016; MacHugh, Larson, and Orlando 2017; Merheb et al. 2019). The study of bioarchaeological collections can help us to better understand the ecological and cultural contexts of animal exploitation (Rowe et al. 2011; Drew, Philipp, and Westneat 2013; Fumagalli et al. 2013; Ottoni et al. 2013; Staats et al. 2013; Fordham et al. 2014), and analyses of additional animal mummies from cultural heritage collections (Kurushima et al. 2012; Wasef et al. 2019) will continue to clarify our understanding of their meaning, the ancient Egyptians' recognition of different species, and the response of those species to changes in the environment, whether of anthropogenic or natural origin.

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