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Short Communications

A toothless bonobo skull challenges the notion of alternative subsistence strategies in early *Homo*

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1. Introduction

Humans are a highly cooperative species exhibiting a remarkable level of prosocial behavior (Richerson et al., 2003). It is hard to trace the emergence of this behavioral trait in the human lineage owing to the difficulty of inferring social behavior from fossil and archeological remains. In search for the origins of our 'hypersociality,' skeletal remains of early hominin individuals that survived despite extreme pathologies have been interpreted as evidence for the occurrence of high levels of altruism and compassion by their conspecifics (Hublin, 2009). The rationale is that, under such handicapping circumstances, only extended social support could have made their survival possible. Examples of extreme pathologies from early humans include individuals with cranial malformations and bone traumata, indicative of motor and cognitive disorders (Trinkaus, 1983; Gracia et al., 2009). The earliest evidence of a hominin surviving with a supposed severe impairment is a toothless skull and mandible of a *Homo erectus* adult from the Dmanisi site (D3444/D3900), the Lesser Caucasus Mountain region of southern Georgia, dated to ca. 1.8 Ma (Lordkipanidze et al., 2005). These authors suggested that such an individual, lacking all but one tooth, could only have survived this masticatory handicap "by virtue of help of other individuals which must have exceeded that capable of being offered by non-human primates" (Lordkipanidze et al., 2005: 718).

One way to evaluate such behavioral inferences from skeletal remains is to use comparative evidence from modern primates (Degusta, 2002). Humans' closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), live in social groups, and their diet consists mainly of fruits supplemented by tubers, leaves, flowers, pith, insects, and meat (Hohmann et al., 2012). Both species exhibit forms of prosocial behavior, including adopting infants and sharing monopolizable food. Overall, the proportion of food accessed by adult individuals via sharing is small, and transfer of processed food between adults is documented only as tolerated theft out of mouth (Yamamoto, 2015). Consequently, if modern human levels of prosociality are necessary for masticatory handicapped individuals to survive, we would not expect chimpanzees or bonobos to survive with severe dental loss in the wild. While there are described cases of wild-shot chimpanzees lacking a substantial portion of their dentition (Schultz, 1956), it remains unclear whether they survived on a natural diet or on crop raiding of domesticated fruits (such as pineapples, papayas, bananas, and so on), thus using an abundant and readily procurable supply of soft and easily digestible food.

Here, I present behavioral and skeletal evidence from a bonobo individual that survived for prolonged time without teeth, without the help of other individuals and without access to domesticated food sources.

2. Methods and results

From March 2016 to December 2018, local trackers and international students followed on a daily basis members of the Kokoalongo bonobo group in the Kokolopori Bonobo Reserve, Democratic Republic of the Congo (N 0.41716°, E 22.97552°). The group consisted of 45 individuals (including 10 males and 13 females estimated to be older than 10 years), which have been under habituation to human observers since 2007 and could be individually recognized since October 2016. On all the days that members of the Kokoalongo group were followed, no one ever saw them raid crops. Bonobos appearing in the agricultural field and feeding on human crops of soft fruits, as in the case of a neighboring group

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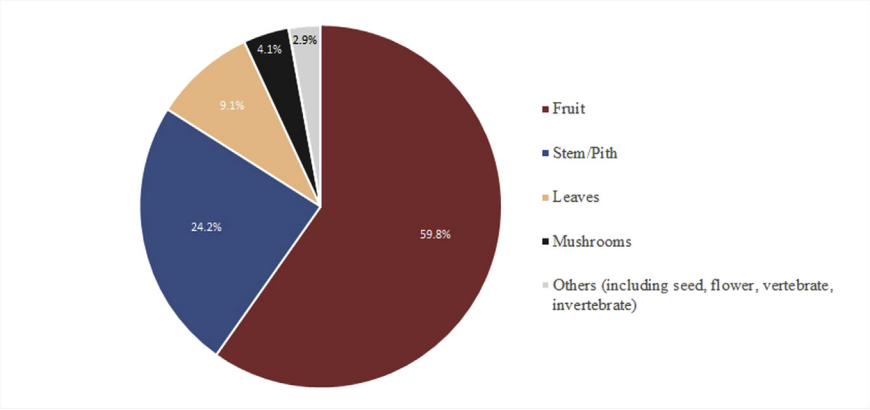

Figure 1. Overview of the proportion of feeding time spent to consume different food items by the Kokoalongo community between October 2016 and December 2018.

Figure 2. Pictures of the bonobo male 'Sting' premortem.

ranging in a forest part closer to the villages and having been observed once to eat a pineapple, are usually noticed by the villagers and reported to the research project. The diet of the Kokoalongo group consisted of about 60% fruits, 24% stems/piths, and 9% leaves (recorded on all occurring feeding events; $n = 11{,}459$; Fig. 1).

In December 2018, an adult male named Sting (Fig. 2) died of so far unknown causes. Overall, he was mostly peripherally associated with the focal subgroup and present in 5.3% of the hourly presence scans (606 of 11,459 scans, average of group individuals: 30.9%). Sting participated in a few grooming events ($n = 5$) but was never involved in the observed food-sharing events ($n = 62$). He occupied the lowest dominance rank among the adult males (based on the outcome of agonistic interactions) and was the victim of 28 agonistic interactions. After his body was discovered in the forest, he was buried and excavated 5 months later using strict hygiene safety measures. Currently, the material is housed at the Institut National de Recherche Biomédicale in Kinshasa (Democratic Republic of the Congo).

Sting's skeletal remains showed classic features of old age as osteoarthritis manifested by osteophytes, or bony projections, on several articular surfaces including the sacrum and lumbar vertebral bodies. The most prominent evidence for advanced age was his edentulous, or toothless, skull (Fig. 3). Sting must have survived for an extended time without teeth before his death as all his teeth were missing. There is nearly complete resorption of the alveolar crest in both the mandible and maxilla. The alveolar crest is absent except for minor traces of alveolar bone at the base of the right M_3 and M_2 roots. In addition, there is some bone resorption in the mandibular corpus and the left mandibular ramus, and most of the alveolar bone that formerly surrounded the tooth roots is completely resorbed and/or remodeled (Fig. 3).

3. Discussion

Evidence that this bonobo individual survived for a prolonged time without teeth and access to processed or domesticated foods calls into question inferences of higher levels of prosociality in hominins based on the finding of an edentulous skull (Lebel et al., 2001; Lordkipanidze et al., 2005). More information on the masticatory requirements of the natural diet and on potential food processing by hominins would be important before reaching such a conclusion. At this stage, it remains speculative whether the fibrous diet of bonobos (Hohmann et al., 2012), or the likely diverse diet of a hominin at Dmanisi, required more chewing (Pontzer et al., 2011; Van Arsdale, 2013; Zink and Lieberman, 2016). In the light of this bonobo skull, it seems adequate to reconsider the skeletal evidence and notions of the evolution of high levels of human prosociality. If we remove examples of tooth loss as strong evidence—specimens Bau de l'Aubesier 11 (Lebel et al., 2001) and D3444/D3900 (Lordkipanidze et al., 2005)—the earliest hominin individuals with presumed cognitive and motor disfunction appear before 500 ka in the fossil record and might be used, in the absence of similar cases in nonhuman primates, as an indication of an emerged human prosociality (Gracia et al., 2009).

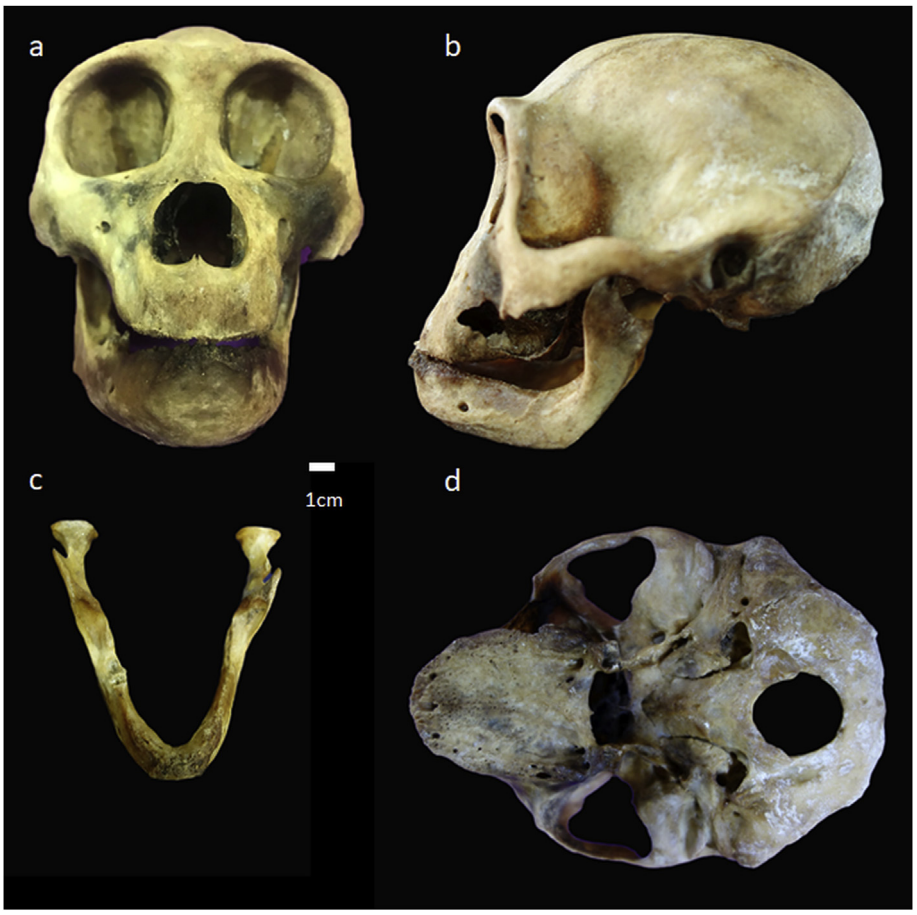

Figure 3. Various views of the toothless skull of the male bonobo Sting: a) frontal view; b) left lateral view; c) occlusal view of the mandible; d) basicranial view.

Conflict of interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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