A possible case of congenital tusklessness in a male African elephant (*Loxodonta africana*)

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The tusks of African elephants (*Loxodonta africana*) have evolved as intra-sexual combat weapons, as well as tools for feeding and digging (Kingdon 2015; LaDue et al. 2021). They are also the target of ivory poaching, which may drive phenotypic and/or genetic selection for tusklessness (Jachmann et al. 1995; Tiedemann and Kurt 1995; Chiyo et al. 2015). Some studies have indeed shown how selective pressures from sustained ivory poaching against tusk-bearing phenotypes could lead to an increase in fitness for tuskless individuals, and thus to the rapid spreading of tuskless phenotypes (Kurt et al. 1995; Steenkamp et al. 2007; Raubenheimer and Miniggio 2016; Campbell-Staton et al. 2021). These studies have, however, focused solely on female African savannah elephants, since congenitally, bilaterally tuskless males (i.e. males that genuinely lack both tusks since birth) seem to be rare to non-existent in this species (see below). However, it should be noted that this condition is common in Asian elephant bulls (*Elephas maximus*), especially from populations with a long history of being hunted for ivory (Kurt et al. 1995; Chelliah and Sukumar 2013).

Here we describe what is, to our knowledge, the first documented occurrence of a potentially congenital tuskless male African elephant with tusklessness present from birth, probably due to genetic causes. We substantiate our claims with photographic evidence and long-term observations, while discussing possible hypotheses to explain such a unique phenomenon.

A genetic study on the elephant population of Gorongosa National Park (NP), Mozambique provides a robust explanation for the apparent lack of congenitally tuskless male African elephants. Campbell-Staton et al. (2021) found that tusklessness in female elephants is an inherited condition, deriving from an X-chromosome-linked dominant gene. They propose that this dominant tuskless allele is connected to male lethality i.e. the dominant tuskless allele in sex chromosome heterozygosity results in the death of male offspring. This was based on the observation that there were no bilaterally tuskless males in the study population, with a bias towards females in the sex ratio of the offspring of tuskless females as all the tuskless male offspring would not survive (Campbell-Staton et al. 2021) unlike in Asia (Kurt et al. 1995). Although comparative demographic data is needed from other sites and the lethality mechanism needs to be further clarified, this seems a plausible explanation for the apparent absence of tuskless males among African elephants.

The hypothesis of Campbell-Staton et al. (2021) is supported by other field observations. Although unilaterally tuskless males have been documented in various African populations (due to yet unknown causes; Jachmann et al. 1995; Whitehouse 2002; Campbell-Staton et al. 2021), bilateral congenital tusklessness in males has not been previously confirmed. In South Africa (Kruger NP and Addo Elephant NP) and in East Africa (Murchison Falls NP, Amboseli NP, and Tsavo NP), long-term research did not produce any evidence for the presence of bilaterally tuskless males (Whitehouse 2002;

Whyte and Hall-Martin 2018; Parker 2023). Similarly, a comprehensive review of data from 15 elephant populations across eastern and southern Africa did not find any evidence for bilaterally tuskless males (Steenkamp et al. 2021), and bilateral male tusklessness seems to be absent also from forest elephants (*Loxodonta cyclotis*) in Central Africa (A. Turkalo, pers. comm., 2023). The only documented case of a bilaterally tuskless male in Addo Elephant NP was the result of the loss of both tusks in fights (Hall-Martin 1987). According to Steenkamp et al. (2007), male bilateral tusklessness is very rare (one case out of 10,000 examined elephant pictures), and suggests that most, if not all, of the very few cases of bilateral tusklessness might derive from tusk loss due to trauma. The only other substantiated observations of tuskless males comes from South Luangwa NP (Zambia, n=2; Jachmann et al. 1995) and Queen Elizabeth NP (Uganda, 9.5% of all bulls examined; Abe 1996). A tuskless male was also observed in 2021 in Murchison Falls NP (D. Daballen, pers. comm., 2022); (Fig. 6). Since it was not reported whether tusklessness was congenital or acquired, these cases may also reflect secondary tusk loss during contests (especially since all tuskless bulls in Queen Elizabeth NP appeared to be 'very old'; Abe 1996). However, contrary to this evidence, we observed a young male African elephant in the Samburu-Laikipia ecosystem of northern Kenya, which appeared to be congenitally tuskless.

The tuskless male elephant is a 13-year-old individual identified as S50.10, and part of a family named the 'Hawaiian Islands'. The family consists of five adult females and their offspring, and has been the subject of monitoring and research since the onset of the Save the Elephants project in Samburu National Reserve (NR) in the late 1990s although only visiting the core study area during periods of very high rainfall (Wittemyer 2001; Save the Elephants, unpublished data). The tuskless male was first identified on 6 September 2011, when he was approximately one year and four months old and therefore too young to bear tusks (the usual age of tusk eruption is generally ~2 years old). We are confident of the estimated age, since ageing an elephant calf tends to be very accurate via comparisons of relative body size with its mother and siblings and with other known age individuals in the same population. The individual was observed on 19 occasions over 13 years with at least one observation per year since identification, except for 2012. This means that, although there are temporal gaps between records, S50.10 could be followed throughout his growth. No tusks or signs of tusk eruption or tusk breakages were observed between 2011 and the present day (Fig. 1).

Figure 1. The tuskless male S50.10, photographed at different stages of his life: (a) 2016 (6 years old), (b) 2021 (11 years old), (c) 2022 (12 years old), and (d) 2023 (13 years old). © Save the Elephants (a), Chris Thouless (b), Giacomo D'Ammando (c) and Olympia Brule (d).

The first possible explanation for bilateral tusklessness is that the individual is not actually congenitally tuskless, but rather broke both off his tusks (or one of them in case he was originally unilaterally tuskless) at an early age. We believe that this is highly implausible for several reasons. First, our long-term records strongly support the conclusion that the individual did not grow tusks at any stage in his development, given that bilateral tusk growth and subsequent breakage at such a young age and between observations was unlikely to go unnoticed. Second, the morphological features of the male face closely mirror those of congenitally tuskless females, based on the examination of close-up pictures. S50.10 presents the characteristic 'pinched' appearance of tuskless females in frontal view, indicating the absence of tusk roots (Fig. 2). His symmetrical appearance makes it improbable that he was unilaterally congenitally tuskless and lost the other tusk to trauma. The morphology of the tuskless male is different from that of an adult male in the Samburu study population who lost his tusks due to trauma during his lifetime: in the latter, tusk sockets are visibly swollen, denoting the presence of tusk roots, with the base of the tusks still slightly protruding from the upper lip (Fig. 3). Finally, potential bilateral tusklessness due to trauma is most likely due to intense fighting, for which the study individual was too young (the age at first full musth is usually around 30 years; Hall-Martin 1987; Poole 1989; Goldenberg et al. 2014).

Figure 2. Morphological characteristics of the tuskless male S50.10 denoting the complete absence of tusks. The 'pinched face' appearance, characteristic of tuskless females, is very visible. Close-ups in lateral view (a, b), three-quarter front view (c, d), and three-quarter rear view (e, f), from pictures taken in 2013, when the individual was 13 years old. © Olympia Brule (a, c), Giacomo D'Ammando (b, f) and Alice Clark (d, e).

Figure 3. Close-up of the tuskless male S50.10 (a,c) evidencing the similarities and differences in tusk socket morphology with a tuskless female (b), and the differences with an adult male who had lost his tusks due to trauma (d). © Giacomo D'Ammando (a), Jemima Scrase (b), Olympia Brule (c) and Save the Elephants (d).

An alternative explanation is that the observed male is truly congenitally tuskless and that this is an inherited trait. This is supported by the fact that his mother (coded as S50 or *Kauai*) is also tuskless (Fig. 4). However, this contradicts the findings of Campbell-Staton et al. (2021) on the lethality of the dominant X-linked tuskless allele for male offspring especially since three of the four known calves of S50 are males (and all tusked except S50.10), contrary to the expectations of female-biased sex ratios in the offspring of tuskless females. There are two potential paths to resolve such contradictions: (i) there could be other genetic mechanisms underlying male tusklessness, possibly varying among different African elephant populations and/or involving interactions between multiple genes driving phenotypic expression, as already proposed by Campbell-Staton et al. (2021); or (ii) the lethality of the dominant tuskless allele is not always complete and might sometimes allow for the survival of a tuskless male into adolescence and possibly adulthood. For example, it is possible that the male-lethal loci on the X chromosome could also carry rare variants that suppress the lethality of the dominant tuskless allele. These hypotheses are for now highly speculative and will need quantitative testing.

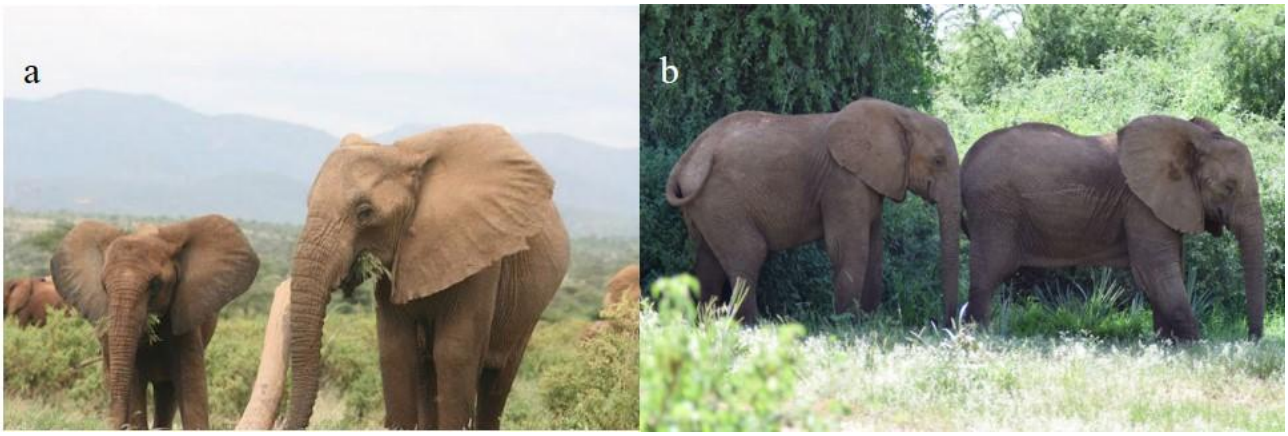

Figure 4. S50, the mother of the tuskless male S50.10, shown here with her calf when the latter was 6 years old (a), and 13 years old (b). The similarities between mother and calf in tusk socket morphology is evident. © Save the Elephants (a) and Alice Clark (b).

It is interesting to note that in at least two elephant populations with very large proportions of tuskless females, namely Gorongosa NP and South Africa's Addo NP (up to 98% of the female population in the latter), congenitally tuskless males have never been observed (Whitehouse 2002; Campbell-Staton et al. 2021; A. Stoeger, pers. comm., 2023). Thus, it is not implausible that the cause of congenital tusklessness in the observed individual is indeed genetic, but connected with rare and unusual mechanisms of inheritance. One possibility involves inactivation of the X-chromosome in the somatic cells of the tusk sockets, in case the male had inherited two X chromosomes from its mother (Pedersen et al. 2014)—an eventuality that could be easily tested via karyotyping.

Another possible explanation is that congenital tusklessness in S50.10 was caused by environmental factors that occurred during foetal or calf development. However, this seems most unlikely since he shows no other signs of mineral deficiency (i.e. similar size to other males of the same age) and soils around Samburu are not mineral deficient (Ihwagi et al. 2011). A last possibility is that the individual is a genetic female that has developed external masculine sexual characters. This has been observed in other mammals, such as lions (*Panthera leo* (Gilfillan et al. 2017), but it is also highly unlikely due to the fact that the individual seems to possess fully developed male sexual organs (unlike masculine females in other species; G. D'Ammando, pers. obs., 17 December 2022).

There is no evidence that tusklessness has affected the behaviour of S50.10, although we have limited information because S50.10 is rarely observed in the core Samburu study area. The tuskless male was observed in December 2022 in a group of young males of similar age and size, while engaging in a sparring 'play' contest. Although he struggled to grapple the tusks and trunks of other individuals, he did not back off from the contest (G. D'Ammando, pers. obs., 17 December 2022); Fig. 5. He seemed to be able to push back against other males using his forehead and trunk.

Figure 5 (a-h). The tuskless male S50.10 in the company of other young bulls and engaging in 'play-fight' or sparring behaviour. From top left, clockwise: the young male was first approached by two other young bulls (a-b); he then engaged in sparring, by approaching a slightly older individual and pushing against him with the base of his trunk in typical face-to-face sparring posture (c-d); after breaking off the trunk engagement and initially retreating from the older individual (e-f), he continued sparring with the other tusked bull (of roughly equal age and size), and managed to hold his ground before the play-fight was interrupted by both parties (g-h). It appears that, during sparring, the tuskless individual was pushed on the side of the head (rather than front), likely due to the absence of tusks and that might have caused the opponents to slip off each other (g-h). This sequence of behaviour strongly suggests that S50.10 has male-like traits except for the absence of tusks. The sequence of events unfolds from left to right in each row. (© Giacomo D'Ammando).

In summary, it appears highly probable that the tuskless African male elephant reported here is the first publicly documented case of congenital male tusklessness in this species and that, due to his tuskless mother, this has a genetic origin. More data is now needed to answer the questions emerging from our observations. We therefore ask the elephant research community to provide any visual evidence of other possible cases of congenital tusklessness in savannah elephant bulls with the aim of collecting as much information on such occurrences as possible. Pictures and videos can be sent to the corresponding author.

Figure 6. A tuskless adult male elephant, immobilized during collaring operations by the Save the Elephants and the Uganda Wildlife Authority team in Murchison Falls National Park (Uganda). The tusk sockets proved to be empty upon manual inspection by David Daballen (co-author of this study), suggesting congenital tusklessness in this individual. © David Daballen.

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