Development of the tush and tusk and tusklessness in African elephant (*Loxodonta africana*)

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The embryologic development of the tush and tusk of the African elephant was studied by means of serial histologic sections prepared from elephant embryos with masses varying between 1g and 240 g. Statistics on tusklessness obtained during a four year population control programme in the Kruger National Park were analysed and compared with those reported in other elephant reserves in Southern Africa. Maxillae of eight elephant embryos, the maternal histories of which were available in six cases, were radiographed, dissected and examined microscopically. This study has shown that the tush and tusk develop from one tooth germ in a deciduous to permanent tooth relationship. Tusklessness was found to be unilateral or bilateral and associated with either the absence or presence of a tush. The possible causes of the differences in the frequency of bilateral tusklessness in different elephant populations are discussed.

Key words: African elephant, embryology of tusk and tush, tusklessness.

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Introduction

The tusk of the African elephant (*Loxodonta africana*) is a pre-maxillary lateral incisor tooth which erupts at an age of approximately one year (Grzimek 1972). It is preceded by a deciduous incisor which is commonly referred to as the 'tush' (Sikes 1971). Although it has been accepted by most that the tusk is a permanent successor to the "deciduous" tush (Sikes 1971; Raubenheimer *et al.* 1995), Anthony (1933) regarded the tush as a rudimentary incisor belonging to a neighbouring position to the tusk. Paleontological data indicate that these two teeth are not homologous and incisors of Proboscideans are teeth of the primary (or deciduous) dentition with no dental replacement by a permanent tooth (Tassy 1987). The tush does not appear to erupt frequently and is pushed aside by growing tusk where it is resorbed in the adjacent tissue (Raubenheimer *et al.* 1995).

The tusk grows continuously throughout life, the size of which is important in determining the hierarchical position of a particular elephant in a herd. The most powerful cow, usually the largest tusker fulfils the role of the matriarch and determines the breeding pattern within her herd (Sikes 1971). Although large tusk-bearing elephant receive considerable attention in the literature (Hall-Martin 1981; Pilgram & Western 1986), little is known of those failing to develop tusks other than their low hierarchal status within the herd. In a study performed on foot in the Mana Pools Game Reserve in the Zambezi valley, 10 percent of 150 adult elephant were found to be tuskless. The tuskless elephant were divided in eight different groups, with one herd consisting of six tuskless elephant and only two with tusks. Amongst immature animals, 23 percent were found to be tuskless. This may indicate an increase in tusklessness in immature elephant in the area (Owen-Smith 1966). Although detailed data could not be obtained from the South African National Parks, the majority of elephant cows in the Addo Elephant Park are tuskless (Hall-Martin 1998). The incidence of tusk-

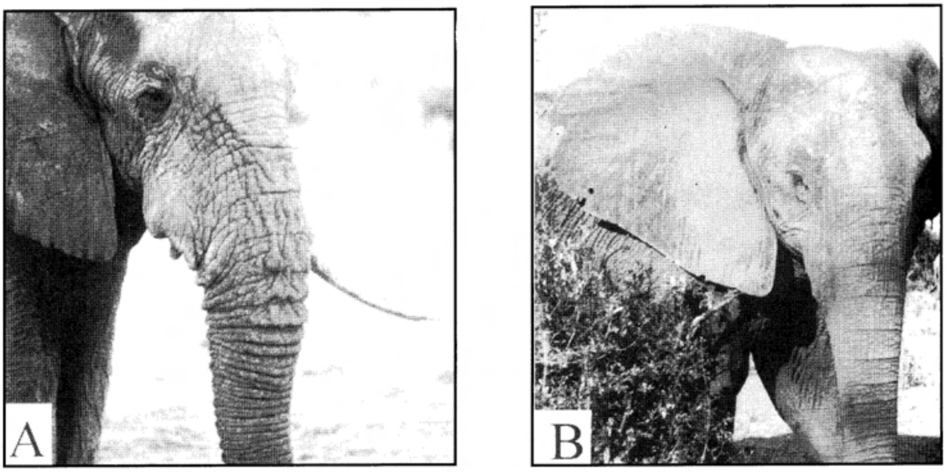

Fig. 1. The external appearances of tuskless elephant. Unilateral tusklessness (A) and bilateral tusklessness (B).

lessness amongst Asian elephant (*Elephas maximus*) is significantly higher than its African counterpart with by far the most animals being born without the capacity to grow tusks (Sikes 1971; Grzimek 1972).

This paper reports on the early development of the tush and tusk and the occurrence and anatomical considerations of tusklessness of elephant in the Kruger National Park. It furthermore proposes a theory on the role human interaction may play in selection for tusklessness in elephant breeding patterns.

Methods

Eight elephant embryos, varying in mass between 1g (less than one month gestation) and 240g (3 months gestational age) were harvested during the population control programme of the Kruger National Park (De Vos 1983). The heads of all but the smallest were hemisected, radiographed, fixed in buffered formalin and processed for routine light microscopy. The heads of all except the smallest embryo (1 g) was hemisected. Serial sections were prepared of each in the sagittal plane and stained with haematoxylin and eosin. The developmental chronology of the lamina dentalis and the primordial of the tush and tusk were recorded through microscopic examination.

Statistics were obtained during the 1990-1993 elephant population control programme of the Kruger National Park (De Vos 1983). The culling programme was carried out on a random basis and across the whole territory of the park. Results were analysed with particular reference to the occurrence of bilateral- and unilateral absence of tusks in adult

Table 1
Distribution of bilateral- and unilateral tusklessness amongst elephant bulls and cows

	Bilateral	Unilateral	
		Left	Right
Bull (n = 229)	2(0.87%)	2(0.87%)	4(1.75%)
Cow (n = 409)	17(4.16%)	6(1.46%)	15(3.67%)

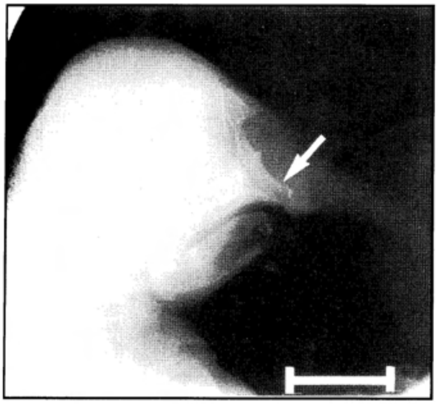

Fig. 2. Os incisivum of a 136-g embryo (arrow) showing a central radiolucent area where the development of the tush and tusk takes place (Bar = 2 cm).

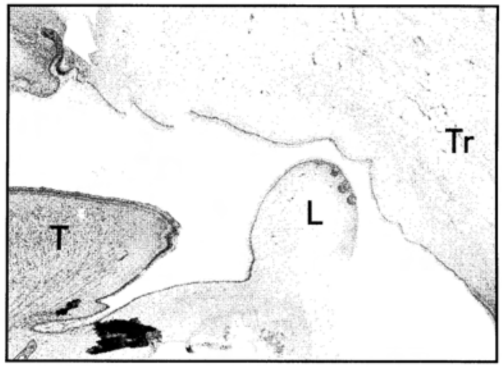

Fig. 3. The early development of the dental lamina (white arrow) in the stomodeum of the 6.5-g embryo. Note the developing tongue (T), lip (L) and trunk (Tr) (H&E stain, magnification x80).

elephant (Figs. 1A & B). The maxillae of four embryos and four foetuses varying in gestational ages from 2-22 months were obtained for radiographic examination, dissection and microscopical examination. The tusked status of the maternal animals of four embryos and two foetuses were known.

Results

The earliest stage at which it was possible to identify the os incisivum (the part of the nasomaxillary complex in which the tush and tusk develop) radiologically was in a 48.8 g (2 months gestational age) embryo. The os incisivum in a 136 g (2-3 month gestational age) showed a central radiolucent area where early development of the tush and tusk was taking place (Fig. 2).

Microscopic examination of the 1g embryo showed a stomodeum lined by primitive squamous epithelium. No dental development could be identified with serial sectioning. Early development of a dental lamina was evident in the 6.5 g (1 month) embryo (Fig. 3) and the formation of the cap stage of the dental organ of the tush was evident in sections of the 48-g embryo. The dental lamina was partially intact at this stage and ectomesenchymal aggregates formed the dental follicle and dental papilla. Formation of bone was present around the dental organ (Fig. 4). A 94-g embryo showed loss of continuity of the dental lamina and maturation towards the bell stage of the dental organ of the tush was evident in sections of the 136-g embryo. At this

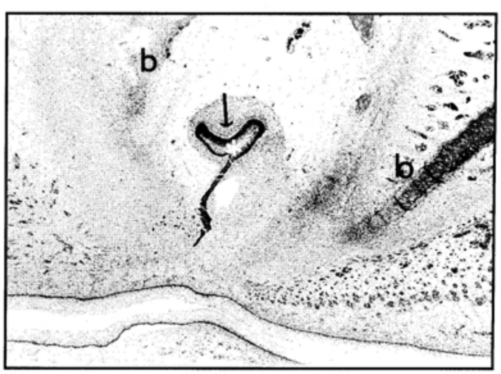

Fig. 4. The dental follicle (asterisk) and dental papilla (black arrow) of the cap stage of the dental organ of the 48-g embryo. Note the partially intact dental lamina (white arrow). Formation of bone around the dental follicle is evident (b) (H&E stain, magnification x180).

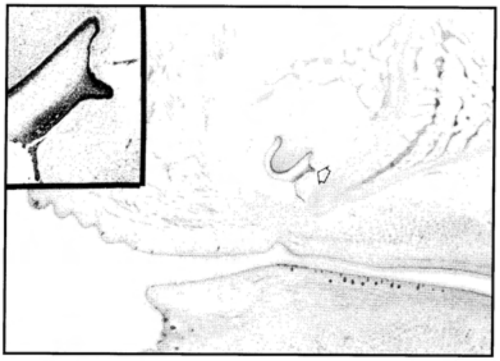

Fig. 5. Formation of the bud stage of the tusk (arrow) from the external epithelial layer of the dental organ of the tush (H&E stain, magnification x100). Inset: High magnification of the bud of the tusk (H&E stain, magnification x250).

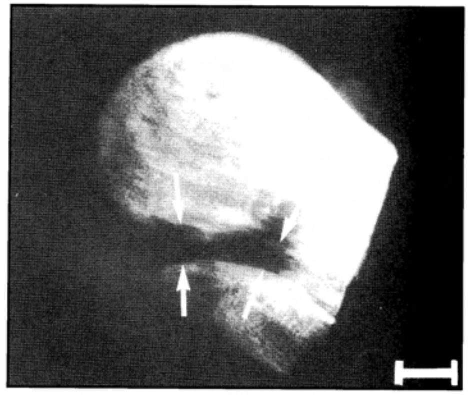

Fig. 7. Lateral radiographic view showing complete absence of tush and tusk (arrows) in the premaxilla of a 59 kg foetus. (Bar = 5 cm).

stage, epithelial proliferation of the external enamel epithelium of the bell stage of the tush formed the bud stage of the succesional tooth germ, the tusk (Fig. 5).

Of the 638 elephant (409 cows and 229 bulls) culled between 1990 and 1993, 46 (38 females and eight males) showed either unilateral or bilateral absence of tusks (Table 1).

Bilateral absence of tusks affected 19 elephant (or 3 % of the total) and the frequency thereof was higher in cows than bulls (17:2). This difference was statistically significant when evaluated with the Chi-square test with Yates correction ($P = 0.03$). Although development of the tush and tusk was recorded in the majority of embryos and foetuses either microscopically or radiographically (Fig. 6).

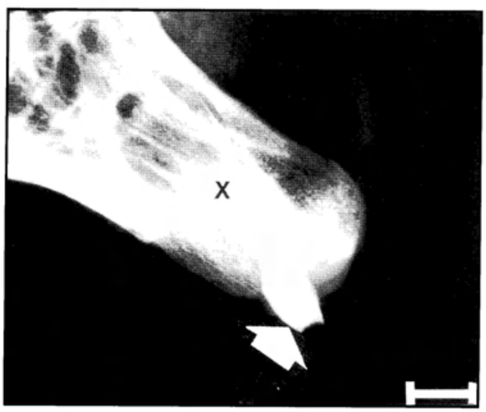

Fig. 6. Radiograph showing normal development of the tush (arrow) and tusk (X) in the premaxilla of the 53 kg foetus. (Bar = 5 cm).

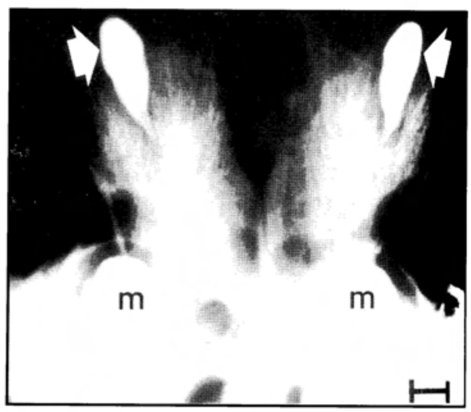

Fig. 8. Occlusal radiograph of the premaxilla of the 90 kg foetus showing the presence of both tushes only (arrows). Note the absence of tusk development between the developing molars ('m') and the tushes. (Bar = 5 cm).

one foetus showed complete absence of both the tush and tusk (Fig. 7) and another the presence of a tush only (Fig. 8). Unilateral absence of a tush or tusk was not seen in any of the embryos or foetuses examined (Table 2).

Discussion

This study has shown that the tush and tusk of the African elephant develop in succession and have a deciduous to permanent relationship. These findings are contrary to those of Anthony(1933) and Tassy (1987) who proposed the tush and tusk to represent separate teeth of the same series of incisors. This observation is supported by the radiograph in which the tush is demonstrated to lie anterior to the developing tusk. After completion of development the tush frequently fails to erupt, is pushed aside by the growing tusk and eventually resorbed in the connective tissue surrounding the os incisivum. The displacement of the tush by the growing tusk, which is clearly evident in dissected specimen of newly born elephant calves (Raubenheimer *et al.* 1994), may have prompted Anthony's observation that the tush develops adjacent to and separate from the tusk. Although the tush seems to be a non-functional vestigial dental structure, it plays an important role in the development of the tusk. The primordium of the tush not only provides the epithelial anlage for the development of the tusk, but also orientates the enamel organ of the tusk in the os incisivum and creates a pathway for the eruption thereof. Furthermore it delays the onset of the development of the tusk by several months during the first trimester of pregnancy. This delay may be important in retarding the eruption of the tusk until well after birth, thereby facilitating breast-feeding during the first year of life.

Absence of both tusks is generally congenital and may follow an inherited pattern. The occurrence of bilateral tusklessness is significantly higher in females (4.16 %) than males (0.89 %) in the Kruger National Park. Tusklessness in this sanctuary, where no selection through hunting has taken place and breeding herds remain intact, probably represents a natural mutation, which appears to be sex linked. Random culling in the Kruger National Park has contributed to this reserve becoming known for its large ivory bearing elephant (Hall-Martin 1981; Hall-Martin 1982), a sight which has disappeared from most of the African continent (Ottichilo 1986; Pilgram & Western 1986). The approach towards hunting within the ecological boundaries of the Kruger National Park

Table 2
Status of tush and tusk development in elephant embryos and foetuses

Mass	Gestational age (mnths)	Tush	Tusk	Maternal status
1 g	< 1	unknown[a]	unknown[a]	tusks L&R
6.5 g	1	L&R	unknown[a]	tusks L&R
48.4 g	2	L&R	unknown[a]	tuskless L&R
107 g	2-3	L&R	unknown[a]	tusks L&R
53 kg	17	L&R	L&R	unknown
59 kg	18	absent L&R	absent L&R	tusk L only
90 kg	21	L&R	absent L&R	unknown
94 kg	21	L&R	L&R	L&R

[a] The stage of embryonal development is to early to determine the presence of tush and/ or tusk.

seems to be changing. A hunting concession was recently granted to a neighbouring community in exchange for an agreement not to settle in an ecologically sensitive part of the park that was handed back after a successful land claim (Steyn 2000). Although limited in extent, this concession may hold consequences for future negotiations on the right to hunt in the Kruger National Park.

Individual animals in a tusked herd may become tuskless in later life as a result of injury or disease (Sikes 1971). This occurrence could be designated as acquired tusklessness and is usually unilateral with normal tusk development on the unaffected side. Unilateral tusklessness could however also be congenital resulting from failure of embryological development of the tusk on one side only. Radiographic examination, dissection and a thorough family history are essential in distinguishing unilateral acquired- from unilateral congenital tusklessness. The right-sided absence of a tusk in a cow in our study is probably genetically linked as her foetus failed to develop tushes and tusks on both sides. The 27 elephant with unilateral tusklessness were not examined thoroughly enough to distinguish the congenital from the acquired type. The higher frequency of right sided tusklessness may be indicative of tusk breakage being the most important cause for the absence of a tusk, as elephant are generally right tusked (Sikes 1971).

The involvement of the tush in tuskless elephant has not yet been recorded. Congenital absence of both the tush and the tusk imply failure to develop a lamina dentalis during the first month gestation. The presence of a tush only indicate arrest of development of the primordium of the tusk wich takes place during the second month of gestation. Tusklessness with or without tushlessness will be indistinguishable with external examination only as the tush of elephant does not appear to erupt and is pushed aside into the surrounding tissue by the growing tusk (Raubenheimer *et al.* 1994).

In order to compare the occurrence of tusklessness in the Kruger National Park with those in other elephant sanctuaries, the unilateral absence of tusks in our study was not be taken into account as in most reports only bilateral tusklessness is recorded. This study has shown that the incidence of bilateral tusklessness varies significantly between different regions. Three percent of our total sample suffered bilateral tusklessness compared to 10 % in Mana Pools. The reasons for the more frequent occurrence of tusklessness in Mana Pools when compared with the Kruger National Park are speculative. An explanation for this can possibly be found in the different population control measures employed in the two regions. In the Kruger National Park, culling has been performed randomly (De Vos 1983) and there is no chance of selection of any kind. The Kruger National Park is fenced and illegal hunting is generally under control. The elephant population in Mana Pools is managed through hunting concessions. The area is not fenced and the elephant population is exposed illegal ivory harvesting. Elephant in the Eastern Cape Province of South Africa reached virtual extinction by 1931 when only 11 survived the onslaught of ivory hunters in the dense Addo bush. Most of these elephant were tuskless. The selection for the tuskless gene is presently, 60 years after hunting was prohibited and the region declared a national park still evident, as most of the cows in the present population of 272 elephant are tuskless (Hall-Martin 1998). The shift towards tusklessness is significantly more pronounced in the elephant populations of Asia (Elder 1970; Pilgram & Western 1986) that has been exposed to modern man – hunter for much longer than its African counterpart. Most Asian elephant cows fail to develop tusks (Sikes 1971) whereas the incidence of tusklessness amongst Asian elephant bulls is much higher than on the African continent. Only 10 % of elephant bulls in Sri Lanka are reported to have tusks (Grzimek 1972). Three thousand years of exposure to man who hunted for ivory and domesticated elephant to perform work, thereby disrupting hierarchal order and breeding patterns.

selected for a phenotype, which generally lacks the genetic capacity to develop ivory tusks.

The modern high velocity rifle no longer respects and in fact selects the large tusk bearing elephant as its contribution to the population control programmes of areas managed through hunting concessions. The undisputed illegal ivory harvesting by those who frequently use armour piercing weaponry in immobilising a large tusker, contribute significantly to the heavy demand placed on the already compromised genetic pool of large tusk carriers. This is in contrast to the methods of hunting employed before the arrival of technology to the African continent. During most of the 19th century and even in the early 20th century elephant hunting and trapping methods like the falling spear, the wheel trap, trunk snare, hamstring and tendon slashing as well as group hunting with heavy short shafted spears (Sikes 1971) were more successful in killing smaller and weaker animals and in fact probably contributed positively towards the selection for a larger tusked phenotype. The arrival of the modern weapons in Africa coincided with the rapid disappearance of large tusk bearing elephant (Sikes 1971; Ottichilo 1986). Although elephant with tusks weighing in access of 80 kg was a common sight in the past century, elephant herds in most areas now consist of small-tusked animals only. Over a long period, this selection will not only lead to a decrease in the large tusked population, but also a relative increase in tuskless animals due to the hunters' lack of interest in elephant without tusks. The trend towards bilateral tusklessness is even higher in the sub adult elephant population in Mana Pools (Owen-Smith 1966), implying that a genetic shift towards tusklessness may have taken place amongst younger animals in certain regions. These changes can possibly be explained by the dominant role the matriarch (usually the cow with the largest tusks - Sikes 1971) play in selecting cows for breeding within her breeding herd. If she is shot (her large tusks usually make her the animal of choice during both trophy hunting and illegal ivory harvesting) a breakdown of the hierarchy within her breeding herd could result in cows of lesser status (i.e., those without tusks) entering the reproductive cycle. Once the genetic balance has swung in favour of tusklessness, a return to normal hierarchical order may not be sufficient to re-establish the ivory bearing genome. This is clearly witnessed in the present day Asian elephant population.

Monitoring of the size of tusks as well as the incidence of bilateral tusklessness are important indicators for genetic selection in nature conservation areas. Randomised population control programmes should be introduced where a reduction of elephant numbers are necessary. Authorities issuing hunting concessions in Africa should take note of the trends reported in this manuscript and introduce a tariff structure, which would encourage hunting of a broader spectrum of elephant in a herd. Restoration of the matriarchal dominance in a breeding herd seems imperative to the long-term survival of the ivory bearing gene. The granting of permits for international trade in ivory should, in the long term, be based on whether a region is successful in maintaining the ivory bearing phenotype during their population control programme.

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