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# Loose front teeth: radiological and histological correlation with grooming function in the impala *Aepyceros melampus*

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(With 1 plate and 1 figure in the text)

Casual observations have revealed that the anterior dentition of impala and other antelope is loosely embedded, with the tips of the teeth movable over a distance of 1·5 to 2 mm. The comb-like anterior dentition of impala *Aepyceros melampus* is utilized extensively for grooming purposes, and it was hypothesized that the looseness of the teeth might be related to the grooming function. A sample of 12 impala mandibles was obtained from Pilanesberg National Park, Boputhatswana. Six of the incisor–canine (IC) complexes were examined macroscopically, radiographically and histologically, while the remaining six were used to determine the alveolar depth relative to total root length. The findings were: (1) wide periodontal ligament spaces, most prominent in the apical region; (2) a loose, highly vascular periodontal ligament; (3) well-developed trans-septal periodontal ligament fibres; and (4) relatively shallow alveoli, with only approximately two-thirds of the roots included within the alveoli. In no case could looseness be ascribed to pathological changes in the periodontal ligament, cementum or alveolar bone. These features suggest that the looseness of the teeth is associated with a see-saw action of the teeth about a fulcrum below the alveolar bone crest, with the maintenance of the closed resting position of the teeth being facilitated by the well-developed trans-septal fibres. It is suggested that the minimal interdental space maintained by this arrangement during grooming assists in the efficient removal of parasites from the pelage by impala.

## Contents



## Introduction

The teeth of mammals demonstrate an impressive evolutionary response to the specialized feeding requirements of the many species of the class that inhabit, or did once inhabit, the earth. Being exposed to the not inconsiderable forces generated during the procurement and mastication of food, mammalian teeth are generally firmly embedded in their alveoli in the mandibular and maxillary processes (Ten Cate, 1989: 244–274). Sometimes, however, teeth are used for purposes other than feeding. McKenzie (1990) has described a specialized array of teeth in small to medium-sized browsing ruminants which are used extensively for grooming of the pelage. As noted (McKenzie, 1990: 119), the anterior teeth in the lower jaw ($I_1$, $I_2$, $I_3$ and the canine, together here referred to as the incisor–canine (IC) complex) are noticeably loosely embedded in their alveoli. Incidentally, Janis & Ehrhardt (1988) also noted that the anterior teeth of ruminants in museum specimens are often lost.

In fresh specimens, the tips of the IC complex elements of impala *Aepyceros melampus* Lichtenstein, 1812 are easily moved over an arc of 1·5–2·0 mm (unpubl. data). The teeth may be manually parted, but return to the resting position with no intervening spaces ($I_2/I_3$ and $I_3/C$) when released. Noting that the loose teeth may be associated with the grooming function in ruminants, one of us (AAMcK) suggested the hypothesis that the looseness of the teeth may be a functional attribute to facilitate a combing action during grooming, allowing the teeth to part and thus permitting the hairs to pass between the otherwise closely adpressed elements of the IC complex.

If indeed the looseness of the teeth is a functional and not a pathological phenomenon, then this should be reflected in the microanatomical relationships between the teeth and their alveoli. In order to define these parameters and relate them to the grooming function, a macroscopical, radiological and histological examination of the IC complexes of adult impala *Aepyceros melampus* was undertaken.

## Materials and methods

The anterior parts of mandibles of 12 adult male impala were collected from freshly killed specimens during a routine culling operation in the Pilanesberg National Park, Boputhatswana. The mandibles were severed midway along the diastema between the incisors and first premolars. Six of the samples were fixed in 10% formalin, the other 6 were stripped clean and allowed to dry. The fixed specimens were macroscopically examined for any evidence of dental pathology and were then individually photographed and radiographed with a conventional dental radiographic apparatus. Specimens were then sawn, decalcified with 10% trichloroacetic acid, and wax-embedded. Sections 5 $\mu$m thick were cut and stained with haemotoxilin and eosin. The sections were examined for evidence of histological correlation with the looseness of the teeth observed in the fresh specimens.

The dried specimens were immersed in a 5% solution of NaOH until the teeth were sufficiently loose to be removed. The samples were then rinsed in water and allowed to dry with the teeth *in situ*. The teeth were then marked at the level of the interdental alveolar bone crest and removed from their alveoli. The roots of the teeth were measured with Vernier callipers, from the apex to the mark, representing the portion of the root within the alveolus, and from the mark to the dentine–enamel junction on the lingual aspect of the tooth, representing the free portion of the root.

## Results

### *Macroscopical examination*

All the teeth of all the sample specimens were intact. Moderate horizontal attrition was present in all specimens, but in no case had the crown height been reduced by more than 30%. Mild discoloration was evident in the neck regions of the teeth on the labial and lingual surfaces. No evidence of caries or gingivitis was detected in any of the specimens.

## *Radiological examination*

All the specimens exhibited two features that were notable in comparison to conventional dental radiographic features.

### *Alveolar bone height*

While proportionality could not be determined from the radiographs, it was apparent that the alveolar bone terminated well below the necks of all the teeth (Plate Ia). The lamina dura was only visible in areas. No pathological alveolar bone loss was seen.

### *Periodontal ligament space*

The periodontal ligament space appeared to be uneven in width but was markedly wider around the apices of the teeth and in the crestal area distal of the canines (Plate Ia)

## *Dry specimen measurements*

The proportion of the root embedded in the alveoli varied from 48·6% to 83·3%, with a mean value of 68·4% (S.D. = 6·4: $n = 48$).

## *Histological examination*

The arrangement of the anterior teeth of an impala in the mandible is illustrated in Fig. 1. The figure also serves to show the areas of origin of Plate I(b–d).

Sections obtained exhibited minimal artefacts, and facilitated detailed examination of hard and soft tissues. The following features were evident in all specimens:

### *Periodontal ligament fibres*

Distinctive, interwoven, horizontal trans-septal fibres occur above the alveolar bone crest. These consist of dense, relatively avascular, acellular collagen (Plate Ib).

The periodontal ligament below the alveolar bone crest is noticeably more cellular and more loosely arranged than that above the bone crest (Plate Ic). Ligament fibres are both horizontally and vertically arranged, and Sharpey's fibres are prominent at both alveolar and dental interfaces.

The ligament is noticeably widest in the apical region (Plate Id), corresponding to the radiographic observation of a wide apical periodontal space. Large, cavernous blood-vessels occur in the periodontal ligament space: most of these lie in a vertical direction (Plate Ic,d). Odontogenic epithelial islands are uncommon in the ligament. Islands of epithelial cells were only encountered in close relationship to the epithelial attachment in the ligament. No signs of periodontal disease were seen in any of the sections.

### *Cementum*

The cementum covers the entire root, and is characteristically uneven and more cellular towards the apex (Plate Ic,d). Periodontal ligament fibres attach via Sharpey's fibres to the cementum

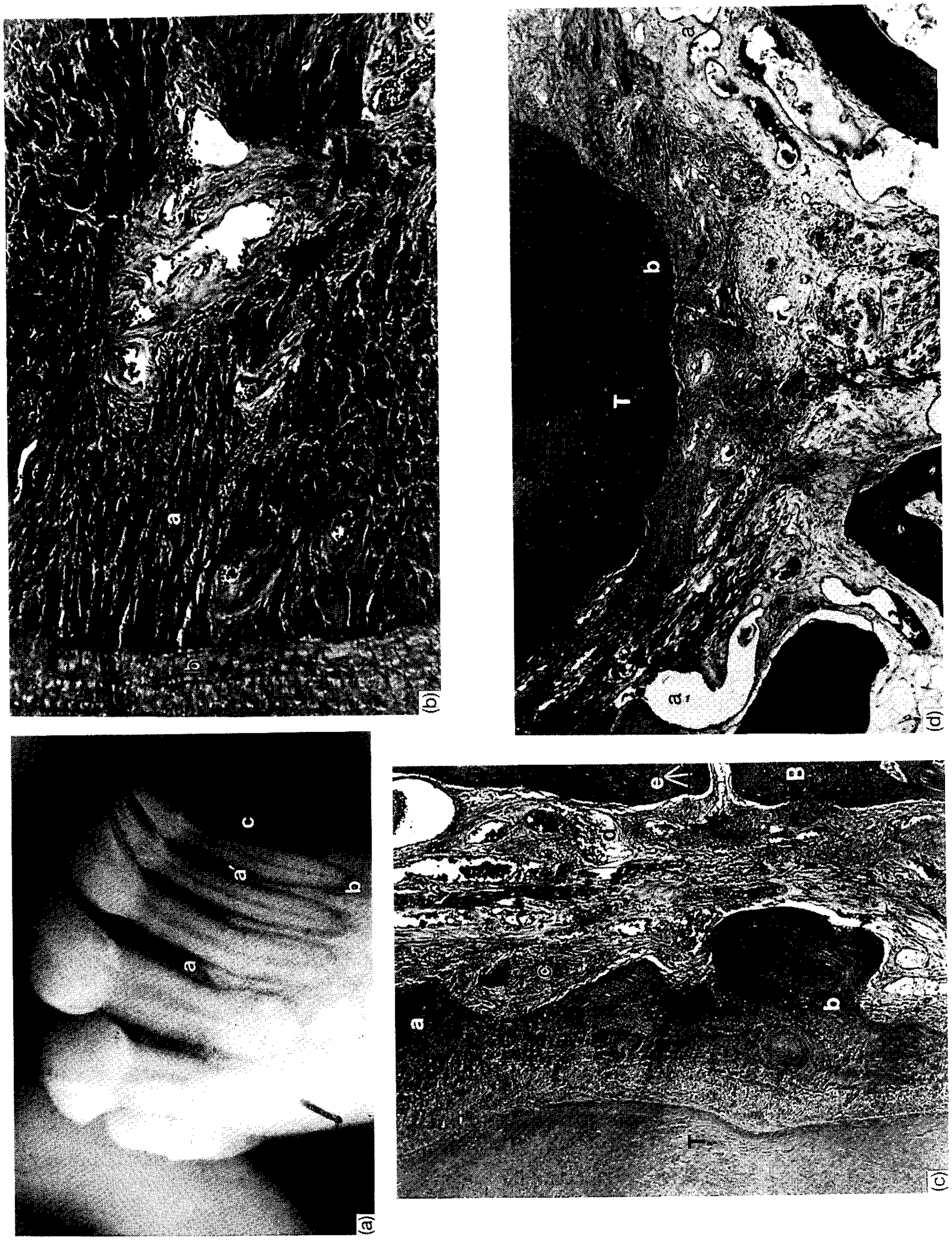

PLATE I

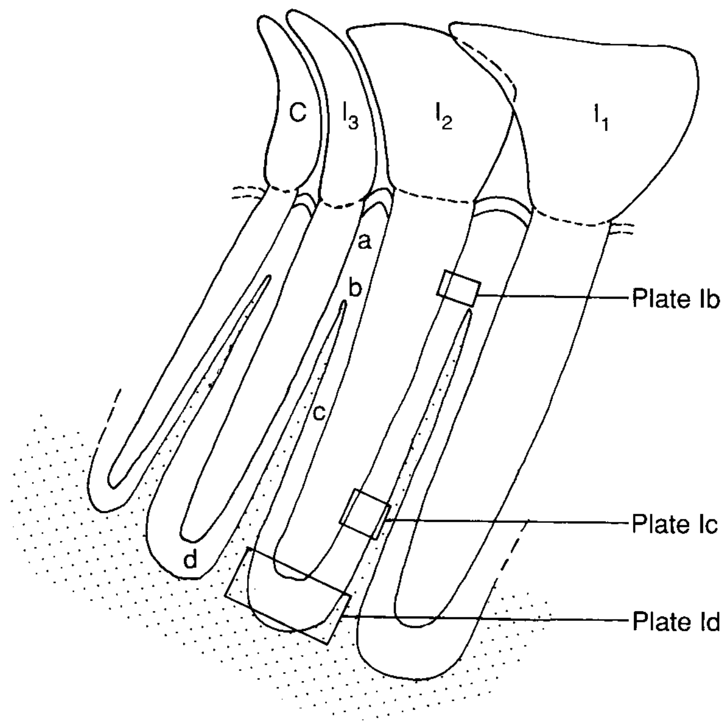


FIG. 1. Lateral sectional view of the incisor–canine complex of an impala mandible. $I_1$, $I_2$, $I_3$ and C: the dental elements of the IC complex. a, Region of the root proximal to the alveolus. This region is characterized by dense, interwoven, trans-septal collagen fibres. b, The alveolar bone crest. c, The wide periodontal space. The periodontal ligament in this region is loosely arranged, with many cavernous vascular spaces. d, The apical region. The periodontal space is widest in this region. The areas of origin of Plate I(b–d) are indicated.

(Plate Ib,c), while the area of epithelial attachment is characteristically acellular. Areas of active restructuring of the cementum, particularly in the apical region, were noted (Plate Ic,d).

### *Alveolar bone*

The alveolar bone crests end at a point half to two-thirds of the distance between the root apex and the neck. Bone surfaces are generally even, with the exception of the alveolar crestal area where marked osteoblastic activity and associated irregularity was recorded. Numerous central as well as peripheral osteoblastic lacunae are present, and Sharpey's fibres are prominent (Plate Ic).

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PLATE I. (a) Antero lateral radiograph of the incisor–canine complex of an impala. Alveolar bone crests occur far below the area of epithelial attachment (a,a′). Wide periodontal spaces are apparent, particularly in the apical region (b) and in the crestal area distal to the canine tooth (c). (b) Region proximal to the alveolar bone crest showing: a, dense, horizontal trans-septal collagen fibres; b, cementum with attachment of the ligament via Sharpey's fibres. ( × 200). (c) Periodontal ligament between tooth (T) and alveolar bone (B). a, Sharpey's fibres. b, Cementum showing irregularities due to active restructuring. Highly cellular periodontal ligament composed of: c, loosely arranged collagen fibres, and d, cavernous vascular spaces. e, Osteoblastic lacunae in alveolar bone. ( × 100). (d) Apical region showing the tip of the tooth root (T) within a wide periodontal ligament. a, Numerous cavernous vascular spaces within the periodontal space in the apical region. b, Irregularity of the root surface indicates active restructuring of the cementum layer. ( × 150).

## Discussion

The casual observation that the elements of the IC complex are functionally mobile in healthy live impala is supported by several observations made in the present study. These will be discussed separately in this context.

The alveolar bone extends only approximately two-thirds of the way between the tooth apex and the neck region of the teeth. This is apparent on dry specimens, radiographs and histological sections. This feature is highly unusual, yet does not explain looseness of the teeth *per se*. What this shallowness of the alveoli does suggest is that any looseness of the teeth due to a wide periodontal space will be magnified at the tip of the crown owing to the absence of restrictive alveolar bone below the neck region of the teeth. Seen in the context of the other features, therefore, the shallowness of the alveoli is integral to the observed mobility of the teeth.

The periodontal space is relatively wide, which accounts for the looseness of the teeth observed in old dry specimens (Janis & Ehrhardt, 1988). A widening of the periodontal ligament space towards the apex of the root is noticeable on histological sections and radiographs. This feature implies that the teeth receive maximum support near the alveolar bone crest. This point then acts as a fulcrum when the teeth are moved, with the root apex moving within the enlarged apical periodontal space.

The ligament within the periodontal space is well secured to both the alveolar bone and the cementum by prominent Sharpey's fibres. However, the ligament itself in this area is loosely structured, with a multi-directional arrangement of fibres, a highly cellular composition, and a considerable number of large blood-filled cavities. From these histological features it is apparent that there is minimal limitation to movement of the apical regions of the teeth within their enlarged periodontal spaces.

Considerable irregularity in the cementum occurs in the regions of the root apices, indicating a continual process of resorption and deposition. These irregularities indicate changes in the cementum in response to stresses imposed on it, presumably by the continual movement of the teeth during grooming. Active bone restructuring in the vicinity of the alveolar bone crest is indicative of similar stresses in this region—the fulcrum about which all movement of the teeth takes place.

Abundant interwoven trans-septal periodontal ligament fibres occur above the alveolar opening. The length of root unencumbered by the alveoli is instead surrounded by these fibres. Relative to the apical areas, the collagen fibres in this region are densely arranged with minimal interspersion by vascular spaces.

The constancy of the features recorded in the present study suggests that the observed looseness of impala teeth is not an aberration. On the contrary, all of these features—the wide, vascular periodontal ligament, the shallow alveoli and the well-developed trans-septal fibres—point to a functional looseness of these teeth. It is readily apparent that these loose teeth are not on the point of exfoliating: the well-developed Sharpey's fibres and trans-septal fibres indicate that the teeth are suitably retained in their resting positions. The marked mobility of the tooth tips is apparently due to a see-saw action of the root centred below the alveolar bone crests, with maximal movement occurring at the crown tips and root apices. In the absence of a firm adhesion along the length of the roots within their alveoli, it would appear that the maintenance of the positioning of the teeth is due in large measure to the cushion of dense trans-septal collagen fibres which lie above the alveolar bone crests. From histological observations, this is the tissue which is most likely to maintain the tendency to close when the teeth are forcefully parted.

As shown by McKenzie (1990), the IC complex of impala is used to comb the pelage, with the hairs being pulled between the teeth during a grooming sequence. It is readily apparent that in order most effectively to scrape parasites off the skin under a dense pelage, a comb-like structure is required. If the teeth used for grooming were in the form of a rigid comb, this scraping action would be equally as effective as in the true situation, where the teeth are inclined to remain closely adpressed. A marked difference would, however, emerge during subsequent events.

Scraping a small parasite (tick larva, louse) off the skin with a rigid comb would allow the parasite either to be carried away from the skin on one of the teeth of the comb, or to pass through the wide spaces of the comb and remain within the pelage. (If the spaces between the teeth were too narrow the rigid comb would become entangled in the pelage.) The alternative arrangement—that of a comb which in the resting position has no interdental spaces, but which can part to allow hair to pass between the teeth—is what is found in impala. Because of the elastic nature of this flexibility, the teeth tend to maintain a minimum interdental space during grooming, the size of which is determined by the thickness of the hairs passing between the teeth. The sequence following the scraping off of a parasite under these circumstances is somewhat different: owing to the hairs of the pelage being pulled through the closely adpressed elements of the comb (particularly $I_2/I_3$ and $I_3/C$), any loose material, including the parasite, would be retained on the lingual surface of the teeth and thus removed from the pelage altogether.

Impala employ oral grooming extensively (L. A. Hart & Hart, 1988), and even exhibit a unique pattern of reciprocal allogrooming in which herd mates groom each other in a reciprocal fashion (B. L. Hart & Hart, 1992; Mooring & Hart, 1992). This grooming may allow impala to utilize habitats in which tick infestation risk is high (McKenzie, 1990; Mooring & Hart, In press). As ticks have been part of the terrestrial environment for at least 200 million years (Hoogstraal, 1978), it is likely that not only behavioural but also morphological adaptations have occurred to allow impala and other antelope to co-exist with these parasites.

## Conclusion

Parasitism is a costly burden to animals (Lightfoot & Norval, 1981; Kim, 1985; B. L. Hart, 1990), yet grooming to remove parasites can be energetically expensive (Lightfoot & Norval, 1981; Dudley & Milton, 1990). We suggest that the loose arrangement of the elements of the IC complex of impala described in the present study facilitate efficient removal of parasites from the pelage. This is achieved by the maintenance of a minimum interdental space, approximately the equivalent of the diameter of an individual hair, during grooming with the tooth-comb. Parasites removed from the skin by the sharp tips of the teeth thereby have little chance of remaining in the pelage to recommence feeding from their host. Evolutionary forces minimizing energy allocation to repeated grooming efforts have led to a 'loose' arrangement of the anterior dentition in impala.

Browsing and mixed-feeding ruminants (equivalent to Hofmann & Stewart's (1972) concentrate selectors and intermediate feeders) possess the small lateral elements of the IC complex as found in the impala (Janis & Ehrhardt, 1988). McKenzie (1990) has suggested that this group is exposed to high levels of parasite infestation in their natural habitat, and that this may explain the presence of a tooth-comb in these species. Similar radiological and histological features to those described in the present study may therefore be expected in the browsers/mixed feeders other than the impala. Impala dentition resembles the ancestral type (Pocock, 1935), and retention of some of these features may explain the general looseness of ruminant anterior teeth as seen in museum specimens (Janis & Ehrhardt, 1988). Such looseness is not typical of groups such as the equids and carnivores:

in these taxa the presence of opposing dentition either precludes a loose arrangement of the teeth or facilitates the alternative biting grooming action of these groups.

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