VELERICORN ANTLERS ON A MATURE MALE MOOSE (*Alces a. gigas*)

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ABSTRACT: Macro- and microscopic descriptions of perennial, velericorn antlers on a male moose are presented. Unlike the proliferating cartilaginous nodules of "peruke" antlers, the growth of velericorn antlers was relatively controlled with evidence of sequestration (separation) of tines and a degree of regeneration where tines and parts of the palm had been lost. In contrast to the centripetal ossification of the pedicles and antlers of normal moose, the slow osteogenic process in velericorn antlers proceeded centrifugally, from the inner core outwards. Proliferation of the integument lead to the formation of epidermal cysts and areas of ectopic ossification. Extra-testicular androgens are believed to cause velericorn antler growth. It is hypothesized that an analogous growth and ossification process characterized proto- and pseudoantlers of the Miocene.

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The absence of testicular androgens in surgically castrated deer does not always have the same impact on growth, morphology, and survival of antler pedicle protuberances among and within cervid species (Acharjyo 1982, Allison 1978, Altreiter 1990, Anonymous 1989, Asdell 1964, Brandt 1901, Bubenik 1963, 1966, 1982, Bubenik unpubl. data on fallow buck castrate, Bubenik and Weber Schilling 1986, Chapman *et al.* 1984, Chevalier 1984, Baber 1987, Dickie 1960, Goss 1983, 1990, Heath 1989, Hohle and Lykke 1986, H.R. 1989, I.H. 1990, Murie 1928, Olt 1927, Robinette and Jones 1959, Seton 1909, Van Bemmel 1952, Wishart 1980). Our knowledge of these differences is limited to studies of antlers which are often grossly malformed with tumor-like growths or protuberances. Such antlers have been termed "perukes" (Olt 1927, Goss, 1990) because the tissue above the pedicle proliferates into cartilaginous nodules which may hang down over the head like curls of a baroque wig (Fig. 1).

In describing peruke antlers, Goss (1983, 1990) uses the term "antleroma", combining the English word antler with the Greek "oma" (tumor-like), due to the tumor-like appearance of the tissue. However, perukes are not malignant (Olt 1927, Goss 1990); the uncontrolled tissue proliferation is limited to protuberances from the antler pedicles. The only known malignant impact of castration is seen in roe deer (*Capreolus* sp.), where castration leads to profound osteoporosis with perforation of the parietal and frontal bones; death may occur within 2 to 3 years (Bubenik 1963, 1990; Fritz 1990, Kübner 1987).

Other types of castrates do not develop perukes. Their pedicle protuberances grow more or less within the species-specific shape (e.g. in red deer, *Cervus elaphus*)(Fig.2). The bony tissue of the surface proliferates into pearls and ridges and the distal parts may become sequestered. The beam of these antlers has the potential to regenerate lost tines, points or palms in an almost specific fashion (Acharjyo 1982, Bubenik 1966, Bubenik and Weber Schilling 1986). To distinguish these antlers with slowly proliferating protuberances from the rapidly growing perukes, and to emphasize their relative species-specific shape and regeneration potential, use of the term "velericorn" antlers (**VCA**) has been suggested (Bubenik 1990). This paper provides the first detailed description of **VCAs** in a moose, a species in which castration usually results in the development of perukes (Bubenik and Timmermann 1982, Murie 1928, Seton 1909). To our knowledge, there have been no studies of the sequestration and subsequent regeneration processes seen in velericorn antlers. Cases of sequestration during the warmer seasons (Acharjyo 1982, Bubenik unpubl. data, Bubenik and Weber Schilling 1986, Bubenik 1983) provide evidence that this process cannot be a consequence of tissue freezing as assumed by Goss (1990).

MATERIAL AND METHODS

A moose, aged 6 to 8 years, was taken from the Big Salmon Range, Yukon Territory, Sept. 21, 1987. The tarsal glands were without the typical smell of a rutting bull (Bubenik *et al.* 1979). The face was pale brown instead of the typical black coloration of a rutting bull (Bubenik *et al.* 1977). The hunter who took the moose did not find a scrotum with testes or hermaphroditic ovaries. The poor state of preservation of the specimen prevented detailed histological investigation.

The right antler was radiographed in segments and a composite negative was later assembled. Transversal and sagital sections of the osteon of the shaft, palm, and re-grown tines, were studied. The surfaces of different ossified parts were polished and stained with Indian ink to enhance the visibility of the lamellae and the density of the osteon. A prominent tine (**T2**) was studied after being soaked for 48 hr in saline to make it pliable.

RESULTS

In frontal view, the veleriform antlers show different stages of regeneration of sequestered parts of the palm and tines (Fig. 3). The left palm exhibits splintered edges across the medial portion of the palm [**MP**] suggesting some of it was recently lost. The two other sequestrations, i.e., of the frontal part of the main palm [**FP**] and that of the brow-tine [**BP**] were probably lost earlier, having rounded edges as a consequence of healing.

The tines **T2**, **T4** and **T5** of the right palm were pliable and probably were still growing. The most medial tine [**MT**] of the palm must have been lost recently as suggested by the splintered rim around the wound. The right brow-palm [**BP**] was apparently dropped earlier and was in a stage of partial regeneration. The velvet had little hair and bled slightly when peeled off. The dorsal side of the right palm had a white triangular area with numerous, flat nodules only partially covered with hair.

The surface of the right antler was covered with scattered areas of desiccated velvet or velvet-like skin, about 3 mm thick. These dried patches could be peeled from an underlying, transparent, corrugated tissue (2 mm thick) with a cartilaginous appearance which adhered to the bony tissue of the antler. The velericorn palm exhibited partially hardened, skin covered, flat nodules. The healed wounds where portions of the antler had been lost were covered by thin, hairless skin.

Radiographic investigations

A radiograph (Fig. 4) revealed that the pedicle of the velericorn antler consisted of homogeneous, dense bone in the center with more porous bone at the periphery. This is the opposite of what is seen in a normal moose where the interior of a growing antler is highly porous (Bubenik 1966). Coronets [**C**] of the velericorn antlers were unusually high and thick (Fig. 4). Remnants of the coronary vessels [**CV**], which develop after the first antlers are cast (Frankenberger 1954), were detectable. Upward projecting blood vessels (arrows) nourishing the VCA were also visible. However, when the vessels began to ramify and crisscross (a sign of developing the palm (Bubenik 1990)), some submerged into the palm's core (Fig. 4, **SV**).

Nodules on the surface of the palm were in various stages of ossification as could be seen where they projected laterally at the edge of the palm [**p**]. Evidently, ossification of the nodules progressed from the periosteum inwards, until they fused with the surface of the palm. The nodules were either scattered across the surface and edges [**p**], or arranged in garlands. The largest nodules developed over the thick blood vessel running across the distal part of the palm [**CV**]. The garland of nodulettes may indicate the development of a 'pseudocoronet', below which a further coronary vessel is detectable. Similar pseudocoronets, were observed on the palms of a castrated fallow deer, *Dama dama*, just prior to sequestration of its distal portion (Fig. 5, from Bubenik 1956).

In the moose velericorn antler, two garlands of nodules in the central part of the palm (Fig. 4) might indicate earlier losses of palm tissue. Tine **T6** and brow-tine **BT** appear to be fully ossified. However, the varying bone density of tines **T1, 2, 3, 5** and **7** may reflect the different times at which they were lost and re-grown. In general, ossification of a tine progressed in accordance with its length. Judging from the length of **T2** and **T5**, the upper portion of the palm may have sequestered and started to regenerate about 3 to 4 months before the animal's death (ie., in the spring).

In transverse section, the pedicle of the VCA (Fig. 6A) revealed a compact interior core surrounded by a layer of porous bone of varying thickness. In contrast, the pedicle of a normal moose antler (Fig. 6B) had a relatively compact outer cortex and a porous centre. Thus, the pedicle of the VCA mineralized centrifugally and almost all of its blood supply was close to the surface.

A transverse section of the shaft of the VCA (Fig. 7A) was compared with the same part of the shaft of a normal moose antler (Fig. 7B) and with that of a Miocene protocervid, *Dicroceros elegans* (Fig. 7C) (from Bubenik 1962, 1982, 1990). The pedicle protuberances of both the VCA and the protocervid antler were mineralized centrifugally, in contrast to antlers of the normal moose in which mineralization progressed centripetally leaving a porous core.

Transverse section of the velericorn palm confirmed the radiographically detected internal vessels and revealed that the core was more porous than the surface. The irregularly thin but relatively compact surface was comprised of fused nodules developed beneath the periostium. Locally, these flat nodules had already begun to engulf some of the superficial vessels.

A sagittal section (Fig. 8) through the base of **T2** revealed that its parallel bony lamellae [**L**] originated from the relative compact bone [**B**] of the palm's edge. This was probably a site of previous sequestration. Despite its length (almost 30 cm), the entire tine [**T2**] was without secondary osteon, typical in the formation of a compact cortex.

A large, partly soft nodule [**N**] located above a well ossified ridge [**B**] was seen in transverse section through the base of **T7** (Fig. 9). Numerous cysts [**cy**] were imbedded in what may have been cartilage with involuted skin [**S**]. Some of the whitish cysts lacked sharp outlines and extended toward the base of the nodule [**N**]. They seemed to infiltrate the 'cartilaginous' tissue [**C**] and undergo ossification. The largest cyst [**P**] expanded toward the palm cortex [**B**] with which it finally fused (arrows). In this way new calcified pearls or 'ridges' may have developed among the vessels, eventually engulfing the superficial vessels [**V**].

Histological examination

The velvet - The integument is characterized by a localized epidermal hyperplasia (Fig. 10 and 11), which in many areas caused a prolific degenerative transformation of sebaceous glands (arrows,Fig. 10; Fig. 11, arrows, **SG**). It appears that after some velvet hair was lost, an outflow of sebum was blocked by proliferating epidermis. Accumulating sebum lead to complete degeneration of some glandular tissues (Fig. 12). This process created numerous cysts varying in size from microscopic follicles (Fig. 12) to large cysts, 5 mm in diameter (Fig. 13). Large cycts were observed in many acral areas, appearing macroscopically as nodules on the palm's surface (Fig. 3, 4, 9). In other areas the integument was fairly thick and of normal appearance. Functioning sebaceous glands were located alongside hair follicles oriented perpendicular to the surface of the velvet (Fig. 10). The deeper parts of the dermis were condensed, forming a characteristic periosteum [**P**] which was attached to the developing primary bone trabeculae by Sharpey's fibers (Fig. 14).

Antler bone - Only immature stages of osteogenesis were observed throughout most of the VCA. Trabeculae of woven bone, richly interspersed with an impressive reticular structure were seen frequently in sections (Fig. 15). Only rarely were Haversian osteons of secondary bone lamellae observed (Fig. 16). Spaces between primary bone lamellae, at the boundary of the periosteum and the osseous tissues, were occasionally filled with a compact material, probably mesenchymal in origin. There was little evidence of rapid bone growth. Very few osteoblasts or osteoclasts were present. This was similar to the appearance of bony tissues seen in autumn in a castrated white-tailed deer (Morris and Bubenik 1982). In contrast to the integument, the bony tissues of the VCA appeared to be in a steady state at the time the animal was killed. In a few areas we have detected ectopic bone formation [**B**] within the velvet (Fig. 17, **D**), indicating abnormal osteogenesis.

DISCUSSION AND CONCLUSIONS

Neither scrotum with testes, nor a blind vagina was found by the hunter who submitted the velericorn antlers. The possibility exists, however, that the moose was a cryptorchid and that the testes were overlooked in the abdominal cavity or, it may represent a very rare case of pseudohermaphroditism in which rudimentary ovaries are conjoint with rudimentary testes (Rörig 1899, Wislocki 1954, Donaldson and Doutt 1965). Atrophy of external testes can be excluded (De Martini and Connoly 1975) because a scrotum was not present on the moose.

If pseudohermaphroditism is rejected as a probable cause, only cryptorchism, accidental castration, or high levels of non-testicular androgens (e.g., adrenal) can explain the relatively well controlled growth of the velericorn antlers described here. In contrast, most of the few known moose skulls suspected of belonging to castrates, seem to develop perukes (Bubenik unpubl. data, Hohle and Lykke 1986, Murie 1928, Peterson 1991).

Our observations indicate that the distal portions of VCAs are probably sequestered and regenerated aperiodically. In contrast to true antlers, in which the core remains spongious, and the cortex develops by 'centripetal' mineralization, in VCAs the process is reversed. We assume that the ossified loci fuse later with the appendage body and finally conjoint themselves by engulfing the superficial vessels. In this way the diameter of the appendage increases permanently or successively and the number and length of regenerated tines is changed. It is a process which may be similar to osteochondrosis which in humans is ascribed to hormonal imbalance (Aegertner and Kirkpatrick 1968) and also occurs in castrated deer .

Of particular importance is the evidence presented here of a periodically decaying and regenerating velvet and a process of subperiosteal ossification. As a result, the bone surface remains alive and growing periodically, despite ossification of pedicles and the relatively compact interior of the palms. The new cartilaginous layers underlying dead patches of velvet may develop from mesenchym beneath the surviving subcutis or from proliferating cartilage of the surrounding nodules. These findings suggest that velvet or velvet-like skin can regenerate beneath dying cutis, thus leaving the bone alive. Rapid proliferation of the integument leads to the formation of epidermal cysts and ectopic ossification centers while a slow osteogenic process occurs in the central parts of the VCA.

The 'centrifugally' progressing ossification is unknown in sexually normal male cervids of all extant deer. However, a progressive petrification of antlers following velvet shedding has been reported in very primitive deer like pudu (*Pudu* sp., *Mazama* sp.) or in muntjacs (Muntiacidae)(Bubenik 1990). This process is similar to the 'centrifugal' ossification seen in protocervids (Dicroceridae), and in North American pseudocervids (Merycodontinae) of the Miocene (Bubenik 1962, 1982, 1990). This leads us to the hypothesis, expressed somewhat differently by Teilhard (1939), that the pedicle protuberances of ancestral deer were facultatively perennial and may have grown by a process similar to that seen in velericorn antlers. Distal parts could sequester and/or regenerate without having to be annually deciduous (Bubenik 1990), as has been assumed by Frick (1937) and Ginsburg (1968).

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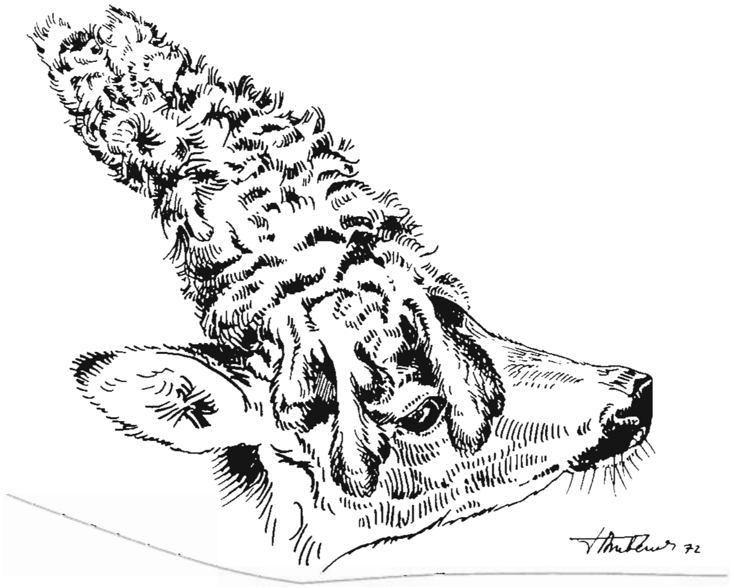

Fig. 1. Peruke of a roe deer, *Capreolus capreolus* (Bubenik personal collection).

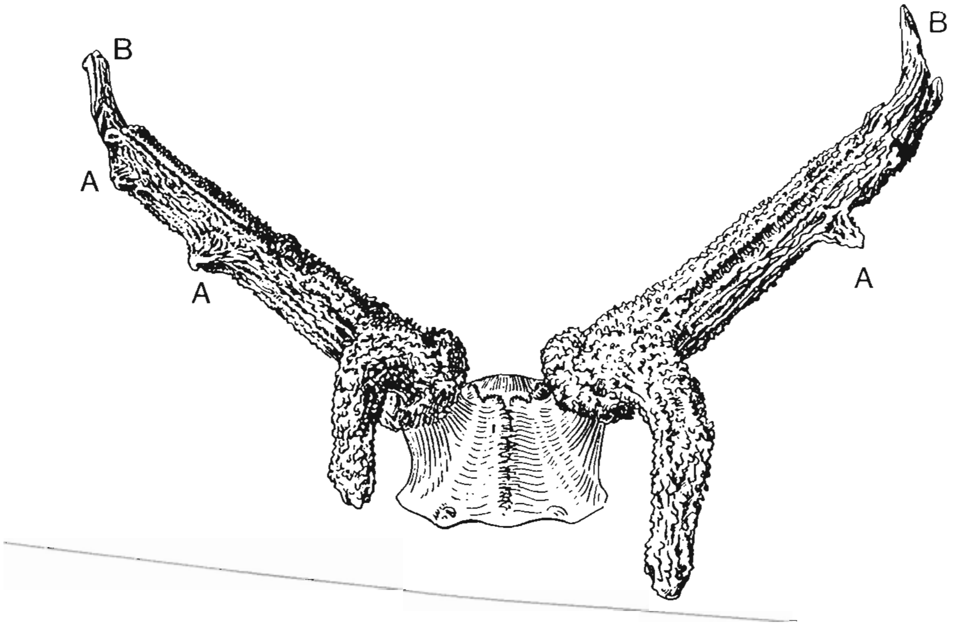

Fig. 2. Velericorn antlers of red deer (*Cervus elaphus*) castrate, with tines [A] and beam ends [B] in different stages of regeneration, due to different timing of sequestration. (from Bubenik 1966).

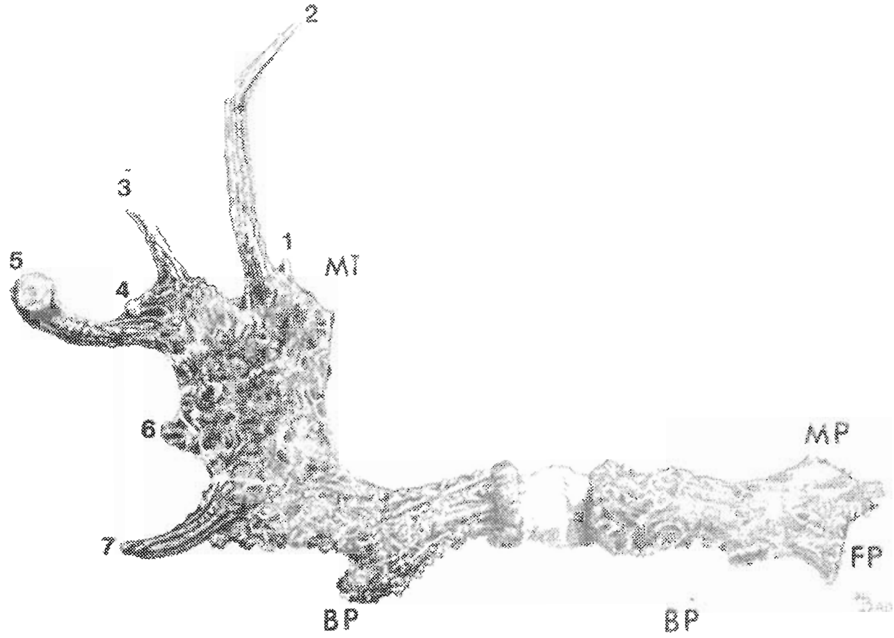

Fig. 3. Velericorn antler [VA] of moose from Yukon Terr., frontal view. The three wounds on the left side, where the palm should be, are marked [MP] = the most recent; [FP] = probably the frontal tines of the main palm; [B] the brow-tine or brow-fork, both in stages of healing. On the right side the pliable tines are marked [T4 and T5]; the others were just hard. [MT] = medial tine of the main palm. The right brow-tine (BP) must have been lost earlier and has been only partially re-grown.

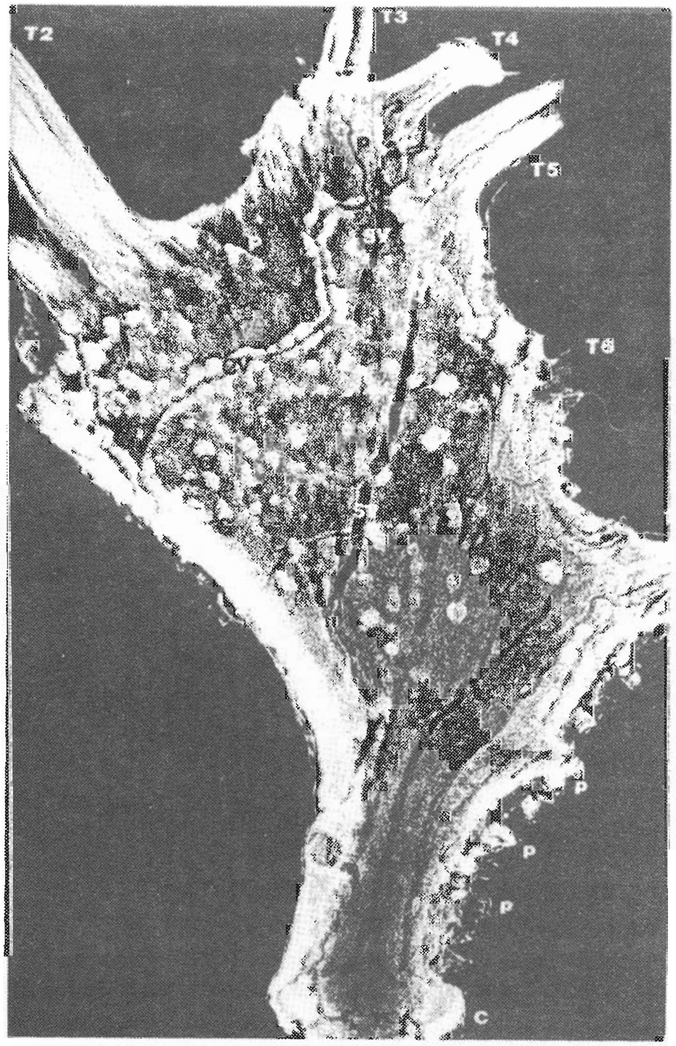

Fig. 4. Composed radiograph of the right palm. [C] indicates the hyperplastic coronet or burr. The black arrows point to the coronary blood vessels. [p] are nodules or pearls in different stages of ossification and fusion with the body. (MT) shows the freshly lost tine. [T1, 2, 3, 4, 5, 6, 7] regenerated or regenerating tines. (P) is probably the regenerated distal portion of the palm. [SV] are submerged vessels and [CV] may be the most recent 'coronary' circuit. (G1, 2, and 3) are garlands, presumably developed as "pseudocoronets" during previous sequestrations.

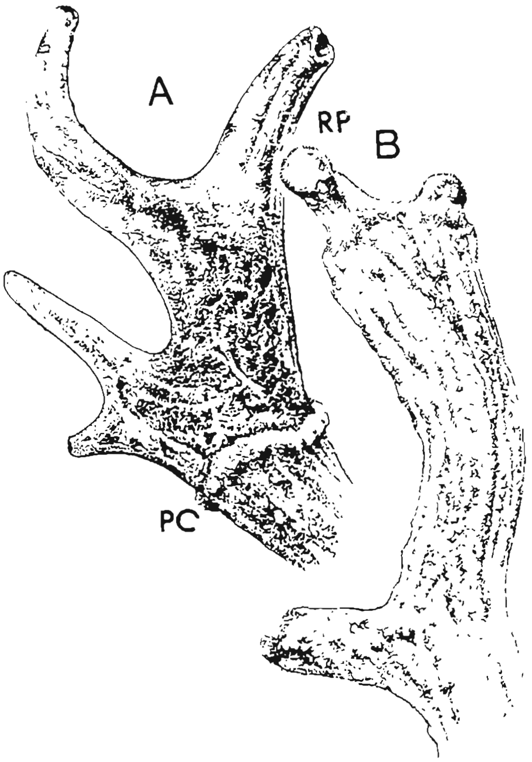

Fig. 5. The right velericorn palm of a fallow buck, *Dama dama*, castrate in a stage of beginning sequestreation. (A.) Development of a 'pseudocoronet' (PC) (from unpublished study).

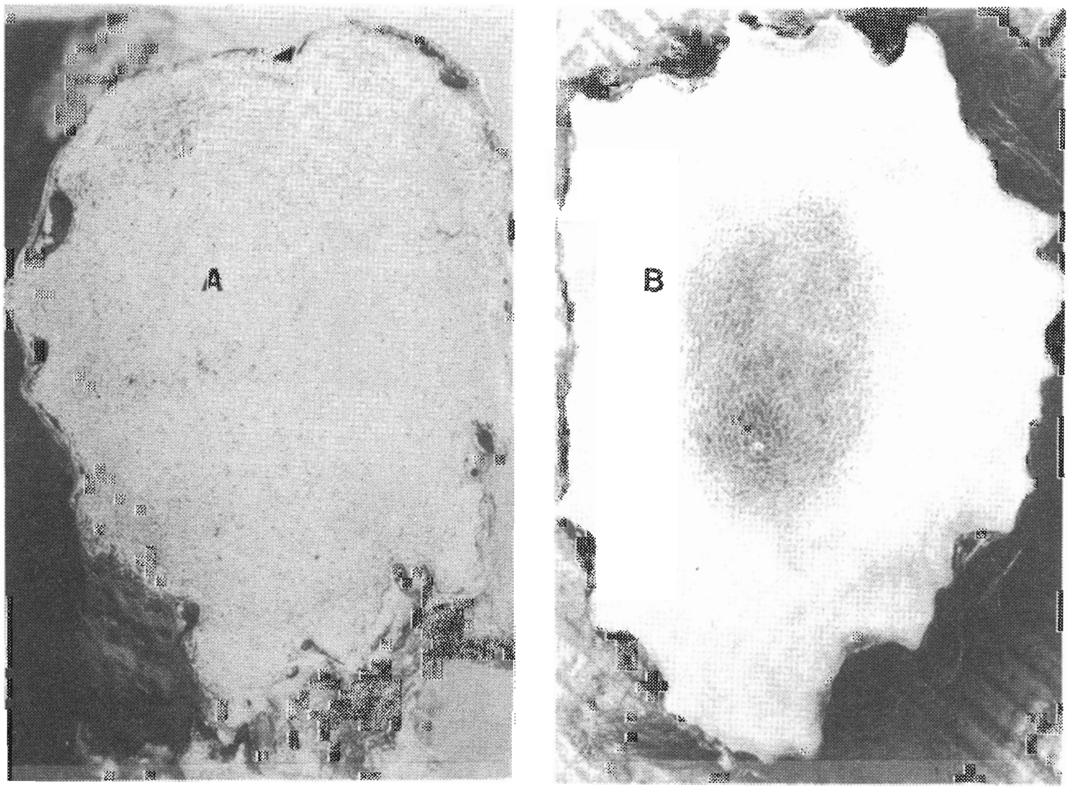

Fig. 6. Transversal-sections through pedicles: A. Velericorn moose antler with partially compact core. B. Transversal-section of normal moose antler with hard antlers.

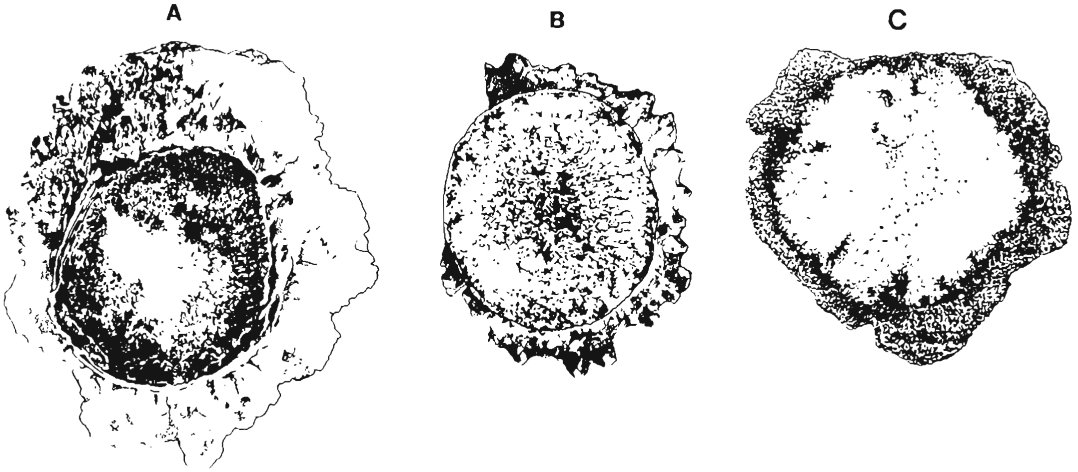

Fig. 7. Transversal section through antler shaft. A. Velericorn antler, B. Normal bull moose, C. Protocervid, *Dicroceros elegans*.

Fig. 8. Sagital section of the base of T2 with parallel lamellae [L], projecting from the more compact osteon of the palm [P].

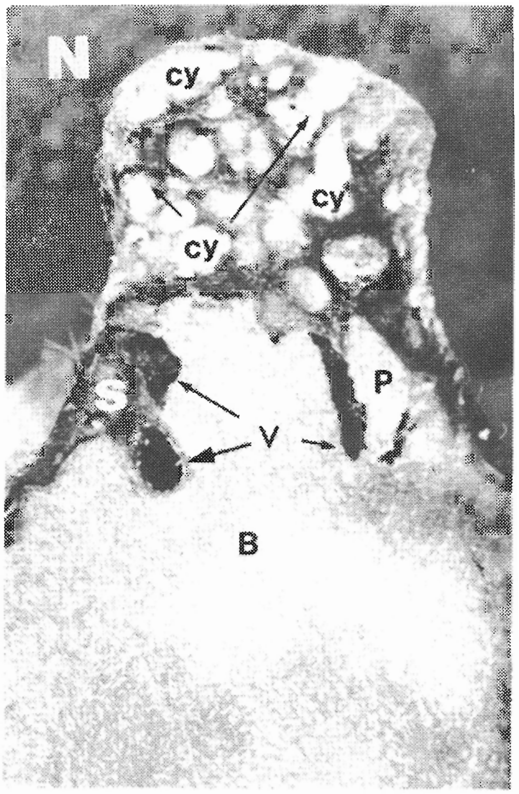

Fig. 9. Transversal-section of a large nodule [N] on the base of T7. The almost white epidermal cysts [cy] interspersed in what is presumed to be cartilage [c]; some seem to be in a stage of expanding ossification with the tendency to fuse (arrows) with the VCA body [B].

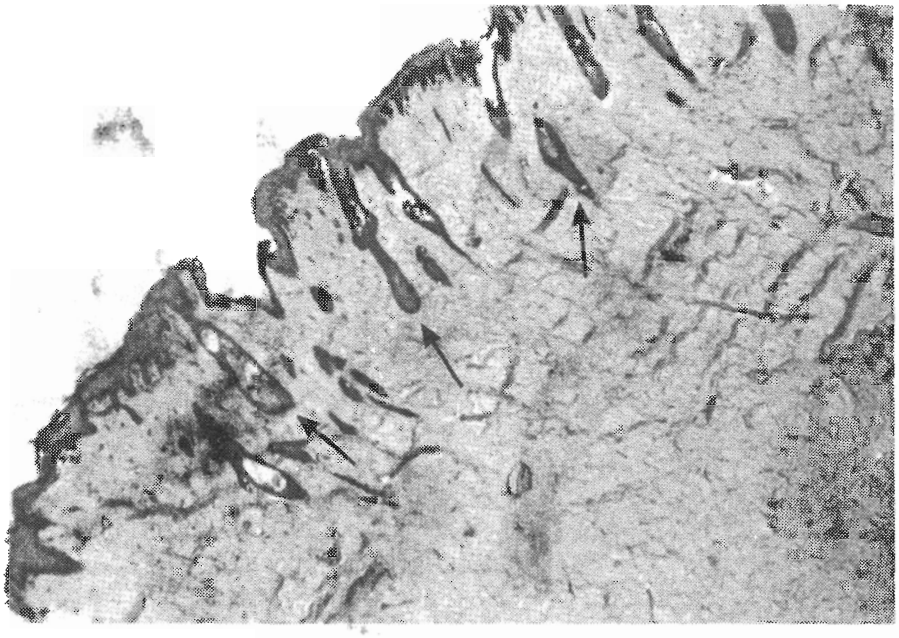

Fig. 10. Ordinary-looking velvet with a thin epidermis containing only a few follicles and sebaceous glands (arrows).

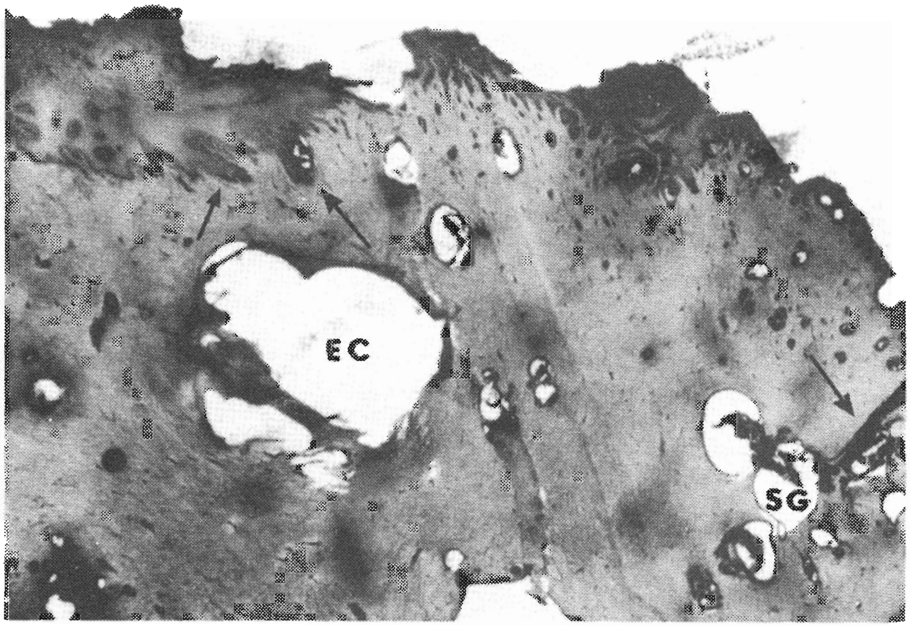

Fig. 11. Epidermal and dermal layers of the velvet. Hyperplasia caused invagination of epidermis (arrow) resulting in a cystic transformation of sebaceous glands [SG]. [EC] = a large epidermal cyst.

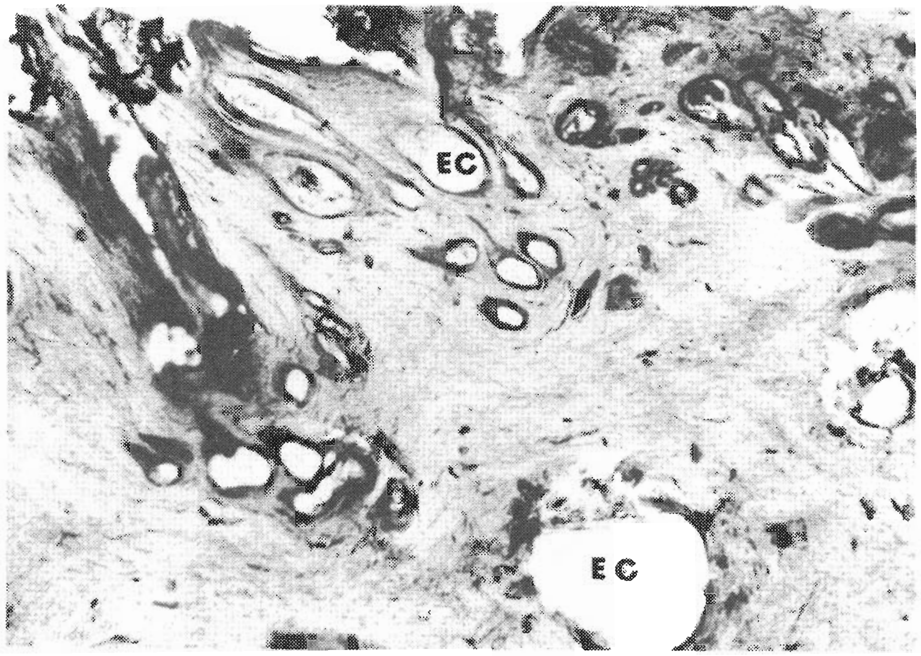

Fig. 12. Numerous epidermal cysts [EC] of various sizes reaching into deeper parts of the velvet dermis.

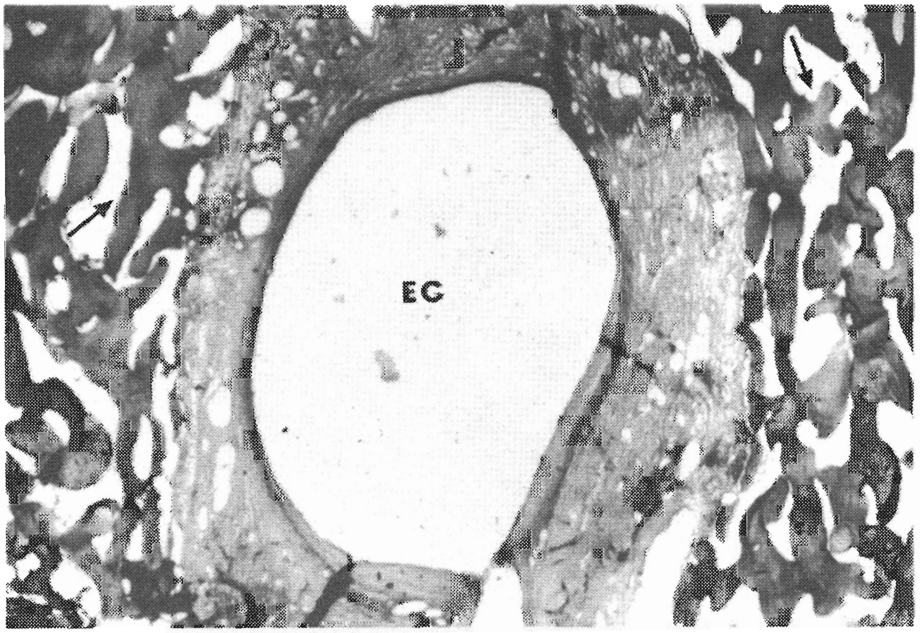

Fig. 13. Large epidermal cyst [EC] located deep in the dermis is surrounded by bony tissue (arrow).

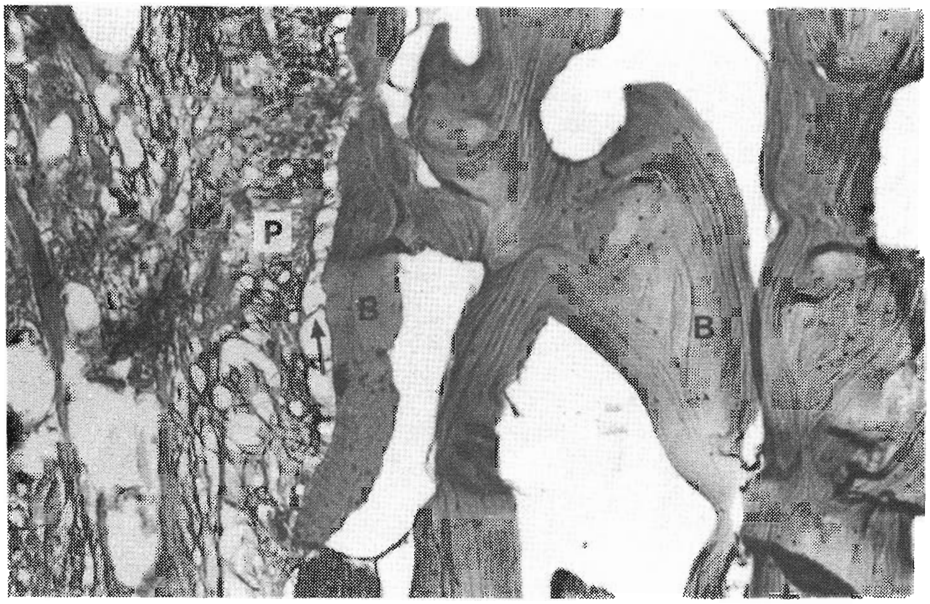

Fig. 14. Sharpey's fibers (arrow) connecting the periosteum [P] to the somewhat more immature primary bone trabeculae [B].

Fig. 15. Immature trabeculae of primary bone [B] are supported by a rich network of reticular fibers (arrow).