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Accessory antlers in male Cervidae

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1 Introduction

Antlers are a unique phenomenon of replaceable head ornament adorning most males of the family Cervidae (BENINDE, 1937 as cited by BUBENIK, A., 1990). The deciduous antlers are paired organs, which grow from permanent bony protuberances of frontal bone, called pedicles. Pedicles grow as a result of stimulation of antlerogenic periosteum, (a specialized type of connective tissue) (HARTWIG and SCHRUDDE, 1974) by male sex hormones during puberty (BUBENIK, G., 1990; LI and SUTTIE, 2001). Normally, only one pedicle will grow on each crest of the frontal bone so two antlers will develop in a more or less mirror image of each other. Only infrequently, accessory (supernumerary) pedicles or accessory antlers will develop in ectopic places, mostly in the area of the frontal, nasal or parietal bones (BUBENIK, A., 1966, 1990; KIERDORF and KIERDORF, 2001). These accessory protuberances, which only rarely will reach substantial height or become branched, are more common in the telemetacarpal deer, such as roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*) or moose (*Alces alces*) than in the plesiometacarpal cervids, such as red deer (*Cervus elaphus*) or fallow deer (*Dama dama*) (BUBENIK, A., 1990). The accessory antlers grow from pedicles, that develop mostly in response to repeated injuries to skull bones belonging to the so called “antlerogenic territory” (GOSS, 1990). In most cases there is only one accessory antler, but a multiple growth of small accessory antlers was also reported (BUBENIK, A., 1966; KIERDORF and KIERDORF, 2001).

The process of initiation of *de novo* osteogenesis, as seen in the development of accessory antlers, can provide an inside to the origin of protoantlers appearing first in the extinct ancestors of the present day cervids (BUBENIK, A., 1990) (Fig. 1). Herein we present three cases of accessory antlers in male cervids and discuss similarities of their development that may be relevant to the evolution of protoantlers.



Fig. 1. Extinct ancestor of deer *Cranioceras skinneri*. Left: Reconstructed head, Right: Fossil skull (Adapted from BUBENIK, A., 1966).



Fig. 2. Supernumerary antler growing from the left pedicle of the European roe deer (*Capreolus capreolus*). Note the formation of a full coronet and the pedicle.

2 Case Histories

Roe deer: A mature (4–5 yrs old) roebuck was shot in the vicinity of Herzogenbuchsee (canton Bern, Switzerland) for the purpose of another study. After the skull was cleaned up and bleached an accessory antler grown from the left side pedicle was detected (Fig. 2). The small antler had its own, fully developed minipedicle and was provided with a complete miniature coronet. Measurements of the accessory antler were as follows: Height of the pedicle: 5 mm, circumference of the pedicle: 54 mm, height of the antler: 16 mm, diameters of the coronet: 22 to 24 mm; circumference of the coronet: 92 mm. The right beam of lateral antlers was 201 mm long; the left beam was 205 mm long. The buck was a six pointer.

White-tailed deer: A hand-reared, 3½-months old, male white-tailed fawn was transported in mid-September in a wooden crate, from the zoo in Peterborough (Eastern Ontario) to the Deer Research Station in Cambridge (Southwest Ontario). During the approximately 3-hour trip, the buck tried repeatedly to stand up, and as a result, it rubbed the top of its head on the wooden planks. The injury was not serious and did not require any surgical treatment of the damaged skin. The buck developed normal pedicles during the puberty but the damaged area between pedicles was left without the skin cover for several months. As the fall approached, the buck became quite aggressive and kept reinjuring the slowly epithelialized wound area by rubbing his head against the posts. The area became finally covered with skin during his second year of life, when he grew lateral antlers, that were normal for his age. Those antlers were forked and reached their final length at 160 mm



Fig. 3. Tiny antler formed at the tip of the accessory pedicle (arrow) of a juvenile white-tailed deer (*Odocoileus virginianus*).

Fig. 4. Premature casting of the ectopic antler tissues left a large wound in the center of the skull.

(right) and 150 mm (left). After the antlers were mineralized, they were cut off for safety reason with only coronets left. Surprisingly, the skin covering the original wound area was shed at the end of the summer and a tiny antler-like protuberance appeared (Fig. 3). This miniature antler (15 mm long, 20×20 mm wide at the base) was cast in mid March of the following year (Figs. 4, 5) and a new antler growth began almost immediately after the velvet skin grew over the wound. The coronets of lateral antlers were cast late in the first week of May, which was more than two months after the average cast-

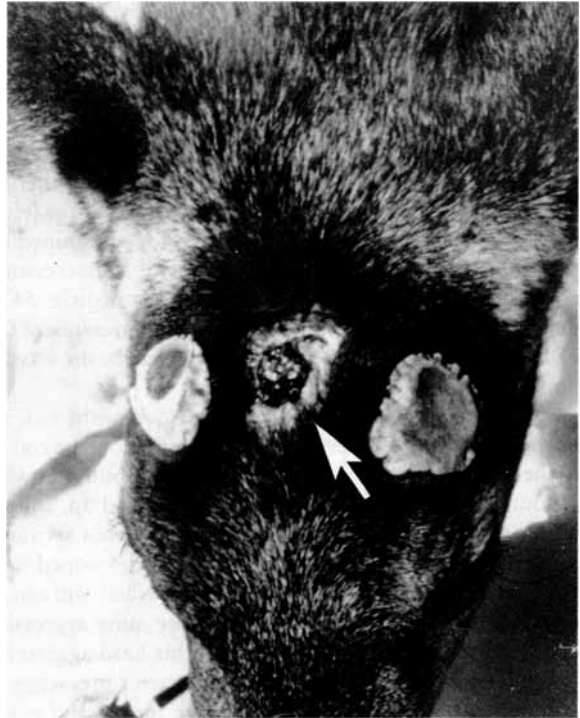




Fig. 5. Cast ectopic antler bone of the yearling white-tailed buck.

ing time (Fig. 4). New antler growth began almost immediately after each casting, thus the growth of the median antler was initially more advanced in its development than the lateral antlers. The median antler eventually stopped growing, however, after reaching the length of 55 mm (Fig. 6). The lateral antlers grew longer, and became branched; the right beam length was 320 mm and the left beam length was 350 mm (Fig. 7). Unfortunately, the buck suffered an infection and died from toxemia in mid August, shortly before the velvet shedding. His skull was saved, cleaned and the 3rd antler was measured and photographed (Fig. 7). Beside the partly curved spike-like beam, the accessory antler exhibited a coronet-like protrusion of the antler base. This bony plate, centered at the confluence of frontal and parietal bones, partially covered both frontal bones and at the posterior end

Fig. 6. Second year growth of the accessory antler in white-tailed buck.

almost reached the occipital bone. The longest diameter of the plate was 71 mm and the widest diameter was 39 mm. The position of the accessory antler beam moved from the original midline (Fig. 4) toward the right lateral antler (Figs. 6, 7).

Moose: Accessory antler tissues developed in captive male moose after fully mineralized and polished antlers were removed immediately prior to the rut. Two mature bulls (older than 5 years) were placed in a common enclosure where

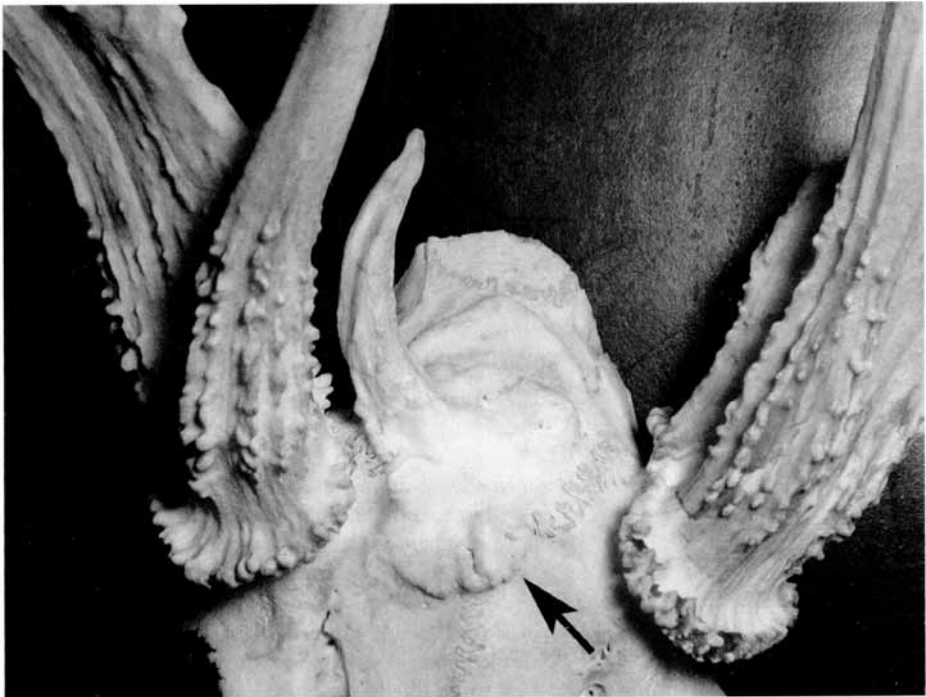


Fig. 7. Polished white-tailed deer accessory antler surrounded by the bony plate with the frontal part forming a coronet-like ring (arrow).

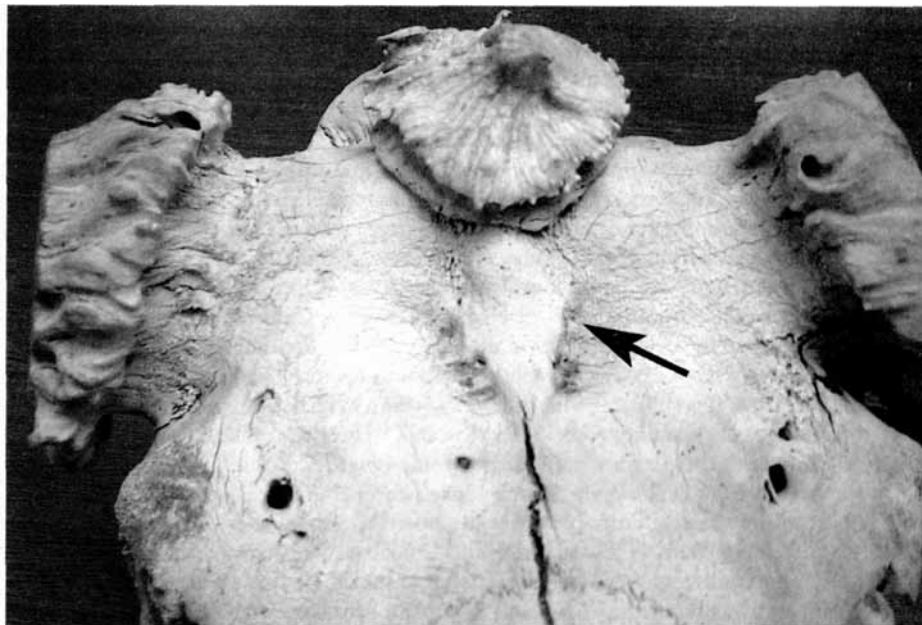


Fig. 8. Medial (accessory) antler tissue formed in the adult moose (*Alces alces*). Note the bony plate covering the interfrontal suture (arrow).

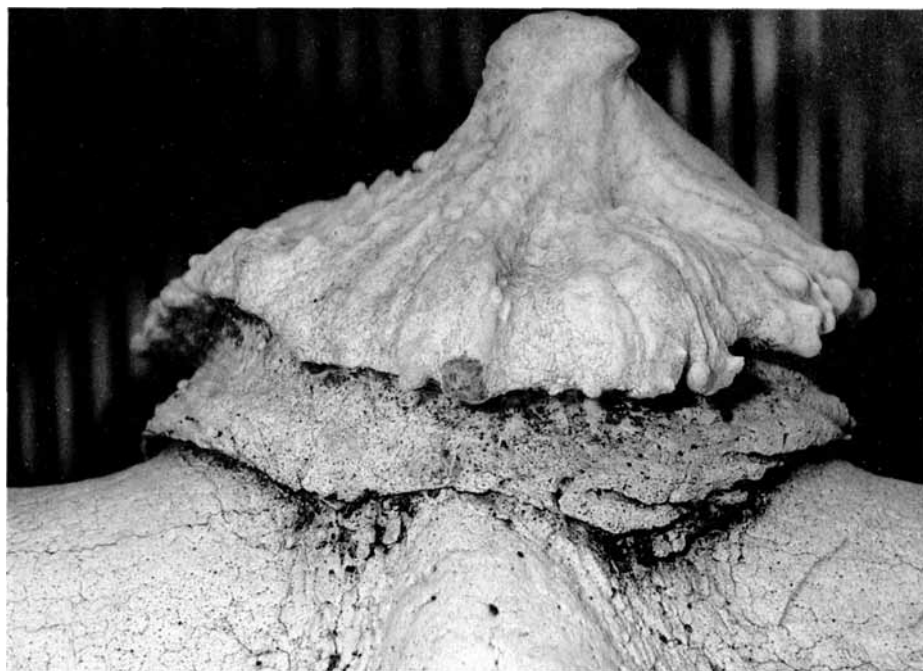


Fig. 9. High power magnification of the medial ossicon. Note the well-developed, roof-like "pedicle". The antler exhibits a well-formed "coronet" with a rosette-like centrifugal grooves.

they proceeded to spar despite the absence of antlers. Sparring took the form of head butting and pushing with the forehead. The repeated trauma resulted in the development of bony protuberances in both animals, which eventually lost the overlaying skin, which had no distinct velvet character. The accessory antler-like ossicones present in both bulls reached their full size at the end of the rut and were shed during the winter. Casual observation of the forehead in one of the animals the following spring indicated a complete healing of the skin of the forehead; there was no visible pedicle detected. The same procedures were followed the next year and once again the accessory protuberances were formed, reaching a larger size than the previous year. No supernumerary ossicones developed during the period of normal antler growth and no measurements of the accessory protuberance were obtained while animals were alive. One bull died the subsequent winter (at 8 years of age), prior to shedding of the coronets and his skull was saved and cleaned. The accessory protuberance (Fig. 8) of that year was formed from a bluntly conical projection growing above the skin, supported by a subcutaneous bony plate (Figs. 8, 9). The upper, coronet-like ring (Fig. 9) had diameters ranging from 73- to 78 mm. The height of the accessory, antler-like structure, including the pedicle-like ossicone, was 44 mm and the circumference of the "coronet" was 242 mm. Although the accessory protuberance was centered at the frontoparietal suture, a massive bony plate was discovered on the posterior side of the "pedicle" of the accessory antler-like structure (Fig. 10). That plate covered a part of the parietal and occipital bones, where it formed a distinct "spur". The plate varied in width from 48 to 63 mm and was raised approximately 5 mm above the normal skull surface. In subsequent years the antlers of bulls were removed only after the rut and the surviving bull never again grew any accessory antler-like tissues.

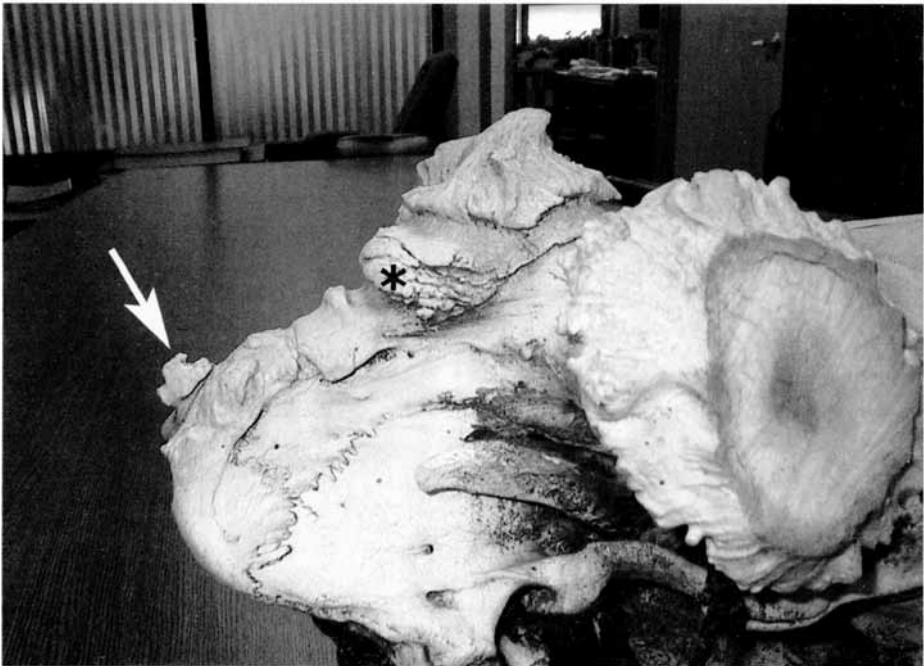


Fig. 10. Lateral view of the posterior skull segment. Note the hyperostoses on the "pedicle" (asterisk) as well as the presence of plates with the protruding occipital spur (arrow).

3 Discussion

Fossil findings revealed that ancestors of cervids carried non-deciduous bony protuberances on various parts of their skull bones (BUBENIK, A., 1990) (Fig. 1). Only later, these seemingly ornamental protrusions became deciduous and their growth and development became controlled by the seasonal changes of sex hormones (BUBENIK, A., 1990; BUBENIK, G., 1990a). In addition, the deciduous antlers grew from the non-deciduous pedicles (developed during puberty) and their location was fixed to the lateral part of frontal bones (GOSS, 1983; BUBENIK, A., 1966, 1990). Occasionally, however, that usual pattern of antler development is broken, and a vestigial, accessory pedicle will develop at ectopic sites from which a miniature replica of the antler will grow. Interestingly, the location of the accessory antler is atavistic, which means it follows the primitive development pattern of cervid ancestors. The accessory (or supernumerary) antlers usually grow in the so called "antler territory", mostly the nasal, frontal, parietal or occipital bones (WISLOCKI, 1952; KIERDORF and KIERDORF, 2001), or even from the zygomatic arch (NELLIS, 1965; BUBENIK, A., 1990). That is the same area where bony appendages and later protoantlers grew in the extinct ancestors of cervids (BUBENIK, A., 1990). Whereas regular pedicle development requires threshold concentrations of male sex hormones (BUBENIK, G., 1990a), the growth of accessory pedicles within the antler territory requires not only high levels of androgens, but also non-physiological stimulation (mostly a trauma to the periosteum or to the developing pedicle) (BUBENIK, G., 1990b; KIERDORF and KIERDORF, 2001).

Growth of supernumerary antlers from the side of the pedicle (Fig. 2) is one of the most common cases of accessory antlerogenesis (BUBENIK, A., 1966, 1990; JACZEWSKI, 1990; KIERDORF and KIERDORF, 2001). It has been hypothesized that the periosteum of the pedicle retains the antlerogenic property and that a non-physiological stimulation can initiate the growth of the ectopic antler (BUBENIK, A., 1966; KIERDORF and KIERDORF, 2001). The presence of the coronet in the accessory antler of the roe buck in our collection indicates that the ectopic antler was already cast at least once. The first-year antlers of males or antlers growing in females usually do not have coronets (BUBENIK, G., 1990a; KIERDORF and KIERDORF, 2001).

In both cases where the cause and the development of supernumerary antler growth were documented (in white-tailed deer and moose) (Figs. 7, 8), the trauma and the successive growth of bony tissue occurred in the fall, the time of rising concentrations of androgens. This corresponds with the normal timing of pedicle development of maturing male cervids during puberty. In the case of the white-tailed buck, the growth of a supernumerary pedicle most probably preceded the development of lateral pedicles. That observation indicated that the trauma was a stronger stimulus for pedicle growth than the usual endocrine stimulus of increasing androgen concentrations. As reported, the casting of the mineralized 3rd antler (Fig. 4) and the subsequent new growth occurred almost 7 weeks before the casting and antler growth of lateral coronets. That would indicate the involvement of other factors than merely endocrine ones, which were common to both, the lateral as well as the accessory antlers. Perhaps a neural factor, such as the hypothetical antler growth center postulated by BUBENIK, A., (1966) may have influenced the different time course of individual stages of the antler cycle of the medial and lateral antlers.

Although the shape of the bony protuberance in the moose resembled the antler tip and exhibited a coronet-like base (Fig. 9), the true nature of that ossicone is difficult to pinpoint. The timing of its development and the integumental cover was more in line with the pedicle development (BUBENIK, G., 1990a). The exostosis grew during the period of rising concentrations of testosterone and was not covered with the typical velvet skin. In addition, there was never any new growth observed in the regular antler growth period of spring

and summer. Conversely, the protuberance lost the skin cover, was cast like an antler in the spring and its shape strongly resembled the antler tissue. Finally, there was never any permanent pedicle tissue left after the casting and after the trauma of head butting was eliminated, the growth of accessory pedicle (or antler) tissues ceased. According to an alternative interpretation of the phenomenon we can speculate that the repeated trauma lead to the growth of a pedicle-like structure which then, despite the rising levels of androgens, continued the growth by forming the antler-like ossicone. Similar growth of antlers during the fall was observed in white-tailed deer treated with melatonin in the spring, which caused a premature casting of antlers (BUBENIK, G., 1990a). Perhaps, the repeated trauma to frontal bones was the stimulus overriding the handicap of the rising levels of testosterone in the fall, which normally would hinder the growth of antler tissue. Conversely, under special circumstances (such as a severe trauma to the pedicle or an ischemic necrosis of the pedicle skin), the entire pedicle can be cast and later regenerated (Fig. 11) (BUBENIK, G., 1990b). Perhaps the difference in ages (prepubertal in white-tailed deer vs mature in moose) played a role in the development of a continuous formation of ectopic antler. It can be hypothesized that the juvenile white-tailed buck developed an accessory pedicle during the period when he was "programmed" to form a neural connection between the pedicles and their antler growth centers (BUBENIK, A., 1966; BUBENIK, G., 1990b). Conversely, in the older, mature bull moose the trauma to the forehead initiated pedicle formation, and antler-like development but this information was never "encoded" to be repeated without additional injury stimulation.

Although the development of the medial antler in the moose was not as well documented as the growth of 3rd antler in white-tailed deer, we detected several features in both species, which indicate that this phenomenon is probably common to all cervids. First, it is the development of the pedicle, which precedes the growth of accessory antlers. Secondly,



Fig. 11. Cast pedicle of a mature white-tailed buck. The pedicle sequestration occurred after the pedicle skin died following repeated injuries. The pedicle fully regenerated in the next two antler cycles.

supernumerary antlers are fully mineralized and repeatedly cast. Third, most accessory antlers grow coronets, or coronet-like structures. Fourth, accessory antlers grow mostly only within the specific antler territory. Finally, the development of the accessory pedicle is often accompanied by a growth of a bony plate or a spur (Figs. 7, 8, 10) (BUBENIK, A., 1966, 1990) surrounding the supernumerary pedicle. These features also were reported in other cases of accessory antlers in Cervidae, resulting either from experimental interventions or occurring spontaneously in nature (BUBENIK, A., 1966, 1990; GOSS, 1990; KIERDORF and KIERDORF, 2001).

The occurrence of accessory antlers, as infrequent as they are, can teach us a lesson in cervid evolution, particularly the evolution of antlers. The primitive, non-deciduous protoantlers of ancestral cervids also grew only within the "antler territory" (Fig. 1). That indicates that either the periosteum in this area has special properties, or that it receives a special signal (perhaps of neural character), which provides the stimulus for pedicle development. So far, no autologous transplant of skull bone periosteum to other regions has succeeded, if it was not taken from the very limited area of the frontal bone, that normally gives rise to pedicles (KIERDORF and KIERDORF, 2001). That trauma provides a stimulus for the pedicle and a subsequent antler development in present day cervids may indicate that a similar process (caused by head-butting or injuries to skull bones) may have initiated development of bony protuberances in the extinct protocervids. Head butting is in the fight repertoire of most *Pecoras*, the group of ungulates that includes both the cervids as well as the bovids (BUBENIK, A., 1990). Both groups developed cranial appendages (antlers or horns), which were then adopted as secondary sex characteristics and are occasionally used as weapons in sexual competition. The deciduous character of antlers, developed in cervids, provided male deer with the additional year to-year flexibility in size alterations, which the continuously growing horns do not provide.

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Summary

Accessory (supernumerary) antlers are an infrequent phenomenon in male cervids. These bony protuberances grow mostly from permanent pedicles, which developed in response to a repeated or a severe trauma to frontal, nasal or parietal bones. They regularly undergo seasonal mineralization, casting and regrowth and may persist for many years. Three examples of accessory antlers in telemetacarpal cervids, roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), are presented. The initiation of accessory antlerogenesis, the progress of growth and development, and the mineralization and casting of accessory antlers were mostly identical or similar to processes observed in the antlerogenesis of lateral antlers. The antlerogenic property of the competent periosteum, located within the "antler territory", appears to play a crucial role in the development of accessory antlers. The variability in location and the progress of development of accessory antlers, which were observed in several antlerogenic cycles, is discussed in relationship to the origin of deciduous antlers in extinct ancestors of cervids.

Key words: Accessory antler, antlerogenic periosteum, antler development, roe deer, white-tailed deer, moose, cervid evolution

Zusammenfassung

Akzessorische Geweihstangen bei männlichen Cerviden

Gelegentlich treten bei männlichen Cerviden akzessorische (überzählige) Geweihstangen (sog. Nebenstangen) auf. Zumeist wachsen diese knöchernen Protuberanzen von permanenten Rosenstöcken, die als Folge wiederholter Verletzungen der Frontalia, Nasalia oder Parietalia entstanden sind. Die überzähligen Geweihstangen werden periodisch mineralisiert, abgeworfen und regeneriert und können über mehrere Jahre existieren. Drei Beispiele solcher Nebenstangenbildungen bei telemetacarpalen Cervidenarten (Reh, *Capreolus capreolus*; Weißwedelhirsch, *Odocoileus virginianus*; Elch (*Alces alces*)) werden besprochen. Beginn und Verlauf des Nebenstangen-Wachstums sowie Mineralisation und Abwurf der Nebenstangen entsprachen zumeist weitgehend den entsprechenden Vorgängen an den Hauptstangen. Die Fähigkeit des kompetenten Periostes des „Geweihbildungsfeldes“ zur Genese von Geweihstrukturen spielt eine entscheidende Rolle bei der Bildung akzessorischer Geweihstangen. Die unterschiedliche Lokalisation der Nebenstangen und deren unterschiedliche Entwicklungsgeschwindigkeit während verschiedener Geweihzyklen werden im Hinblick auf die Entstehung von periodisch gewechselten Geweihen bei den ausgestorbenen Vorläufern der Cerviden diskutiert.

Schlüsselwörter: Akzessorische Geweihstangen, Geweihbildungsperiost, Geweihbildung, Reh, Weißwedelhirsch, Elch, Cerviden-Evolution

Résumé

Bois accessoires chez les Cervidés mâles

Des bois accessoires (surnuméraires) constituent un phénomène peu fréquent chez les Cervidés mâles. Ces protubérances osseuses procèdent le plus souvent de pivots permanents qui se développent en réponse à un traumatisme sévère causé aux os frontaux, nasaux ou pariétaux. Ils présentent normalement une minéralisation saisonnière, une mue et une nouvelle croissance et peuvent persister plusieurs années. Trois exemples sont présentés de merrains accessoires observés chez des Cervidés télémetacarpaliens, soit chez le Chevreuil européen (*Capreolus capreolus*), chez le Chevreuil à queue blanche (*Odocoileus virginianus*) et chez l'Elan (*Alces alces*). L'initiation de la genèse de bois accessoires, la progression de leur croissance et de leur développement ainsi que leur minéralisation et leur chute se révélèrent essentiellement identiques ou similaires aux processus observés dans la genèse de bois principaux. La faculté, pour le périoste concerné, situé au cœur de l'espace territorial des bois, de générer des bois semble jouer un rôle crucial pour le développement de merrains accessoires. La localisation variable et la progression du développement de merrains accessoires, lesquels ont été observés dans de nombreux cycles de bois, fait l'objet d'une discussion en relation avec l'origine de bois caducs chez des ancêtres de Cervidés aujourd'hui éteints.

Trad.: S. A. DE CROMBRUGHE.

Mots clefs: bois (merrains, perches) accessoires, périoste de genèse des bois, développement des merrains, Chevreuil européen, Chevreuil à queue blanche, Elan, évolution des Cervidae

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