INTRODUCTION

Antlers are paired bony appendages of the deer cranium that undergo cyclic shedding (antler casting) and regrowth (Goss, 1983; Landete-Castillejos et al., 2019; Lincoln, 1992). Among extant cervids, antlers are missing only in the Chinese water deer (Hydropotes inermis), whose lack of antlers is considered a case of secondary loss (Wang et al., 2019). Except for the reindeer (Rangifer tarandus), antlers are grown only by male deer (Goss, 1983; Landete-Castillejos et al., 2019; Lincoln, 1992). Periodic antler regrowth is an impressive case of appendage regeneration in mammals, a clade that is generally characterized by an only very limited regenerative ability (Price et al., 2005; Kierdorf et al., 2007; Kierdorf et al., 2009; Kierdorf & Kierdorf, 2012; Li et al., 2014).

Antlers do not sprout directly from the skull roof, but are grown and cast from permanent outgrowth (apophyses) of the frontal bones known as pedicles (Goss, 1983; Kierdorf & Kierdorf, 2002). Pedicle formation is initiated by a transient surge in circulating testosterone in male deer during their first year of life (Bubenik, 1990b). Growth of the first set of antlers, the so-called primary antlers, commences once the pedicles are fully formed (Kierdorf & Kierdorf, 2002). It is with the casting of its primary antlers that a deer enters into the lifelong cycle of antler regeneration.

Antlers elongate at an unparalleled speed for bones. Thus, a peak daily antler growth rate of 2.75 cm has been reported for wapiti (Cervus canadensis), and in the extinct giant deer (Megaloceros giganteus), whose antlers spanned up to 3.5 m, maximum growth rates must have been even higher (Goss, 1970; Landete-Castillejos et al., 2019). Growing antlers are enveloped in a special type of hairy integument known as velvet (Goss, 1983). The arteries responsible for the blood supply of the growing antler are branches of the superficial temporal artery that are located in the vascular layer at the

KEYWORDS

antler casting, autotomy, osteoclasia, testosterone deficiency, velvet shedding

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base of the velvet (Rhumbler, 1929; Rörg, 1900; Waldo et al., 1949). Antler elongation occurs through a modified form of endochondral ossification (Banks, 1974; Banks & Newbrey, 1983; Gruber, 1937; Kierdorf, Kierdorf, Szuwart, & Clemen, 1995; Kierdorf et al., 2007). There is only very limited circumferential growth of antlers by direct (intramembranous) ossification (Banks & Newbrey, 1983; Kierdorf, Kierdorf, Szuwart, & Clemen, 1995; Kierdorf et al., 2007). Mature antlers consist of an outer layer of compact bone, the antler cortex, and a central portion of cancellous bone, the antler spongiosa (Gomez et al., 2013; Goss, 1983; Landete-Castillejos et al., 2019; Rolf & Enderle, 1999).

In deer species from higher latitudes, the annual antler cycle is closely linked to the reproductive cycle and under strict photoperiodic control (Bubenik, 1990b; Goss, 1983; Lincoln, 1992). This control is basically exercised via changes in circulating levels of androgens, testosterone in particular (Bubenik, 1990b; Goss, 1968; Lincoln, 1992; Suttie et al., 1995). During antler growth, plasma testosterone concentrations are low (Lincoln, 1992). It is debated whether or not androgen levels above a low threshold are required as an antler growth stimulus (Bartoš et al., 2000, 2009; Bubenik, 1990; Sadighi et al., 2001; Suttie et al., 1995). There is, however, widespread consensus that insulin-like growth factor 1 (IGF-1) is the main endocrine stimulator of antler growth (Price et al., 2005; Suttie et al., 1985, 1988). A rise in testosterone at the end of the growth phase leads to dense ossification of the antler cortex and to the death of the velvet and its shedding from the antlers (Bubenik, 1990b; Goss, 1983; Lincoln, 1992; Suttie et al., 1984). The bare bony antlers, also referred to as hard antlers, are then ready for use in inter-male fighting during the rutting period.

Some authors suggested that antlers survive velvet shedding and that there is even ongoing bone formation in hard antlers (Brockstedt-Rasmussen et al., 1987; Rolf & Enderle, 1999). Others, however, provided evidence that antlers die from ischemia when the velvet is shed (Currey et al., 2009; Gomez et al., 2013; Gruber, 1937; Waldo & Wislocki, 1951; Wislocki, 1942). Hard antlers can thus be characterized as dead bony structures. A marked drop in testosterone after the end of the rutting season is associated with the onset of osteoclastic activity that eventually causes antler casting (Bubenik, 1990b; Goss, 1983; Goss et al., 1992; Lincoln, 1992; Suttie et al., 1984). Injection of testosterone (or estradiol) late in the hard antler phase inhibits both antler casting and regrowth (Goss, 1968; Lincoln, 1992), while premature casting of hard antlers can be brought about by castration or administration of antiandrogens (Goss, 1983; Jaczewski, 1985; Kierdorf et al., 1993; Kierdorf, Kierdorf & Knuth 1995; Suttie et al., 1995; Wislocki et al., 1947). The shape of the base of the cast antler (the sequestration plane or seal) can be convex, flat or concave (Bubenik, 1990a).

The drop in testosterone also enables the start of antler regrowth in a process of epimorphic regeneration, which, depending on the species, occurs directly after casting or after a lag period of up to some months (Goss, 1983; Kierdorf & Kierdorf, 2012). Although the casting of the old antlers and the start of antler regeneration occur in a temporally coordinated manner, the former is not the cause for the latter (Goss, 1983; Kierdorf & Kierdorf, 1992a; Kierdorf & Kierdorf, 1992b). The independence of the two processes is illustrated by the so-called double-head antlers that consist of the undetached hard antler from the previous year and a new antler grown from the sides of the pedicle. It has been argued that the trigger for antler regeneration is the death of the antlers at velvet shedding, and that regeneration is delayed until plasma testosterone drops below a threshold (Kierdorf & Kierdorf, 1992a; Kierdorf & Kierdorf, 1992b).

The dependence of the antler ossification process and velvet shedding on higher levels of testosterone explains why insufficient androgen production in hypogonadal males or individuals with testicular lesions causes antler abnormalities, including incomplete ossification and associated breakage of antlers and velvet retention (Bubenik, 1990a; Bubenik et al., 2001; Carrasco et al., 1997; Fox et al., 2015). The present paper describes a case of belated antler casting and abnormal location of the sequestration plane above the coronet in a red deer (Cervus elaphus) stag. Following the dictum "pathologia physiologiam illustrat", we discuss the implications of this case for our understanding of antler casting.

2 | MATERIALS AND METHODS

The studied antlers originate from a free-ranging red deer stag that was observed by local hunters near Bad Laasphe (county Siegen-Wittgenstein, federal state of North Rhine-Westphalia, Germany). The individual, whose age was estimated at 4 years, was first spotted in October 2013 with its antlers still completely covered by velvet. On 15 January 2014, the stag’s freshly sequestered antlers that had been cast above the coronets were found. The coronet (or burr) is the enlarged bony rim at the base of a regenerated antler. The seals of both antlers were covered with clotted blood. Observation on 28 January 2014 revealed that the stag still carried the proximal antler portions (stumps) that had retained their velvet cover.

Normally, velvet shedding in young adult red deer occurs in July or early August, and antlers are cast in March or April (Wagenknecht, 1988). The stag from Bad Laasphe had thus belatedly and incompletely shed the velvet from its antlers, followed by premature casting of the distal antler portions that had lost their velvet cover. The cast antlers of the red deer stag were collected by local hunters and submitted to the authors for study in February 2014. As the antlers had been naturally cast by a free-ranging wild deer and their collection did not involve interaction with the animal, no ethical approval was required for the study.

Upon arrival at our laboratory, the antlers were photographed with a digital camera (Canon EOS 80D), weighed and measured using a measurement tape and sliding calipers. Subsequently, a medial segment was cut from the basal portion of the left antler. Adherent organic remains were removed from this segment by digestion with an enzyme solution (Enzyrim OSA), followed by thorough rinsing with tap water and air-drying. The antler segment, which comprised both compact and spongy bone, was photographed with a digital microscope (Keyence VHX-500F) under reflected light. Subsequently,
the specimen was sputter-coated (Leitz EM ACE 2000) with gold-palladium and viewed in a scanning electron microscope (Zeiss EVO MA15) operated in the secondary electron mode at 10 keV.

3 | RESULTS AND DISCUSSION

The cast antlers exhibit five points each, that is a brow tine, a bez tine, a trez tine and a terminal fork (Figure 1). Antler measurements are given in Table 1.

Both antlers are largely denuded of velvet, but in the more proximal portions small remnants of velvet are still attached to the bone surface. Interestingly, in the middle and distal antler portions, several dried arteries have been retained (Figure 1). Portions of these vessels are still situated in the grooves on the antler surface in which they were located during the growth phase. This denotes that fraying behaviour of the stag had not been of normal intensity, since typically the velvet is completely removed in the shedding process.

The sequestration planes of both antlers are located at the level of the brow tines and exhibit a distinctly concave shape (Figures 1 and 2). In the spongy antler portion, the sequestration plane is located some millimetres more distally than in the cortex (Figures 2 and 3). A relatively thin cortical layer is separated by a distinct furrow from a transition zone that itself gradually merges with the spongy core portion of the antler (Figures 3 and 4a). Scanning electron microscopic inspection revealed that the base of the cast antler is densely covered with resorption pits left by osteoclasts, that is, Howship's lacunae (Figure 4b-d), demonstrating an intense osteoclastic activity.

FIGURE 1  Pair of red deer (Cervus elaphus) antlers cast above the coronets. On both sides, casting occurred at the level of the brow tine. Both antlers possess five tines, viz. brow, bez, and trez tines (identified in the left antler) and a terminal fork. Note marked concavity of the sequestration planes and presence of dried arteries (arrows) still attached to the antler surface.

The aggregation of large numbers of osteoclasts along the future 'abscission line' is a very rapid process (Goss et al., 1992). Normally, this zone of intense osteoclastic activity is located in the living bone of the distal pedicle (Goss et al., 1992; Gruber, 1937; Kölliker, 1873). Accordingly, a small portion of the pedicle is lost along with the cast antler (Kierdorf & Kierdorf, 1992b, 2012). Bone resorption occurs both within the pedicle's interior and sub-periosteally along the pedicle periphery, the latter process leading to the formation of a circumferential furrow at the pedicle surface (Kölliker, 1873; Gruber, 1937; Goss et al., 1992; Kierdorf & Kierdorf, 1992b) The osteoclastic process within the pedicle results in the formation of extended, frequently confluent resorption spaces that Kölliker (1873, p. 60) termed "resorption sinuses". These are arranged in a somewhat uneven plane (Goss et al., 1992; Waldo & Wislocki, 1951). Our findings on the specimens under discussion suggest that the antler casting process had occurred in a typical way but at an abnormal location, that is, within the antlers. It might be assumed that the furrow separating the cortex from the interior of the cast antlers represents the border up to which the peripheral (sub-periosteal) bone resorption had progressed centripetally.

Various observations demonstrate that antler casting does not occur at a fixed (pre-determined) location, but that the sequestration plane is always located directly proximal to the border between dead and living bone regardless of the position of this border. Thus, when the permanently velvet-covered antlers of castrated fallow bucks (Dama dama) suffered from frostbite, only the frozen (dead) antler tips were sequestered (Kierdorf, Kierdorf & Knuth 1995). The basal surfaces of these sequestra were densely covered by Howship's lacunae, corresponding to the situation observed in the present case. It has further been reported that when red deer stags are prevented from antler casting at the normal time by treatment with exogenous testosterone or estradiol, the border between dead and living bone gradually shifts proximally along the pedicle, a phenomenon referred to as "die-back" (Lincoln, 1992). When the antlers were belatedly cast following cessation of sex steroid application, a larger than normal portion of the pedicle was accordingly detached along with the antler. These observations indicate that that the sequestration of dead bone can occur at any level of the cranial appendages of deer.

The present case of antler casting above the coronet in a highly symmetric fashion is attributed to a systemic cause. The condition was likely related to a testicular abnormality that resulted in abnormally low testosterone levels. As we could not examine the animal, our conclusions on the cause of the antler abnormality are, however, indirect. They are based on the recorded deviations from a regular antler cycle in the individual, our observations on its cast antlers, and on similar cases reported in the literature (see below). The belated and only incomplete velvet shedding from the antlers suggests a lower than normal and delayed rise of testosterone at the end of the antler growth period. In consequence, only the more distal antler portions died off after having lost their velvet cover, while the basal antler portions retained their velvet and stayed alive. The sequestration plane at the level of the brow tine accordingly marks the boundary between living and dead bone within the antlers. Premature antler casting in January
suggests that following the (lower than normal) peak causing incomplete velvet shedding, testosterone levels declined again. As long as testosterone levels are high, the hard antlers are retained, that is the onset of osteoclastic activity and the resulting sequestration of the dead bony appendages are hormonally inhibited (Goss, 1968; Kierdorf & Kierdorf, 1992a). A decline in testosterone after the rut then triggers the processes leading to antler casting (Kierdorf et al., 2009; Lincoln, 1992; Suttie et al., 1984). In the present case, it is suggested that the drop in testosterone started from an abnormally low level and that the bone resorption processes eventually leading to antler casting above the coronets therefore started earlier than normal after testosterone levels had fallen below a critical threshold.

Antler casting above the coronets has been previously observed in red deer. Thus, Raesfeld (1920) described a case in which a stag cast its right antler that was still completely covered in dry velvet at the normal time (30 March), while in the left antler the velvet was shed only from the distal portion down to immediately below the trez tine. Only the denuded portion of this antler was then belatedly cast on 23 April. Similarly, Bubenik and Weber-Schilling (1986) observed bilateral antler casting above the brow tine in a cryptorchid red deer stag. The case of a hermaphrodite red deer (bilateral hermaphrodite) was reported by Schulte (2011). At the time of death, the individual had cast its left antler above the coronet, with the remaining velvet-covered antler stump showing a convex surface. The antler on the right side had been (largely) cleaned of velvet in its distal portion. However, the basal coronet was still covered in velvet and a demarcation line was present at the border between the two antler portions. We assume that also in these three cases, the antler abnormality had been caused by an insufficient testosterone level. In line with the views

| Side  | Antler mass (g) | Antler length (mm) | Circumference above bez tine (mm) | Extension of sequestration plane along anterior-posterior axis (mm) |
|-------|----------------|-------------------|-----------------------------------|---------------------------------------------------------------|
| Right | 811            | 695               | 128                               | 78.5                                                          |
| Left  | 865            | 725               | 125                               | 72.0                                                          |

*Measured with a tape along the posterior side of the antler from the rim of the antler base to the antler tip.

*Measured with sliding calipers as a straight line.
expressed by Bubenik (1990a) and Bubenik et al. (2001), velvet retention in proximal antler portions and location of the sequestration plane within the antler is therefore regarded as indicative of a deficient testosterone production.

Antler casting has been characterized as a kind of autotomy by Goss (1983). However, when comparing antler casting to tail autotomy in lizards, the best known example of self-induced loss of a body part in vertebrates (Alibardi, 2010; Emberts et al., 2019; Gilbert et al., 2013), several major differences between the two processes are apparent. First, in the case of caudal autotomy a living body part is detached, while the cast antler is a dead structure. Second, contrary to antler casting, tail loss occurs at a pre-determined breakage location. Thus, most lizards capable of caudal autotomy possess pre-formed transverse intravertebral fracture planes. These align with fibrous partitions in the surrounding muscular and connective tissues of the tail, which enables tail loss without extensive tissue damage (Alibardi, 2010; Gilbert et al., 2013). Third, contrary to antler casting, caudal autotomy is not brought about by osteoclastic activity. Only during the wound healing stage following autotomy, osteoclasts are active at the fracture site (Gilbert et al., 2013). It therefore seems advisable to follow Rhumbler (1929) and Gruber (1937, 1952), who regard normal antler casting as a case of “abacterial sequestration” (Gruber, 1952, p. 338).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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FIGURE 4  Overview (a) and scanning electron micrographs (b-d) of a segment from the base of the left antler. In both the cortical (b) and the spongious portions (c, d), the sequestration plane is densely covered with Howship’s lacunae. Asterisk: blood vessel canal in antler cortex. C: cortex, S: spongiosa, TZ: transition zone.
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