

REVIEW

Antler tine homologies and cervid systematics: A review of past and present controversies with special emphasis on *Elaphurus davidianus*

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Abstract

Antlers are the most conspicuous trait of cervids and have been used in the past to establish a classification of their fossil and living representatives. Since the availability of molecular data, morphological characters have generally become less important for phylogenetic reconstructions. In recent years, however, the appreciation of morphological characters has increased, and they are now more frequently used in addition to molecular data to reconstruct the evolutionary history of cervids. A persistent challenge when using antler traits in deer systematics is finding a consensus on the homology of structures. Here, we review early and recent attempts to homologize antler structures and objections to this approach, compare and evaluate recent advances on antler homologies, and critically discuss these different views in order to offer a basis for further scientific exchange on the topic. We further present some developmental aspects of antler branching patterns and discuss their potential for reconstructing cervid systematics. The use of heterogeneous data for reconstructing phylogenies has resulted in partly conflicting hypotheses on the systematic position of certain cervid species, on which we also elaborate here. We address current discussions on the use of different molecular markers in cervid systematics and the question whether antler morphology and molecular data can provide a consistent picture on the evolutionary history of cervids. In this context, special attention is given to the antler morphology and the systematic position of the enigmatic Pere David's deer (*Elaphurus davidianus*).

KEYWORDS

antler traits, *Elaphurus*, hybridization, phylogenetic conflicts, *Rucervus*

1 | INTRODUCTION

The most characteristic trait of deer is the presence of antlers in male individuals that constitutes a shared derived

character (synapomorphy) of cervids (Geist, 1998; Heckeberg, 2020). Among extant deer species, only the water deer (*Hydropotes inermis*) lacks antlers, which is considered a case of secondary loss (Hassanin et al., 2012;

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Heckeberg, 2020; Wang et al., 2019). The reindeer/caribou (*Rangifer tarandus*) is the only species in which both sexes regularly have antlers (Geist, 1998; Goss, 1983).

Antlers are paired osseous appendages that grow from permanent apophyses of the frontal bones (pedicles) and undergo periodic shedding (antler casting) and regrowth throughout the life of an individual (Goss, 1983; Davis et al. 2011; Landete-Castillejos et al., 2019). The process of annual antler regrowth constitutes a unique case of epimorphic regeneration in mammals (Goss, 1984; Kierdorf et al., 2007, 2009; Kierdorf & Kierdorf, 2012; Li, 2012), a taxon that otherwise exhibits only very limited capacity for appendage regeneration (Daponte et al., 2021; Seifert & Muneoka, 2018). In all deer species, the first (primary) antlers are simple, unbranched structures, also known as spike antlers or spikes (Geist, 1998; Goss, 1983). The first antlers of young individuals are produced while their body is still growing, which allows only limited investment in antlers. In *Mazama*, *Pudu*, and *Elaphodus*, the antlers of adults are also spikes, whereas in most deer species they are branched structures (Goss, 1983). The antler cycle of male deer is closely linked to the reproductive cycle and controlled by seasonal fluctuation of hormone levels (particularly androgens). In deer from higher latitudes, the changes in circulating androgens are under photoperiodic control (Bubenik, 1990b; Goss, 1983; Lincoln, 1992).

Antlers elongate in an appositional mode by proliferation in apically located chondrogenic growth zones (Banks, 1974; Kierdorf et al., 1995; von Korff, 1914). During their growth, antlers are covered by a special type of integument referred to as velvet (Goss, 1983; Li & Suttie, 2000) that, along with the periosteum, is shed once the antlers are fully formed. Velvet shedding exposes the bare bony (hard) antlers that are used for inter-male fighting during the rut (Goss, 1983). Antlers are the fastest growing bones in vertebrates (Goss, 1983; Landete-Castillejos et al., 2019), and to sustain this high growth rate, the developing antlers are richly supplied with blood (and thus nutrients and oxygen) via branches of the superficial temporal artery (Rhumbler, 1916, 1929a; Rörig 1900, 1906; Waldo et al., 1949). The arteries directing the blood to the antler growth zones are located in the vascular layer at the base of the velvet. The walls of these arteries are very thick, possess a high resistance to compression and can rapidly close by constriction when they are severed (Wislocki & Singer, 1946).

Despite claims to the contrary (e.g., Rolf & Enderle, 1999), there is strong evidence that hard antlers are dead structures (Currey et al., 2009; Kierdorf et al., 2021; Wislocki, 1942). Previous studies assumed that during the evolution of the Cervidae deciduous antlers were preceded by permanent appendages (Azanza & Ginsburg, 1997;

Bubenik, 1990a; Ginsburg, 1989; Ginsburg & Azanza, 1991; Rössner, 1995). However, more recent studies convincingly argued that right from their first appearance in the fossil record, antlers were deciduous structures that underwent a cycle of necrosis, casting and regeneration similar or identical to that occurring in extant cervids (Azanza et al., 2022; Heckeberg, 2017a; Rössner et al., 2021).

Due to their periodic replacement, antlers, along with teeth, constitute the most abundant fossil remains of deer. Therefore, and because they exhibit species-specific branching patterns, antlers have been widely used to classify both extant and fossil cervids (e.g., Azanza, 1993a; DiStefano & Petronio, 2002), especially during times when molecular data were not yet available. Given the high variability of antlers, both intraspecifically and ontogenetically, the use of antler traits in species diagnosis and classification is, however, difficult. Remarkably, despite these difficulties, many subdivisions in the first classification of Cervidae by Brooke (1878), which was based on morphological characters including antlers, were later confirmed by molecular analyses.

However, several controversies regarding the systematic relationships within Cervidae, the homology of antler structures and their use in phylogenetic reconstructions remain (Heckeberg, 2020; Samejima & Matsuoka, 2020; Wang et al., 2019). The internationally most common antler terminology was proposed by Pocock (1933), and the homologies of antler structures suggested by him are still widely accepted. Among the unresolved issues is the homology of the antler structures of the Père David's deer (*Elaphurus davidianus*) with those of other cervid species. This question has puzzled researchers ever since Garrod (1877, p. 16) stated that “[t]he antlers of *Elaphurus davidianus* are at present quite beyond my comprehension”. The use of antlers in systematic reconstructions was recently addressed anew by Samejima and Matsuoka (2020) who (again) tried to homologize antler tines across different cervid taxa. These authors analyzed the branching pattern of antlers based on the vessel impressions on the antler surface. They concluded that their morphological findings and molecular genetic data provide a consistent basis for classification that allows a deeper insight into the evolutionary history of the Cervidae.

Here, we review early (Brooke, 1878; Garrod, 1877; Pocock, 1933; Weber, 1904) and recent (Samejima & Matsuoka, 2020) attempts at homologizing antler structures and objections to this approach (von Lehmann, 1959). We further introduce some developmental aspects into the discussion of antler branching patterns and their potential for reconstructing cervid phylogeny. In addition, we address current discussions on the use of molecular markers in cervid systematics and the question of whether antler morphology and molecular data can provide a consistent

picture of the evolutionary history of deer. Special attention is given to the systematic position of *Elaphurus*, an issue that has been a matter of controversy for more than a century, as demonstrated by Pocock's (1912; p. 777) claim that there "is no stag whose systematic position has troubled zoologists as much as *Elaphurus*".

2 | FUNCTION AND BIOMECHANICS OF ANTLERS

The function of antlers has been a matter of discussion for long, and various hypotheses have been proposed why males annually produce these costly appendages (Bubenik, 1990a; Clutton-Brock, 1982; Geist, 1998; Gould, 1974; Janis 1995). In a thorough review of the issue, Clutton-Brock (1982) concluded that the principal function of antlers is their use as weapons in intra-specific combat between males for establishing dominance and access to females during the rut. However, other researchers emphasized the role of antlers as display organs that allow competing males to assess their opponents without fighting (e.g., Andersson, 1994; Bubenik, 1990a; Caro et al., 2003; Geist, 1998; Gould, 1974; Kitchener, 1991). Thus, antler morphology seems to be primarily influenced by intraspecific competition for females and possibly also over other resources (Caro et al., 2003; Geist, 1966).

An eco-functional link was suggested for antler size and complexity with different mating systems. Compared with males from smaller breeding groups, those from males of larger groups would require relatively larger (and often more complex) antlers in order to successfully compete for females (Caro et al., 2003; Clutton-Brock et al., 1980; Kitchener, 1985; Roberts, 1996). An additional adaptive explanation for antler size and complexity is female choice. According to this view, females prefer males with relatively larger antlers that indicate a "superior" genetic quality of these males. Antler size and complexity would thus (at least partly) be the product of sexual selection (Clutton-Brock, 1982).

A further hypothesis linking antler morphology and environment posits that species living in closed habitats possess simpler and shorter antlers enabling them to move quickly through dense vegetation, while more complex and larger antlers are found in species from open habitats (Caro et al., 2003; Colbert, 1955; Simpson, 1949). In this context, it has been suggested that the large antlers of the giant deer (*Megaloceros giganteus*) were unsuited for life in wooded landscapes and that this contributed to the species' extinction (Gould, 1974). However, in western Europe, *M. giganteus* disappeared at the onset of the Younger Dryas cold phase (about 12.9 kya), a period of open habitat (Stuart, 2021). In the eastern part of its range, the species persisted into the early Holocene,

and it is currently unclear why the giant deer failed to recolonize western Europe in the Holocene and which factors caused its extinction (Stuart, 2021).

As has been demonstrated in red deer (*Cervus elaphus*), the mechanical properties of the dry hard antlers carried by stags during the rut are very well suited for their use in intraspecific fighting (Currey et al., 2009; Landete-Castillejos et al., 2019). However, there remains a certain risk of antler breakage during fighting. For the very large antlers of the giant deer it has been argued that they were largely unsuited for fighting as they would not have resisted the resulting mechanical loads (Gould, 1974). This view was refuted by other authors, who suggested that the antlers of *M. giganteus* could actually be used for fighting (Kitchener, 1987; Klinkhamer et al., 2019). Based on results of finite-element analysis, the latter study concluded that, contrary to older views, the antlers of *M. giganteus* were capable of withstanding some fighting loads if they were interlocked proximally and that they were better adapted to withstand loads from twisting rather than from pushing actions. Klinkhamer et al. (2019) further suggested that the fighting of male giant deer was probably more constrained and predictable than in males from extant cervids.

The use of antlers in intraspecific fighting is a two-step process that consists of an initial clash followed by a phase of pushing and twisting in an attempt to break the opponent's balance and to inflict injuries on him (Lincoln, 1992). To withstand the initial clash, the antlers need a high resistance to impact loading, while during the second phase additional resistance to torsional forces is important (Klinkhamer et al., 2019; Landete-Castillejos et al., 2019). In deer species with large and complex antlers, these are often interlocked by the opponents prior to the start of the pushing contest. In this case, the tines not only have a protective effect but also allow a firm contact between the fighting males and an effective transmission of force. In rare cases, the interlocking between antlers can be so "effective" that the opponents are unable to separate, which normally is a death sentence for both (e.g., von Raesfeld, 1920).

Regarding the protective role of the antler tines, the lowermost tine (brow tine in many species) serves to protect the eyes and the facial region (Croitor, 2021b; Goss, 1983). Regarding the trez tine, it has been suggested that it provides an additional protection in larger cervines, thereby "increasing the safety of both combatting stags in large-sized deer" (Croitor, 2021b, p. 23). According to the latter author, the importance of the trez tine as an evolutionary acquisition in mid-latitude deer is indicated by the independent development of this trait in different lineages of large-sized deer such as *Cervus*, *Dama*, and *Praeelaphus*. Croitor (2021b) further suggests

that the regular presence of brow and trez tines in larger antlers is evidence of the vital importance of these tines and is maintained by stabilizing selection. The antlers of mature stags of extant European red deer are characterized by the presence of a crown, that is, a complex of three or more distal tines (Beninde, 1937; Lister, 1987). It has been argued that the selective explanation of the crown is basically its role in display rather than in fighting, as it only rarely participates in the interlocking of the antlers (Lister, 1987).

The function of antlers in female reindeer/caribou (*Rangifer tarandus*) is currently unclear. Whether, or to which extent, they are an adaptation for intra-specific competition over resources with males, a defense against predators, or function as male mimicry is one of the unresolved questions in cervid evolution (Caro et al., 2003; Roberts, 1996).

3 | ANTLER MORPHOLOGY, MORPHOGENESIS, AND TERMINOLOGY

The species-specific morphology of antlers in mature males indicates that antler size and shape are under genetic control, and it has been shown that heritability varies among different antler traits (e.g., Williams et al., 1994). However, antlers are notoriously variable and exhibit high phenotypic plasticity, and they should therefore not or only cautiously (fossils) be used as the sole classification criterion. Regarding antler size and shape, clearly the genetically controlled reaction norm is wide and allows the formation of various phenotypes (Gilbert, 2010). Thus, antler size and complexity vary greatly with an animal's age, which is evident when one compares the spike antlers of a red deer yearling with the impressive multi-tined rack of a prime-aged stag. Among the extrinsic factors affecting antler size and shape, nutrition is likely the most important one (Bartoš, 1990; Brown, 1990; Demarais & Strickland, 2011; Vogt, 1936).

In extant cervids, ontogenetic variation in antler morphology can be addressed by comparing antlers sequentially grown by individual deer (Beninde, 1937; Drechsler, 1988). Intraspecific variability of antler traits can be studied by measuring larger numbers of antlers, followed by a statistical analysis of the data. The degree of phenotypic plasticity of the antlers in extinct cervid species was very likely similar to that of their living relatives. However, in the case of early deer species, often only few fossil antlers are available, raising the question to which extent these antlers show the “typical” morphology of the species. In this context, an important issue arising from the study by Samejima and Matsuoka (2020)

is how representative the diagrammatic patterns and 2D-projections provided by these authors are for certain species. The question of how to identify and interpret phenotypic plasticity in the fossil record has recently been discussed in greater detail by Lister (2021).

Given the high phenotypic plasticity of antlers, it is considered unlikely that each tine is controlled by a specific gene. Regarding the developmental control of antler morphogenesis, it seems more likely that the species-specific antler bauplan is controlled by genetically encoded “branching rules” that specify under which conditions the growth apex of a developing antler bifurcates (Wang et al., 2019). However, our current mechanistic understanding of the factors controlling antler growth, including the potential role of morphogenetic signaling substances like retinoic acid (Allen et al., 2002; Kierdorf & Kierdorf, 1998) in this process, is still very limited. According to a hypothesis proposed by Bubenik (1966), antler growth and morphogenesis are controlled by “centres of antler growth” (one for each side) located in the brain. However, thus far, the existence of these centers, which are thought to exercise their effects via neural or neuroendocrine signals, has not been convincingly demonstrated.

There is evidence that the size of the regeneration blastema forming on the pedicle stump after casting of the previous antler and the amount of blood supplied to the growth zones greatly influence size and shape of the regenerating antlers (Goss, 1961). Thus when a pedicle is diminished in size (by resection), the subsequently formed antler is reduced in length and number of tines, suggesting that the degree of morphogenetic expression (complexity) is a function of the pedicle stump area and the resulting size of the regeneration blastema established on it (Goss, 1961). The relationship between antler size and shape is also illustrated by the fact that antlers with a species-specific number of tines do not occur in miniature, as a decrease in antler size is always associated with reduced morphological complexity (Goss, 1983).

The formation of a multi-tined antler involves the repeated dichotomous splitting of its growth apex (Beninde, 1937; Rhumbler, 1916). Resulting from this splitting, initially a Y-shaped structure is formed. Both split halves have the potential to grow further; however, in most cervids the anterior half has the lower growth potential and will develop into a tine, while the posterior half (representing the “main beam”) will grow further until the next bifurcation event (Figure 1). The main beam of a fully formed antler therefore consists of the sequentially formed dominant split halves from successive bifurcation events (Rörig, 1906). In Old World deer, like red deer or fallow deer (*Dama dama*), in which the first anterior tine (brow tine) is situated directly above the burr, separate growth

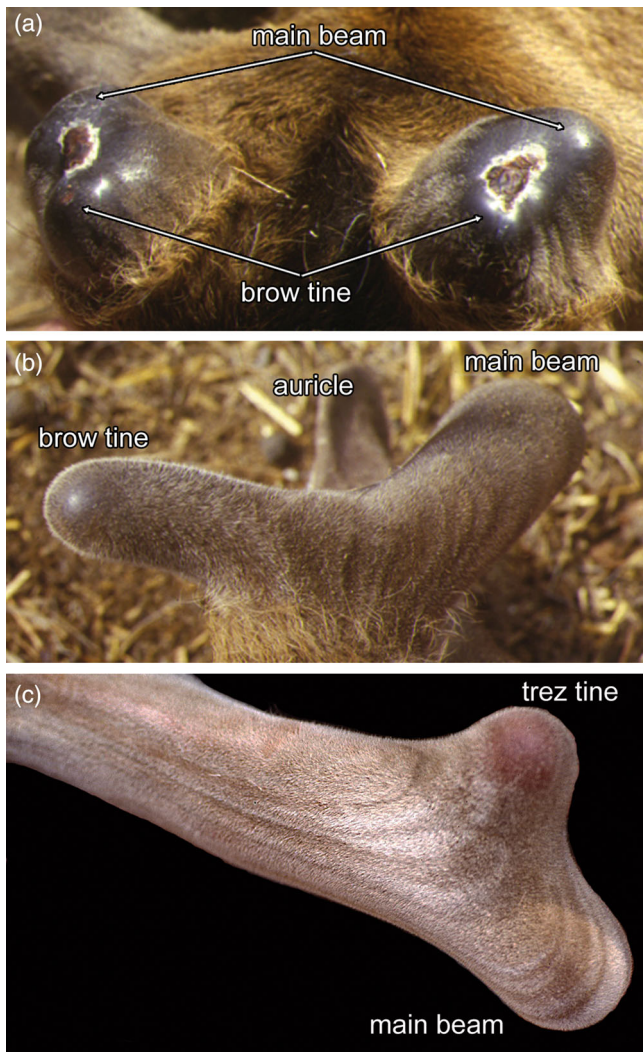


FIGURE 1 Different stages of antler growth in fallow bucks (*Dama dama*). (a) Budding stage of antler regeneration with separate growth centers for the brow tine and the main beam. The central depression of the bud still contains the scab from wound healing. (b) Early stage of antler regeneration with growing brow tine and main beam. Note the difference between hairs of the antler velvet and pedicle skin. (a) and (b) shows that a bifurcating antler growth apex forms very early in the antler development separating the brow tine from the main beam. (c) More advanced stage of antler regeneration shortly after splitting of the growth tip into main beam and trez tine. Note the growth lines on the velvet in (b) and (c). Photographs by UK.

centers for this tine and the main beam are already discernible before a dome-shaped growth tip has formed, which can be considered a certain departure from the rule of dichotomous splitting (Li et al., 2004, Kierdorf & Kierdorf, 2012; Figure 1).

The idea of relating the branching pattern of antlers to the arrangement of their blood supply as reflected by the system of blood vessel impressions on the surface of hard antlers goes back to Rhumbler (1911, 1916) who

studied these impressions with special emphasis on the antlers of red deer. A corresponding approach was later also used by Samejima and Matsuoka (2020), albeit without reference to these earlier studies. Rhumbler (1911, 1916, 1929b) also performed detailed studies of the arterial arrangement in velvet antlers, by analyzing specimens that had been injected with colored gelatine, and proposed a terminology for the different types of arteries. The distribution of these vessels influences the shape of the antler. To facilitate locating the origin of the vessels on the (circular/elliptical) cross-section of the burr, Rhumbler (1911) divided the antler into four quadrants (anterior, posterior, lateral, and medial). He concluded that no tine is nourished by arteries from more than two quadrants. Apparently unaware of Rhumbler's work, Samejima and Matsuoka (2020) applied a similar method in their attempt to homologize antler tines. They used the blood vessel impressions to determine the orientation of the tines that was projected onto the burr represented by a circle. Tines having the same (projected) position on the circle were considered homologous.

Based on his investigations, Rhumbler (1916) noted that the lateral side of the antler grows faster than the medial side since it has a more intense blood supply. He further concluded that the bez tine does not constitute a regular tine, but is a lateral accessory to the rest of the antler. Building on previous work by Rörig (1906), Rhumbler (1916) divided the red deer antler into different segments along the proximo-distal axis that represent temporal stages of antler growth.

Hoffmann (1901) proposed the following three rules for the growth of antlers. (1) The main beam of a multi-tined antler bends backwards from the point of bifurcation at the base of the (new) tine. (2) There is a compensatory curvature of the main beam with an anteriorly directed concavity between two successive tines. (3) At the point where a tine originates, the main beam is laterally flattened. Rhumbler (1916) added a fourth rule stating that the tip of each tine tends to bend upwards and simultaneously towards the median plane.

4 | HOMOLGY OF ANTLER STRUCTURES

4.1 | General considerations

The term homology and the related concepts are complex and often contentious (Rieppel, 2015), and doing justice to this historical and present debate is beyond the scope of this review. Often, homology is defined as the presence of the same feature in two organisms (or taxa) whose most recent common ancestor also possessed this feature

(Hall, 2003; Mayr, 1982), and this is how we use the term here. Mostly, homologous features are realized through shared developmental mechanisms, but exceptions exist (Hall, 2003).

Most systematists working on deer hold that, in principle, antler structures can be homologized. This view is, for instance, expressed by Grubb (1990, p. 176) who stated, “If antlers are found to be very similar in form, then it is possible to regard them not only as homologous as whole organs, but also as homologous part-for-part. For example, brow tines, beam and front-outer or back-inner tines of the terminal fork must be homologous between different individuals of a three-tined deer species; between different subspecies of the same; and perhaps even between different species, such as *Hyelaphus* [= *Axis*] *porcinus* [...] and *Rusa unicolor* [...], when the proportions and dispositions of tines are very similar.”

However, this view is not unanimously accepted. Thus, von Lehmann (1959) argued that the alleged homology of antler structures across species can often not be tested due to the scarcity of the fossil record. He acknowledged the existence of certain basic developmental mechanisms/rules in antler development, such as the dichotomous splitting of growth tips and the compensatory curvature of the main beam, but denies that this can justify attempts to homologize antler tines. Instead, he considers the tines mainly to represent what he refers to as analogous structures or convergent features. This leads von Lehmann (1959, p. 56) to conclude that “homologization of antler parts must be performed with utmost reservation; in no way is it justified to identify individual antler tines or parts with symbols (letters and numbers), because this pretends something that may not actually exist (*viz.*, homology) [original in German, translated by the authors]”.

We hypothesize that the potential of antlers for branching developed only once in the evolutionary history of cervids, which is more parsimonious than to assume that this potential evolved separately in different lineages. Accordingly, the potential for branching is considered a constitutive feature of the cranial appendages of deer. In this context, we suggest considering all antler-associated features, such as branching potential, short antler lifespan, periodic replacement, and velvet as a special type of skin cover, as parts of a synapomorphic character set, that together constitute the trait complex referred to as “the antlers”. This trait complex apparently existed already in the first representatives of the cervid lineage (Heckeborg, 2017a; Rössner et al., 2021). If or to which extent the branching potential of antlers is realized primarily depends on the size of the antler growth region/blastema and thus, on body size, and the antlers' blood and associated nutrient supply. It is further hypothesized that the realization of the shared branching

potential occurred independently in different lineages of deer, which could also explain why, for example, a three-tined antler looks different in Capreolinae and Cervinae.

In deer species with simple, unbranched adult antlers, this feature can theoretically represent a primary or a secondary condition. In the first case, the necessary conditions for splitting of the antler growth region were never met during the evolutionary history. In the second case, the spike antlers would constitute a derived condition that evolved from branched antlers, thus representing an example of reduction of morphological complexity in an evolutionary lineage (Geist, 1998). In species typically possessing unbranched antlers, rare cases of antler splitting have been observed. As an example, Figure 2 shows the skull of an adult southern pudu (*Pudu puda*) and a living adult male of this species with (unilateral) antler bifurcation. The causes underlying such exceptional instances of antler branching are probably varied, including exogenous factors like trauma. The occurrence of these cases suggests that a (latent) potential for antler branching exists also in deer species in which adults normally produce only spike antlers.

Given the ontogenetic component in antler formation, that is, the variation in shape between antlers successively grown by an individual, it seems prudent to use the most complex antlers produced by prime-aged males as the basis for attempts to compare and homologize antler structures (Lister, 1987). The latter author recommended this approach because these antlers “provide a fixed point for assessment and comparison of size and form, since they represent the fullest expression of the genotypic and environmental forces acting on each population” (Lister, 1987, p. 89). Indeed, most attempts to establish homologies of antler tines are based on comparisons of fully formed antlers (Pocock, 1912). As an exception to this rule, in the case of palmated antlers in mature males (e.g., in *Alces alces*) the unpalmated or less palmated antlers of younger individuals may provide a better basis for establishing tine homologies (Croitor, 2021a; Pocock, 1933).

It is sometimes possible to identify evolutionary change of antler form within certain lineages. For example, Lister (1987) noted a trend towards a reduction in strength of the bez tine in the antlers of European red deer from the Middle Pleistocene to the Holocene. This trend was paralleled by the development of a crown, which is mostly lacking in mature antlers from early Middle Pleistocene populations while it is typically present in specimens from late Middle Pleistocene localities (Beninde, 1937; Kahlke, 1958, 1960; Lister, 1987).

The classification of antler tines and their homology across different cervid taxa are the matter of long-standing debates. Sometimes different diagnostic criteria are used to identify specific tines, as is for instance the

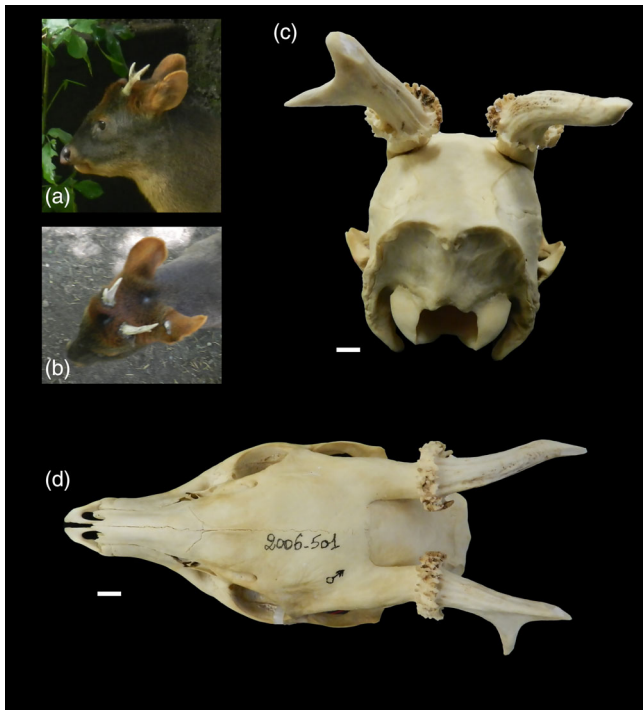


FIGURE 2 Bifurcating antlers in two southern pudus. (a) *Pudu puda* male in lateral and (b) dorsal view. The right antler is bifurcated; the left antler has an accessory tine. Photographed by NSH at the Ménagerie du Jardin des Plantes, Paris, 2012. (c) Occipital and (d) dorsal views of the skull of a male *Pudu puda* (Muséum National d'Histoire Naturelle, Paris; specimen MNHN 2006-501) showing unilateral antler bifurcation. Scale bars equal 1 cm.

case with the brow tine (Table 1). In our view, a tine may be considered a brow tine if three criteria (main criterion A and the secondary criteria C and D) are fulfilled (Table 1). Tables 2 and 3 and Figure 3 provide an overview of the terms used for different antler structures. Mostly, the situation in *Cervus elaphus* has served as the starting point for attempts to identify homologous antler structures, and the terminology developed for red deer antlers has been extended to other species. Unbranched first antlers and the spike antlers grown by adults of some species cannot readily be included in a system of antler tine homology. Therefore, in Figure 4 adult spike antlers are colored differently.

Garrod (1877) assumed that the fundamental plan of branched antlers is an apically dichotomously branched beam (branches B and C) with a basal brow tine (A). Brooke (1878) adopted Garrod's interpretation of tine homology and extended it to all existing cervid species. He argued that antlers of all deer in principle follow the same branching pattern and that the three main branches (A, B, C) are traceable in nearly all of them (Table 3 and Figure 3). Extending this system, Pocock (1912) reasoned that more complex, multi-tined

TABLE 1 Definition criteria of selected antler structures/tines that often lead to controversial homologies.

Main beam

- A Spike in single-tined antlers as p1
- B posterior branch in two-tined antlers as p1
- C succession of p* branches as continuation of the p1 from which a* tines bifurcate

Brow tine

- I the brow tine is equated with a1 (single criterion, here: criterion A)
- A the lowermost/first anterior (and upward) directed tine above the burr
- II to be classified as brow tine, some (or all) of the other listed (secondary) criteria (B-D) must be fulfilled *in addition to A*
- B the angle between a1 and p1 is larger than 90° (e.g., *Cervus elaphus*)
- C the relative position of a1 is close to the burr, that is, a1 actually protects the eye/brow (e.g., *Cervus canadensis*)
- D a1 is subordinate compared with p1 and/or the main beam (e.g., *Dama*)
- E a1 is unbranched (e.g., *Cervus*)

Trez tine

- A tine directly below the terminal bifurcation
- B tine directly below the terminal crown or crown-like tines
- C tine directly below the palmation

antlers represent exaggerated developments of either B or C or both. He further concluded that in *C. elaphus* and *C. canadensis* (in the form of the bez tine) as well as in *Rangifer*, the brow tine/first anterior tine is duplicated due to the size of the antlers. Pocock (1912) further noted that the bez tine arises from the main beam, not from the brow tine.

Simple forms of this basic bifurcation scheme are realized in *Rusa* and *Axis*. In *Rucervus duvaucelii*, B is more developed than C. This is even more pronounced in *Rucervus eldii*, similar to the situation in *Odocoileus* and *Rangifer*. In *Dama* and *Cervus nippon*, B is reduced in size, in *C. elaphus* and *C. canadensis*, C has multiple points, and in *Rucervus schomburgki*, B and C bifurcate (Garrod, 1877). Garrod (1877) interpreted the anterior distal tine of *Rusa unicolor* as a homologue of the trez tine and the posterior apical tine as being homologous to the surroyals above the trez tine, so that the main beam is only the antler segment up to the trez tine, and the bez tine is a duplicated brow tine. Brooke (1878) adopted a system similar to that of Garrod (1877), and used the letter a as designation for the first anterior branch, x for the main beam, b and c for the elements forming the first

TABLE 2 Antler terminology and definitions.

English	German	Description
Pedicles (stalks)	Rosenstöcke	Paired, permanently skin-covered outgrowths of the frontal bones from which the antlers are grown and cast
Antlers	Geweih	Paired bony outgrowths from the pedicles that are periodically cast and regrown
Antler	Geweihstange (Stange)	One of the paired outgrowths that constitute a set of antlers
Burr (coronet)	Rose	Circular thickening on the most proximal end of the antler, directly dorsal to the antler-pedicle junction
Pearls	Perlen	Small button-like or granular protrusions that form the burr and are part of the perlaceous ornamentation of the antlers of some deer species
Main beam (beam)	Hauptstange (Blasius, 1857) Stangenachse (Nitsche, 1898)	Main antler structure formed by the sequentially developing dominant split halves from successive bifurcation events. During the growth process, the dominance of the split halves can change (Table 1)
Groove (gutter) (furrow) (channel)	Riefe (Rinne) (Rille)	Longitudinal blood vessel impression on the antler surface
Spike (spike antler)	Spieß(/ss)	Unbranched antler; first antler in all cervid species and also adult antler in <i>Mazama</i> , <i>Pudu</i> and <i>Elaphodus</i>
Bifurcated antler	Gabelstange	Antler consisting exclusively of the brow tine/a1 and an unbranched main beam/p1
Tine (branch)	Spross(e) (Ende)	Subordinate branch of an antler bifurcation with limited growth potential and early cessation of growth
Palm(ation)	Schaufel	Laterally flattened distal part of (adult) antlers, typical of antlers in <i>Alces</i> , <i>Dama</i> and <i>Megaloceros</i>
Brow tine	Augspross(e)	First tine above burr in most species, directed anteriorly (main criterion, additional (secondary) criteria for identification listed in Table 1)
Bez tine (bay tine)	Eisspross(e)	Tine originating from p1/main beam and situated between brow tine and trez tine, close to the brow tine. Common in <i>Cervus elaphus</i> , and <i>C. canadensis</i>
Trez tine (tray tine)	Mittelspross(e)	Tine situated between brow tine and antler tip. The three-tined antlers present in many deer species only consist of brow tine/a1, trez tine/a2 and distal tine/p1 (Table 1)
Surroyal (dagger)	Wolfsspross(e)	Irregular tine between trez tine and crown, sometimes present in <i>C. elaphus</i>
Angular tine	Winkelspross(e)	Irregular tine of Cervini originating from the antler base at the vertex between a1 and p1
Crown	Krone	Association of three or more tines at the distal end of the antler
Back tine	Hinterspross(e) (Rückspross)	Subordinate tine projecting posteriad

Note: Comparison of English and German terms; mainly based on Nitsche (1898) and Kirchhoff (1976). Alternative or less commonly used terms are given in brackets.

distal bifurcation, a' for the bez tine and d for the back tine or fourth tine in cervine deer (Table 3 and Figure 3).

Weber (1904) stated that a brow tine is present in *Hippocamelus*, *Axis*, *Rusa*, *Cervus*, *Dama*, *Alces*, and *Rangifer*, but missing in *Capreolus* and that a bez tine is

present in *C. elaphus* and *Rangifer*. The trez tine (Mittelspross) is present in *Rusa*, as the anterior distal tine, and in *Cervus*, *Dama*, *Alces* and *Capreolus*. He further stated that the "Hinterspross" (posterior tine, different from the back tine sensu Lister et al., 2005 except for *Dama* and

TABLE 3 Overview of homologies of antler structures by different authors.

	Pocock (1933)	Garrod (1877)	Brooke (1878)	Weber (1904)	This article
Base of antler	b				b
Proximal anterior branch	a1	A	a	Augenspross ^a	a1
Proximal posterior branch	p1		x		p1
Bez tine	x		a'	Eisspross	x
Anterior branch from a1					a1a
Posterior branch from a1					a1p
Anterior branch from p1	a2	B	b	Mittelspross ^b	a2
Posterior branch from p1	p2	C	c		p2
Anterior branch from a2					a2a
Posterior branch from a2					a2p
Distal anterior branches originating from p2-p*	a3-a*		(c)		a3-a*
Distal posterior branches originating from p2-p*	p3-p*		d		p3-p*

Note: Most a1 branches are considered as brow tines, some a2 branches are considered as trez tines, the bez tine is an individually sprouting tine from p1, the main beam usually consists of the posterior branches (p*), palmated beams consist of a* and p*, which can be difficult to track in fully palmated antlers of adult individuals. Terms introduced in this study are highlighted in bold.

^aIf brow tine; exception: *Capreolus*, in which he homologized a1 with the trez tine.

^bIf trez tine; exception: *Capreolus* (see above), *Rangifer*, in which he homologized the back tine with the trez tine.

Rangifer) is present in *Axis*, as the short distal tine, as well as in *Cervus*, *Dama*, *Alces*, *Capreolus*, and *Rangifer*.

The antler terminology and system of antler tine homology introduced by Pocock (1933) differs in a few cases from the homologies suggested by his predecessors, but has recently also been used by Samejima and Matsuoka (2020). Figure 4 shows these homologies, along with cases, where in our view different homologies are possible. We also discuss deviating opinions of other authors (Table 3). Thus, for instance not all a1 are considered as homologous with the brow tine and not all a2 as homologous with the trez tine (see Table 2 for the definitions of different antler structures), raising the question on which criteria the identification of these tines should be based. The trez tine is typical of *Cervus* and *Dama* and their fossil relatives, such as *Eucladoceros* and *Megaloceros* (Figure 5; Azzaroli & Mazza, 1992; Croitor, 2006; Croitor & Robinson, 2020). The bez tine is only present in *C. elaphus* and *C. canadensis*.

4.2 | Muntiacini

There is general consensus about the antler homologies of *Muntiacus*, which consist of a1 as the brow tine and p1 as the main beam (Brooke, 1878; Pocock, 1933; Samejima & Matsuoka, 2020; Figure 4). The antlers of *Elaphodus* consist of short, unbranched spikes. Pocock (1933) described the antler of *Elaphodus cephalophus* as a “minute, irregular, undivided snag.” It is not possible to unambiguously homologize this spike with structural elements of

branched antlers. (Figure 4). The antler morphology of *Elaphodus* could be a case of a secondary simplification that evolved from a *Muntiacus*-like, two-tined antler morphology. Assuming such a derived condition would be in principle accordance with the fossil record. The first fossil *Muntiacus* are known from the upper Miocene, *M. nor-ingensis* (11–9 mya) and *M. leilaoensis* (9–7 mya), and resemble extant muntjacs (Dong, 2007; Dong et al., 2004). The split between *Muntiacus* and *Elaphodus* was estimated to have happened between 4.8 and 3.4 mya (Lan & Shi 1993, 1994) or at about 2.5 mya based on total evidence dating (Heckeberg, 2017b). The first certain *Elaphodus* fossils are known from the Middle Pleistocene (around 700 kya) (Hooijer, 1951; Leslie et al., 2013). An alternative interpretation would be to assume that bifurcation of the antler growth tip has never occurred in the evolutionary history of this taxon due to the small size of the blastema (primary lack of branching). *Elaphodus* was not included in the study by Samejima and Matsuoka (2020).

4.3 | Cervini

According to Pocock (1933), *Axis* antlers consist of a1, p1, a2 (the longer of the two distal tines), and p2 (the shorter, mediad directed of the two distal tines), which is similar to Garrod's (1877) and Brooke's (1878) views and was adopted by Samejima and Matsuoka (2020). Weber (1904) considered the longer distal tine as the main beam and the shorter one as the back tine. In *Axis*, Lydekker (1915) regarded the tine later referred to as a2 by Pocock (1933)

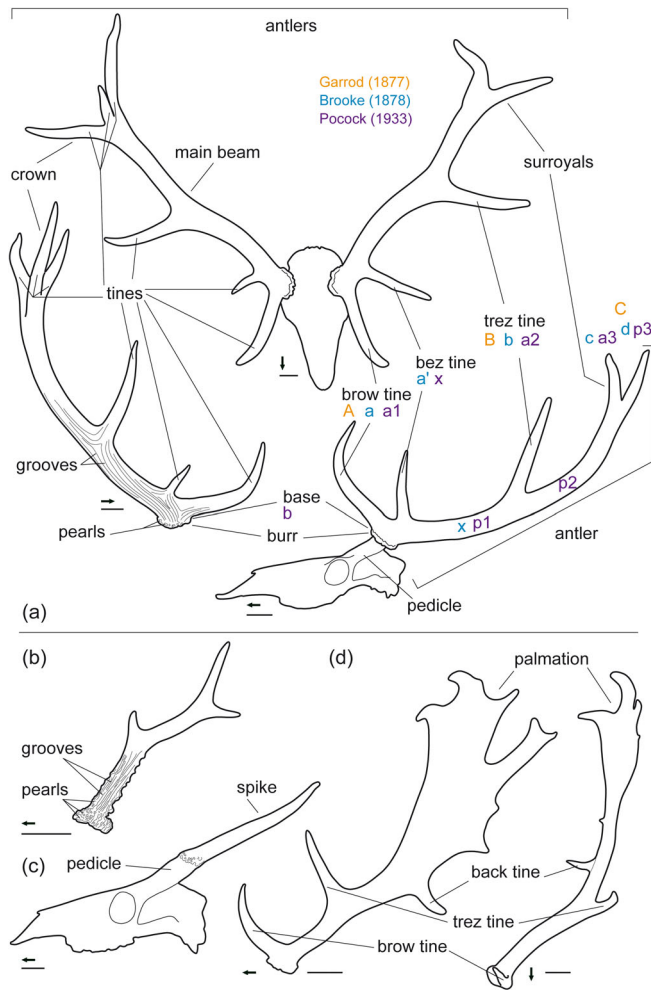


FIGURE 3 Overview of the antler terminology. (a) Dorsal view of the skull and antlers, lateral view of the right antler and lateral view of the skull and left antler of *Cervus elaphus*. Terms for different antler parts, structures, and ornamentation are shown including terms used by Garrod (1877), Brooke (1878) and Pocock (1933). (b) Left antler of *Capreolus capreolus* showing extensive ornamentation with pearls and prominent grooves. (c) Left lateral view of the skull and first antler of a young *Rusa unicolor*. Note the initial perlaceous ornamentation and thickening at the position where the burr develops in successive antler generations. (d) Lateral and dorsal view of the left antler of *Dama dama* showing palmation and p3 as the back tine. All scale bars equal 5 cm. The arrows point towards anterior.

as homologous to the tine in *Rusa* classified as p2 by that author, which is similar to our views. Lydekker (1915) also considered p2 in *Axis* and a2 in *Rusa* as the trez tine, which was adopted by Samejima and Matsuoka (2020) but is contra Pocock (1933), who stated that p2 in *Axis* is not homologous to the trez tine. We consider the longer distal tine as p2, representing a continuation of the slightly twisted beam p1, and the shorter mediad pointing distal tine as a2, which is not homologous to the trez tine (Figure 4). The angle

between a1 and p1 is obtuse in *A. axis*, while in the other three *Axis* species the angle is acute.

According to Pocock (1933), all *Cervus* species have a1 as the brow tine, a2 as the trez tine, p2, a3, and p3. *C. elaphus* and *C. canadensis* have a bez tine originating from p1 with varying position and size, which is not present in any other extant deer. It is also the first tine not to be developed in reduced (“set-back”) antlers of old individuals, and it is absent in certain populations under unfavorable conditions (e.g., the Mesola deer, *C. e. italicus*, Zachos et al., 2014). *Cervus* species often have additional distal tines. Pocock’s (1933) view was already suggested by Brooke (1878) and Garrod (1877), and is shared by Samejima and Matsuoka (2020). We likewise agree with the proposed homologies and further suggest that the shorter, mediad pointing distal tine in *C. nippon* represents a3 and the longer distal tine p3 (Figures 4, 6, and 7).

von Lehmann (1959) discussed the presence of a tine that is variably present in Cervini species, which he referred to as the angular tine (German: Winkelspross). This tine originates from the antler base at the vertex between the brow tine/a1 and main beam/p1. According to his accounts, the angular tine occurs most frequently in *Axis*, but also appears in *Cervus*, *Dama* and *Rusa*.

There is great individual variation within the antlers of *Dama*, with simpler forms of *Dama dama* antlers being similar to those of *C. nippon*, while more complex forms resemble those of *M. giganteus* (Garrod, 1877; Pocock, 1933). There is consensus about the homology of the antler structures, which consist of a1 as brow tine, p1, a2 as trez tine, p2, a3 (palmated in older individuals), and p3 as back tine sensu Lister et al. (2005) (Figures 4 and 5; Brooke, 1878, Pocock, 1933, Samejima & Matsuoka, 2020).

The tine homology of *Elaphurus* antlers and the systematic position of this taxon have been much debated over the last 150 years. Lydekker (1915) and Cameron (1892), whose cervid classifications were based on antler morphology, did not attempt to homologize the antler tines of Pere David’s deer with those of other cervids. They stated that the antlers of *Elaphurus* were fundamentally different from those of any Old World deer and classified the Pere David’s deer as a New World cervid despite all Old World characters of the taxon. In contrast, Brooke (1878), based on the metacarpal bones, and Weber (1904) placed *Elaphurus* within Old World deer, a classification later confirmed by molecular data. Brooke (1878) suggested that *Elaphurus* has no brow tine; instead, he considered the anterior tines as homologous to the anterior tine of *Rusa* and *Rucervus* and to the trez tine of *Cervus*, and the posterior tine as homologous to the anterior surroyal tine of *Cervus*. However, other authors did not follow this view. The growth series shows

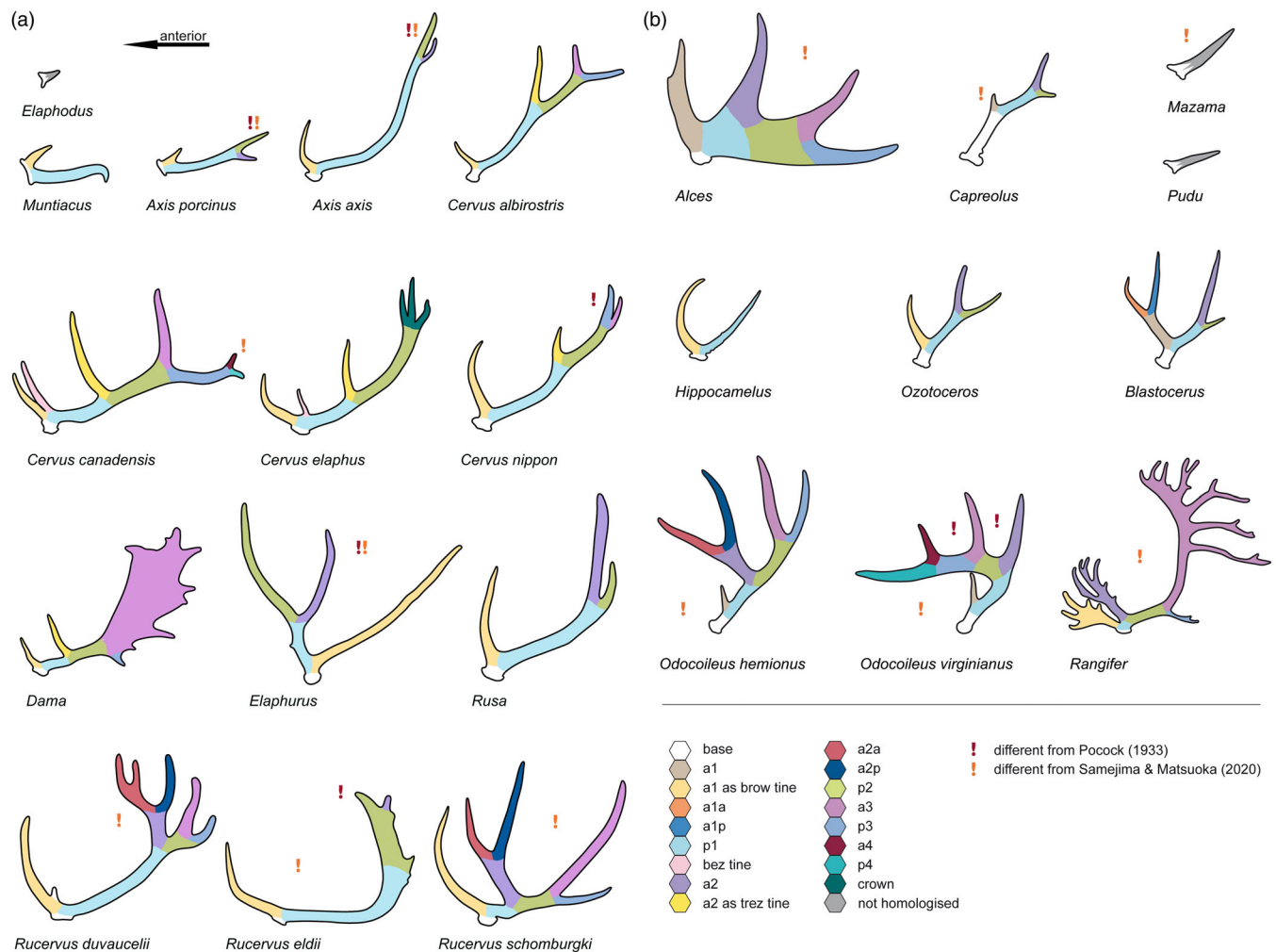


FIGURE 4 Homologies of antler structures in (a) Cervinae and (b) Capreolinae. The tines considered homologous are shaded in the same color (color code in part b). a1 and a2 have different colors when considered as brow tine or trez tine, respectively. p3 in *Dama* and *Rangifer* is short and often referred to as the back tine (e.g., Lister et al., 2005; Weber, 1904). Differences in homology patterns to Pocock (1933; red exclamation mark) and to Samejima & Matsuoka (2020; orange exclamation mark) are highlighted.

that the brow tine (a1) is vertical, slightly curved forward, and terminates in a pair of tines, and that the posterior branch (p1) is slender, long, mostly simple (sometimes divided) and projects posteriad. Anterior and posterior branches can have multiple accessory tines. *E. davidianus* is the only species where a1 is more developed than p1 (Pocock, 1912, 1933). Hoffmann (1959) homologized the posterior branch as the main beam because it has more bifurcations and is longer than the anterior branch (Figures 4 and 6).

Samejima and Matsuoka (2020) adopted a similar system of tine homology, including a1 as brow tine and p1 as the posterior branch, and also indicated the position of a hypothetical, non-existent trez tine (Samejima & Matsuoka, 2020, SI 3, figures 29 and 30).

We agree that the antlers of *Elaphurus* are dissimilar to those of any other cervid and therefore consider two

homologizing alternatives (Figures 4 and 6). The first would be that the anterior branches are homologous to a1 with a further bifurcation, for which we suggest the terms a1a and a1p, and the posterior branch would be a homologue of p1 (not shown in Figure 4). The second and new hypothesis (see Figure 4) is that the growth pattern and thus the position of the branches in *Elaphurus* antlers may simply be reversed, that is, the anterior half develops as the main beam and the posterior half remains simpler. Beninde (1937) already observed that the antlers of *Elaphurus* resemble reversed red deer antlers. A potential reversal of the anterior–posterior antler axis might be due to the mixture of two genomes resulting in patterns entirely different from the parental patterns (see below). Regarding mechanistic aspects of antler morphogenesis, experimental studies by Goss (1991) in fallow deer suggested that the anterior–

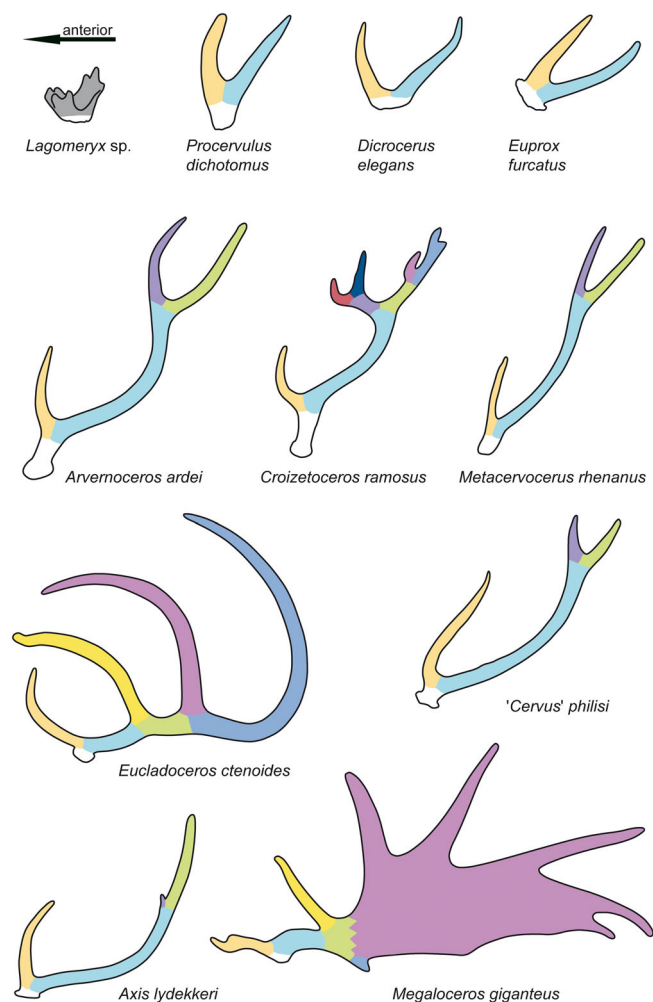


FIGURE 5 Antler tine homologies for a selection of fossil cervids. Colors are as described in the legend of Figure 4. “*C. philisi*” has been suggested to be a junior synonym for *Metacervoceros rhenanus* (Croitor, 2018a).

posterior axis of antler orientation is determined by the antlerogenic periosteum (AP) that is located at the future pedicle/antler sites of the frontal bones. Thus, when the AP overlying the incipient pedicles was experimentally rotated by 180°, the subsequently grown antlers exhibited a reversed anterior–posterior polarity. Later studies by Gao et al. (2012) in *Cervus nippon* indicated that the morphogenetic information of the antlers is primarily held in the anterior-medial portions of the AP.

Generally, the outcomes of hybridization events are difficult to predict. Morphological characters of hybrid species may be unique instead of intermediate between the parent species as is the case in *Elaphurus* (Groves, 2014; Rieseberg & Wayne, 1999). For example, hybrids between the two closely related sea urchin species *Heliocidaria tuberculata* and *H. erythrogramma* deviate in development from both parental species (Raff & Byrne, 2006). When a *H. erythrogramma* egg was fertilized with a *H. tuberculata*

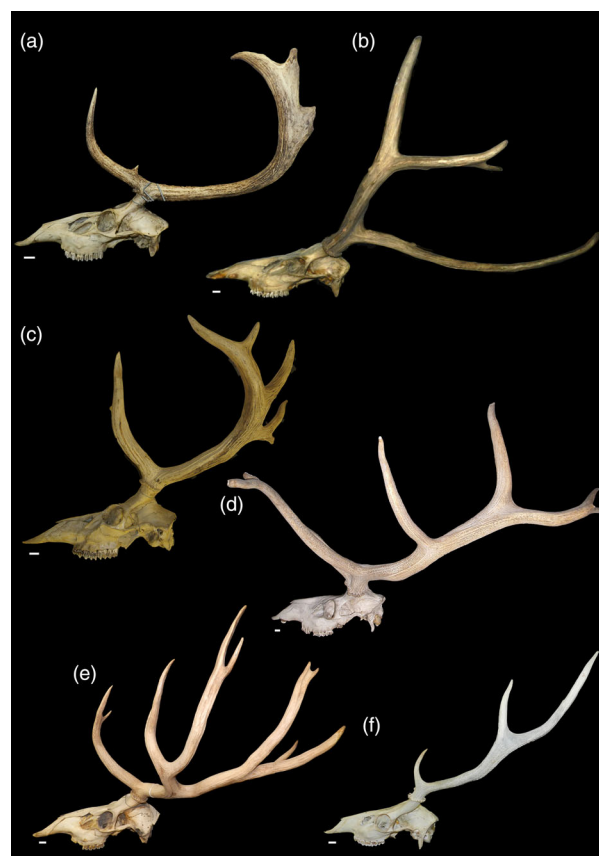


FIGURE 6 Skulls of selected cervine species. (a) *Rucervus eldii* (ZSM 1905/3018)—the angle between a1 and p1 is almost 180°; a1 is long and points upwards after the horizontal extension; p1 bends upwards and anteriorad after the horizontal extension with multiple smaller tines on p1. (b) *Elaphurus davidianus* (ZMB_MAM 106005)—the anterior beam of the antler shows the bifurcating pattern usually present in the posterior beam of cervids within Cervini; the posterior beam does not bifurcate similar to the brow tine in cervids within Cervini; tiny accessory tines may be present in some individuals (not here). (c) *Rucervus duvaucelii* (NMS 1913-178)—the angle between a1 and p1 is relatively wide; a1 has a lesser horizontal component than the other two *Rucervus* species and points upwards; p1 bends upwards and anteriorad with multiple smaller tines. (d) *Cervus canadensis* (NMB C2642)—brow tine and bez tine are long and point anteriorad (the bez tine largely obscures the brow tine in this photograph); p1 bifurcates in the pattern typical of *Cervus*. (e) *Rucervus schomburgki* (NHM 75.1393)—the angle between a1 and p1 is wide; a1 is long (and terminally forked) and points upwards after the horizontal extension; p1 bifurcates shortly after the lateroposteriad extension; a2 and p2 and following tines bifurcate. (f) *Cervus nippon* (ZSM 1961/285)—the angle between a1 and a2 is acute; there is no bez tine; p1 further bifurcates in the pattern typical of *Cervus*. Note there is a fourth tine (a3) at the bifurcation of p2 directed mediad, which is not visible in lateral view. All scale bars equal 2 cm. NHM, Natural History Museum London; NMB, Naturhistorisches Museum Basel; NMS, National Museums of Scotland Edinburgh; ZMB_MAM, Museum für Naturkunde Berlin; ZSM, Zoologische Staatssammlung München.



FIGURE 7 Advanced stage of antler growth in a red deer stag (*Cervus elaphus*). Brow, bez, and trez tines are well developed, and formation of the crown has just begun. Photo courtesy of H. Arndt.

sperm, this resulted in a novel morphology of the larva that was able to undergo metamorphosis. However, the reciprocal hybrids (*H.tuberculata* egg \times *H. erythrogramma* sperm) failed to develop beyond gastrulation due to lack of proper axis specification. The latter finding indicates a decisive role of the *H. erythrogramma* egg cytoplasm in axis differentiation (Raff & Byrne, 2006).

We hope that the role of the AP in determining the anterior–posterior polarity of antlers and the hypothesis of a reversed polarity of the antlers in *Elaphurus* can be addressed in more detail in the future. There is also need for a detailed analysis of the antler morphology and ontogeny of *E. davidianus*, which is, however, beyond the scope of the present study.

Pocock (1933) considered the antlers of *Rucervus* to be more specialized than those of *Axis* and *Rusa*, but the pattern can be derived from either of the two taxa. The antlers of *R. duvaucelii* show greater individual variation than those of the other two *Rucervus* species. Some are more similar to antlers of *R. eldii*, while others have a branching pattern similar to *R. schomburgki*. All *Rucervus* species have a1 as the brow tine, p1 as the main beam, a2, and p2 (Pocock, 1933). Usually, the antlers of *R. schomburgki*, and sometimes those of *R. duvaucelii*, have additional bifurcations on both a2 and p2. In some *R. duvaucelii*, a2 continues forward and upward as the main beam with smaller tines, while p2 is shorter and sometimes exhibits additional tines (Figures 4 and 6). This is similar to *R. eldii*; however, in most individuals of *R. duvaucelii*, a2 and p2 are of approximately equal length and both bifurcate further (Lydekker, 1898; Pocock, 1933). Antlers of *R. eldii* are characterized by a1 as the brow tine and a long p1 as the main beam.

According to Pocock (1933), the main beam of *R. eldii* continues into a long a2, from which a short p2 diverges. He further stated that a2 and p2 correspond to a2 and p2 in *Axis* and *Rusa* and that p2 in *R. duvaucelii* and *R. eldii*

are homologous. Garrod (1877) and Lydekker (1915) had previously proposed the same view. In addition, Lydekker (1915) homologized p2 with the trez tine, which is incorrect according to Pocock (1933). The antlers of *R. schomburgki* are slightly different and consist of a1 as the brow tine, a short p1, and a2 and p2 that both bifurcate further (Figures 4 and 6). We generally agree with the homology proposed by Pocock (1933); however, we consider p2 rather than a2 as the continuation of p1 and thus the main beam in *R. eldii* and, if applicable, in *R. duvaucelii*. We also introduce new terms for the tines bifurcating from a2, viz. a2a and a2p (Table 3, Figure 4). This is a logical deduction from Pocock's (1933) system, and the introduction of new terms for these regularly present tines seems justified. Samejima and Matsuoka (2020) did not follow Pocock's (1933) homologies and applied their own terminology. For example, the p2 and a3 in *R. duvaucelii* are stated to be missing, instead p3 is considered as the “back beam with distal tines”. Samejima and Matsuoka (2020) present similar homologies for *R. schomburgki*. In *R. eldii*, p1 and a2 have been combined into the “lower beam” by these authors, p2 is named the “medial tine”, and the position of a (non-existent, that is, lost) trez is indicated. The “higher beam” was not homologized with Pocock (1933), instead new terms were introduced.

According to Pocock (1933) *Rusa* antlers consist of a1 as the brow tine, p1, a2 (anterior branch) as trez tine and p2 (posterior branch). There is a consensus about the homology of antler tines in *Rusa* (Brooke, 1878; Pocock, 1933; Samejima & Matsuoka, 2020; Weber, 1904). We generally agree with the proposed scheme; however, whether a2 is homologous to the trez tine is debatable, because it does not fulfill any of the criteria listed in Table 1 (Figure 4).

4.4 | Capreolinae

Croitor (2021a) stated that the antler bauplan in Capreolinae was more conservative than that of the Cervinae. Based on our review of the matter, we think the opposite is the case, and that different species within Capreolinae show more disparity in antler morphology than Cervinae (see Figure 4). Antler morphologies of Capreolinae include single-tined, two-tined, three-tined, multi-tined and palmated antlers. Particularly the palmated antlers of *Alces* and *Rangifer*, but also the forward curving antlers of *Odocoileus virginianus* are disparate. We could not recognize a “*Capreolus*-bauplan”, which according to Croitor (2021a) underlies all antler baupläne of Capreolinae species other than those of the genus *Capreolus* and very closely related fossil taxa like *Procapreolus*.

The branching pattern of *Alces* antlers is similar to that of *Cervus* and best observable in younger individuals, where the palmation is not yet fully developed (Pocock, 1933). As soon as the palmation develops, the tines are often no longer traceable. There is a1 and the palmated part consists of a2-a* + p1-p* (Table 3; asterisks indicating consecutive numbers). We agree with this homology (Figure 4). Weber (1904) adopted a similar homology as Brooke (1878) with the exception that he homologized the palmated part with the trez tine, which is incorrect according to Pocock (1933). Samejima and Matsuoka (2020) considered the antler base as the lower and upper beam, which is inconsistent with other homologies, and the antler to consist of a1 and p1. Contra Croitor (2021a), we find no particular resemblance between the antlers of *Alces* and *Capreolus*.

The individual variation of *Capreolus* antlers is remarkable, although the general structure is very similar; they have a long base, a1, a2 and p2. Many authors considered a1 as the brow tine (Blasius, 1857, Brooke, 1878, Nitsche, 1898, von Raesfeld, 1923, Samejima & Matsuoka, 2020). Others homologized a1 with the trez tine (Lydekker, 1898; Pocock, 1933; Weber, 1904). Hoffmann (1959) argued that the position of the tine is irrelevant for its homology; nevertheless, he considered a1 in *Capreolus* as the trez tine, suggesting that the brow tine had possibly been lost in this taxon. von Lehmann (1959) declined to homologize a1 with either the brow tine or the trez tine and instead referred to this tine as the “sub-basal” tine. We think that it is currently not possible to unambiguously homologize a1 with the brow tine. In *Capreolus*, a1 fulfills four criteria for the brow tine, that is, A, B, D, and E (Table 1, Figure 4), while the relatively distal position of a1 is an argument against its classification as the brow tine.

The antlers of *Blastocerus* consist of a relatively long base, a1 directed forward and upward with another (unique) bifurcation, p1 that is almost as long as a1, a2, and p2, and rarely a3 and p3 (Pocock, 1933). We agree with this view and name the two tines bifurcating from a1 a1a and a1p (Figure 4). Samejima and Matsuoka (2020) named the base “lower tine” and combined p1 and a2 into the upper beam with p2 as the “rear tine”.

The antlers of *Hippocamelus* consist of a short base and more or less equally long a1 (as the brow tine) and p1. The latter sometimes has small accessory tines (Pocock, 1933). We agree with this proposed homology (Figure 4). *Hippocamelus* was not included in Samejima and Matsuoka (2020).

The antlers of *Mazama* and *Pudu* resemble the short unbranched first antlers (spikes) present in all deer species (Pocock, 1933). As in *Elaphodus*, the question arises whether this simple antler morphology represents the ancestral character state or a derived condition. In the

latter case, a comparable reduction of morphological complexity must have occurred in both lineages (Geist, 1998). Since *Mazama* and *Pudu* are secondarily reduced in size, and a simplification of antler morphology could well be associated with this body size reduction, we consider the latter as the more likely scenario. In addition, the rare occurrence of bifurcating antlers in *Pudu* (Figure 2) supports a latent potential for antler splitting that is usually not realized. Samejima and Matsuoka (2020) reported small tine-like projections from the spike antlers of *Mazama*, and accordingly distinguished lower beam, rear tine and upper beam. *Pudu* was not included by Samejima and Matsuoka (2020).

The antlers of *Odocoileus hemionus* share some similarities with those of *Blastocerus* (Pocock, 1933). Pocock (1933) agreed with Brooke (1878) that the similarity, referring to the double-bifurcating branching pattern, is superficial and that the structures in question were independently acquired, that is, in *O. hemionus* a1 is developed before the double-bifurcation, while in *Blastocerus* a1 is part of the double-bifurcation (Figure 4). In contrast, Cameron (1892) and Lydekker (1915) suggested certain homologies between the main branches of both species. The antlers of *O. hemionus* consist of a simple, upward pointing a1 not considered homologous with the brow tine, p1, a2, and p2. The latter two both bifurcate further (Pocock, 1912, 1933). We agree with this view and suggest naming the two tines bifurcating from a2 a2a and a2p. (Tables 1 and 3 and Figure 4). Since a1 is mostly short and points upwards rather than anteriorly we suggest not to homologize this tine with the brow tine.

The antlers of *O. virginianus* consist of a simple, upward-pointing a1 not homologous with the brow tine, a long p1, a2 (curved beam), p2 (long upward tine), a3 (anterior continuation of a2), and p3 (long upward tine) (Pocock, 1933). We consider the long forward curving main beam to be a continuation of the p* branches, rather than the a* branches, and the upward pointing tines to be the equivalent to the a* branches, due to a strong compensatory flexion on the anterior side. We suggest to continue to name the tines a3, p3, a4, p4, etc. (Figure 4). Since a1 is pointing upwards instead of anteriorly, we do not consider it to be homologous to the brow tine (Table 1). Samejima and Matsuoka (2020) consider a1 as the “rear tine”, combine p1 and a2 into an “upper beam” and assign p2 to one of the remaining tines. This homology pattern seems inconsistent with that of other deer species, particularly concerning the introduction of a “rear tine” and not following the numbering scheme suggested by Pocock (1933). Contrary to the suggestion by Croitor (2021a), we do not find a particular resemblance between *Odocoileus* and *Capreolus* antlers. For example, the a1 in *Capreolus* is at a distal position and can be considered a brow tine, while a1

in *Odocoileus* originates close to the burr; *Capreolus* antlers have exactly one distal bifurcation on relatively short and straight antlers, while *Odocoileus* antlers have several bifurcations along the long main beam, which is also curved anteriorly as described above.

The antlers of *Ozotoceros* are three-tined with a moderately long base, a1, a long p1, a2, and p2 (Pocock, 1933). We agree with this view and propose that a1 could be homologized with the brow tine, since it fulfills several of the criteria listed in Table 1. This taxon was not included in Samejima and Matsuoka (2020).

The individual variation of antlers in *Rangifer* is remarkable, although they do not differ much in their fundamental structure from those of other cervids. They consist of a1 as a very variable, often palmated brow tine, a short p1, a2, which is also often palmated, p2, a3 as the main beam with multiple accessory tines and p3 as the back tine (Lister et al., 2005; Pocock, 1933). Brooke (1878) considered *Rangifer* antlers to be similar to *Dama* and also to include a trez tine (a2). The latter view was supported by Lydekker (1898). Garrod (1877) found the antlers of *Rangifer* to be similar to those of *R. eldii*, homologizing a2 with the bez tine. The presence of a bez tine (instead of a trez tine) was also supported by Weber (1904), who homologized the back tine with the trez tine. Samejima and Matsuoka (2020) adopted similar homologies, using different terms and did not homologize any tine with bez or trez tines. We agree with the homology pattern of Pocock (1933) and adopt the term back tine (Lister et al., 2005; Figure 4). The asymmetry of the brow tines is a peculiarity of *Rangifer* antlers, which makes it difficult to establish its relation to the brow tines of other deer species. Thus, in *Rangifer* one brow tine is usually well developed, palmated and extends diagonally across the nose (in dorsal view). The contralateral brow tine is reduced, straight and not palmated or may even be absent (Goss, 1995). The more developed brow tine can change sides from year to year as successive sets of antlers are regenerated. However, sometimes, both brow tines can be palmated. Goss (1995) considered the “brow tine phenomenon” in *Rangifer* as one of the unsolved problems in antler research. Despite its variability, palmation and usually asymmetrical appearance, we agree with homologizing a1 with the brow tine (Table 1).

4.5 | Antler homologies in fossil cervids

A plethora of literature on comparative morphology of fossil antlers is available (e.g., Azanza, 1993; Azanza Asensio 2000; Azanza & Ginsburg, 1997; Azanza et al., 2011, 2013, 2022; Böhme et al. 2012; Croitor, 2018a, 2021a; DiStefano & Petronio, 2002; Heintz 1970).

Therefore, we provide here only a few examples of the different types of antlers from the Miocene to the Pleistocene. There is consensus that all antlers known from the fossil record were deciduous and underwent a cycle of death, loss (casting) and regeneration comparable to extant cervids (Azanza et al., 2022; Heckeberg, 2017a; Rössner et al., 2021). It is, however, controversial whether the antler cycle of early cervids was strictly seasonal as in extant deer or of a more irregular nature (Azanza et al., 2022).

Antlers of fossil cervids can be divided into two groups. The first is represented by Miocene cervids with simple and/or unique antler morphologies that have no parallel in any extant cervid. The second group consists of cervids from the Plio- and Pleistocene with larger and more complex antlers. The latter group can be further subdivided into (1) cervids typical of the Plio- and Plio-/Pleistocene epoch whose antlers partly resemble those of extant cervids but also possess some unique morphological features, and (2) Pleistocene cervids that are largely similar to extant cervids regarding their antler morphology and that are partly even assigned to extant genera (Heckeberg, 2017b).

In Miocene cervids, a dichotomous antler morphology is most common, for example, in *Acteocemas*, *Procervulus*, and *Dicrocerus* (Figure 5) with a1 as the brow tine and p1 as the main beam (Azanza, 1993b; Azanza et al., 2011, 2013, 2022). The antler base is short and there is no burr. The antlers of *Euprox furcatus* represent a special case in that they are similar to those of extant muntjacs and, in contrast to all other antlers of Miocene cervids, possess a burr. Therefore, *Euprox* has been considered the first representative of Muntiacines (Azanza, 1993a, Rössner 2010), while others are more cautious regarding this assignment (Heckeberg, 2017b). Lagomerycine antlers are multi-tined, crown-shaped structures with a variable number of tines. It is not possible to homologize antler structures of Lagomerycines with those of other cervids because the number and size of tines are inconsistent and inference of the orientation of cast antlers is mostly not possible.

The antler morphology of Plio- and Plio-/Pleistocene cervids is more complex, and there is an increase in antler (and body) size. The bauplan of many taxa is already similar to that of extant cervids, for example, *Arvernoceros*, *Metacervoceros* (Croitor 2009; Croitor & Robinson, 2020; Croitor & Stefaniak 2009), while others are unique, for example, *Croizetoceros* (Heintz 1970). Three-tined antlers are very common with a1 as the brow tine and a distal bifurcation of a long p1 with a2 and p2. Croitor (2018a, 2018b) found similarities in the antlers of *Rucervus* and *Arvernoceros*. Antlers of *Croizetoceros* have a1 as the brow tine, p1, which can be longer or shorter depending on the number of distal bifurcations, a2 and p2, which both have the potential to bifurcate further.

The antlers of most Pleistocene cervids resemble those of extant deer, with some species assigned to extant genera, for example, *Axis lydekkeri* (Zaim et al. 2003). A three-tined antler bauplan is common with a1 as the brow tine, p1, a2, and p2. The antlers of *Eucladoceros ctenoides* are similar to those of extant *Cervus* species, developing a trez tine and often even a bez tine. Croitor (2018a) concluded that *Eucladoceros* does not belong to the *Cervus-Rusa* lineage, but phylogenetic studies analyzing the bony labyrinth as well as other recent morphological approaches show a close relationship of *Eucladoceros* with *Cervus* (Mennecart et al., 2017). Palmated antlers as in *Megaloceros* and early relatives of *Alces* become more common in the Pleistocene (Azzaroli & Mazza, 1992; Croitor, 2006, 2021b, 2021a). The antlers of *Megaloceros* are similar to those of *Dama dama* (Lister et al., 2005; but see Croitor, 2021b for different views) and therefore, are partly difficult to homologize. There is a1 as the brow tine, which can be palmated, p1, a2 as the trez tine, p2, a3 constituting the palmated part, and p3 as the back tine. Alternatively, the upward pointing tines could be homologized as a3-a*. In order to infer homologies with certainty, ontogenetic series would be helpful.

The difficulty of applying antler tine homologies of extant cervids to the more complex antlers of fossil taxa is due to the absence of ontogenetic series and often the lack of a sufficient number of specimens to allow an estimation of intraspecific variability.

5 | THE USE OF MORPHOLOGICAL AND MOLECULAR DATA IN CERVID SYSTEMATICS

5.1 | General considerations

The difficulty of homologizing antler structures across cervid species is evident and should be accounted for when using antler characters as classification criteria. Nevertheless, a consensus on homology patterns exists for many cervids. Antler traits were for a long time—in addition to dental, other osteological, and additional morphological characters—the only information available for establishing a classification (e.g., Azanza, 1993a; Brooke, 1878; DiStefano & Petronio, 2002). Molecular data (e.g., Douzery & Randi, 1997; Randi et al., 1998) much later confirmed large parts of the systematics proposed on the basis of morphological data, for example the division of Capreolinae and Cervinae by Brooke (1878). While for some morphological characters (e.g., the bony labyrinth, Mennecart et al., 2017) phylogenetic

reconstructions fit molecular-based topologies relatively well, some discrepancies between molecular-based and morphology-based phylogenetic reconstructions remain (Heckeberg, 2017b). In addition, different molecular data sets, particularly mitochondrial (e.g., Hassanin et al., 2012) vs. nuclear (e.g., Cronin et al., 1996; Hu et al., 2019) genetic markers, suggest different evolutionary histories of cervids. These conflicting hypotheses about the systematic relationships need to be considered, especially when attempting to establish new classification schemes and trying to map these with only one phylogenetic reconstruction, ignoring alternative hypotheses on the evolutionary history of the taxon. Here, we highlight the conflicting hypotheses within cervid systematics arising from different data sources.

Probably due to the larger available datasets, high levels of variability, and its maternal inheritance, it has been common practice to predominantly rely on mitochondrial markers when reconstructing a taxon's evolutionary history, which has increasingly become contentious in recent years (e.g., Galtier et al., 2009; Nabholz et al., 2008, 2009; Sánchez-Gracia & Castresana, 2012). In line with this trend, most current analyses and interpretations in cervid systematics are based on topologies inferred from mitochondrial markers (e.g., Duarte et al., 2008; Hassanin et al., 2012). Nuclear markers are available for fewer species than are mitochondrial markers, and therefore less often used in phylogenetic reconstructions. Nevertheless, the topologies based solely on mitochondrial markers or on datasets dominated by mitochondrial markers that outweigh all other characters are often considered to be more reliable than they really are (e.g., Ghazanfarullah et al., 2021; Samejima & Matsuoka, 2020). For cervids, different phylogenetic studies repeatedly used (almost) identical mitochondrial datasets resulting in the same topologies, thereby strengthening the above assumption and creating the false impression of a robust, recurring signal (e.g., Ghazanfarullah et al., 2021; Heckeberg et al., 2016; Lorenzini & Garofalo, 2015; Samejima & Matsuoka, 2020; Wang & Yang, 2013; Wong et al., 2021).

Focusing on mitochondrial data is, however, problematic because it ignores conflicting hypotheses arising from reconstructions based on other characters, including morphological and nuclear genetic data. Mitochondrial DNA also only represents part of the evolutionary history (that of the maternal lineage), which makes it liable to well-known shortcomings, including a biased study design, misinterpretations, and/or erroneous conclusions due to hybridization signals and others. Accordingly, we recommend not focusing exclusively on mitochondrial data as a basis for systematic analyses.

5.2 | Monophyletic *Rucervus* and the case of *Elaphurus*

5.2.1 | Systematic position

Within cervids the use of mitochondrial vs. nuclear genetic markers has a most striking impact on the position of *Rucervus eldii* (Figure 8). Depending on the molecular markers analyzed, *Elaphurus* is nested either within *Cervus* (non-mitochondrial markers), or placed as the sister taxon of *R. eldii* (mitochondrial markers). The latter position would render *Rucervus* polyphyletic, because the other two *Rucervus* species are part of a different clade not closely related to *R. eldii*/*E. davidianus*. Analyses using restriction fragment length polymorphisms (RFLPs) of mtDNA (Cronin, 1991), allozyme electrophoresis (Emerson & Tate, 1993), κ -casein sequences (Cronin et al., 1996), and karyotype (Meijaard & Groves, 2004) all yielded *Elaphurus* as nested within *Cervus*. In line with this, *Elaphurus* shows some behavioral parallels with *Cervus* (Geist, 1998). The karyotype of *Elaphurus* is the same as that of *C. elaphus* ($n = 68$) (Eroglu, 2021; Hsu & Benirschke, 1969). Still, numerous studies analyzing mitochondrial DNA resulted in the classification of *R. eldii* as the sister taxon to *E. davidianus* (e.g., Ghazanfarullah et al., 2021; Hassanin et al., 2012; Kumar et al., 2021; Pitra et al., 2004; Randi et al., 2001; Turvey et al., 2017; Wong et al., 2021). With reference to these findings, it is often incorrectly stated that all phylogenetic reconstructions based on molecular data unequivocally unite *E. davidianus* and *R. eldii* as sister taxa, thus rendering *Rucervus* polyphyletic (Ghazanfarullah et al., 2021; Hassanin et al., 2012; Kumar et al., 2021; Pitra et al., 2004; Randi et al., 2001; Turvey et al., 2017; Wong et al., 2021). It must be emphasized, however, that the claim that *R. eldii* is phylogenetically not closely related to the other two *Rucervus* species solely rests on the same mitochondrial data that were repeatedly analyzed and, expectedly, always generated the same topology. Thus, these reconstructions do not represent independent, mutually corroborating, consistent results from different approaches, which has, however, often been neglected in subsequent studies (e.g., Samejima & Matsuoka, 2020; Wong et al., 2021). The problem of conflicting systematic positions of *Elaphurus* and *R. eldii* in previous studies was recently addressed, and it has been found that the apparent position of *R. eldii* as sister taxon to *E. davidianus* is likely an artifact of the mtDNA shared with *Elaphurus* (Heckeberg, 2020).

Because of these conflicting views, *R. eldii* has often been re-assigned to a different genus, *Panolia* (Croitor, 2021b; Groves & Grubb, 2011; Pocock, 1943; Samejima & Matsuoka, 2020; Turvey et al., 2017), and *R. duvaucelii* was considered the only living member of the genus *Rucervus*

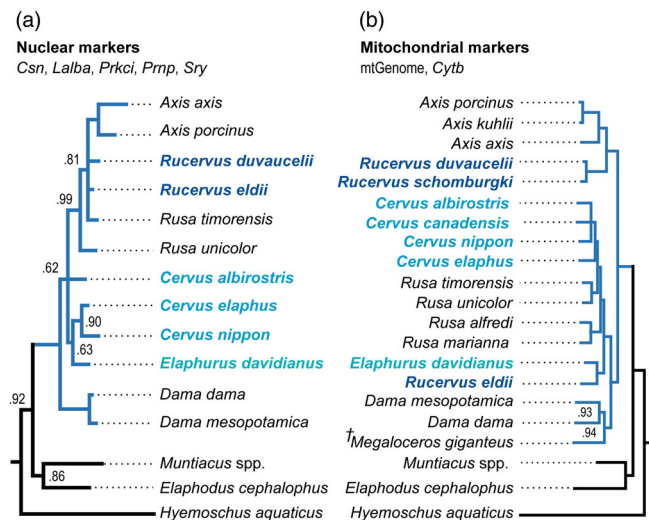


FIGURE 8 Comparison of phylogenetic reconstructions of Cervinae based on (a) nuclear vs. (b) mitochondrial markers. *Hyemoschus aquaticus* (Tragulidae) is used as the outgroup; Capreolinae not shown. Both topologies are results of Bayesian inference analyses and modified after Heckeberg (2020). Support values are equal to 1 unless specified otherwise. *Rucervus*, *Cervus*, and *Elaphurus* are highlighted. Note the differences between the trees in the phylogenetic position of *R. eldii* with respect to *Elaphurus*.

(Kumar et al., 2021). Other studies assigned *Elaphurus* to the genus *Cervus* (Emerson & Tate, 1993; Gilbert et al., 2006; Lydekker, 1915; Maqbool et al., 2007; Pitra et al., 2004; Slate et al., 2002; Tate et al., 1995). Ghazanfarullah et al. (2021) follow a similar approach when suggesting assigning *R. eldii* together with *E. davidianus* and all four *Rusa* species to the genus *Cervus*, based on the significant evolutionary and systematic distance between *R. eldii* and the other *Rucervus* species. These authors further hold that this re-assignment is in agreement with the previous molecular phylogenetic studies.

5.2.2 | Hybridization

The origin of *Elaphurus* may have been a hybridization event between a male *C. canadensis* and a female *R. eldii* or closely related ancestors of these species (Groves, 2006; Meijaard & Groves, 2004; Pitra et al., 2004; Taru & Hasegawa, 2002). The presumed origin of *Elaphurus* was in eastern Asia during the Late Pliocene (Taru & Hasegawa, 2002), and northern or eastern China would be among the potential hybridization areas. From the early Pleistocene onwards, fossils of *E. davidianus* are well known from North, East and Northeast China, Taiwan, and Japan (Dong et al., 2019). Fertile hybrids between *E. davidianus* and *C. elaphus* have been

observed in captivity (Dong et al., 2019; Otway, 1992; Tate et al., 1997). The polyphyletic status of *Rucervus* suggested by the position of *R. eldii* in mitochondrial analyses or combined datasets in which mitochondrial markers largely outweigh other markers, would then reflect this hybridization event. The maternally inherited mitochondrial markers yield *E. davidianus* and *R. eldii* as sister taxa. In contrast, using nuclear markers, particularly paternally inherited *Sry* (sex determining region on the Y-chromosome), results in polytomous (but not polyphyletic) *Rucervus* species more closely related to each other than to *E. davidianus* and yields the latter as closely related to *Cervus* (Figure 8). In accordance with this classification, a sister group relationship of *R. eldii* and *R. duvaucelii* is also supported by dental and cranial (including antler) morphology (Heckeberg, 2017b, 2020).

Discordance between mitochondrial and nuclear phylogenies is widespread, and within Cervidae it is particularly well-known with regard to *C. elaphus* and *C. canadensis*. The two are morphologically very similar (to the point that they have often been considered conspecific), but mtDNA consistently placed *C. nippon* (and sometimes even other *Cervus* species) as closer to *C. canadensis* than *C. elaphus* (Hassanin et al., 2012; Heckeberg, 2020; Kuwayama & Ozawa, 2000; Lorenzini & Garofalo, 2015; Ludt et al., 2004; Polziehn & Strobeck, 1998; Randi et al., 2001). This has usually been considered an example of a misleading gene tree, and indeed, the first nuclear analysis recently resulted in red deer and wapiti being sister taxa to the exclusion of all other *Cervus* species, sika included (Hu et al., 2019).

Similar phylogenetic conflicts occur within cattle (Bovini), in particular the systematic relationship of the American bison (*Bison bison*) and European bison, or wisent (*Bison bonasus*) (Soubrier et al., 2016; Verkaar et al., 2004; Wang et al., 2018). In mtDNA analyses, the American bison is close to the yak, and the wisent seems closely related to domestic cattle (Nowak & Olech, 2008). In contrast, Y-chromosome markers, similar AFLP fingerprints of nDNA and morphological resemblance all showed the close phylogenetic relationship of American bison and wisent, which also produce fertile offspring (Verkaar et al., 2004). Already Janecek et al. (1996) proposed three explanations for the mitochondrial divergence of the two bison species. (1) phenotypic convergence, which is considered highly unlikely; (2) lineage sorting, in which two lineages in the branch leading to both bison species would have persisted; and (3) an ancient hybridization event (Verkaar et al., 2004). The social structure of herd species with dominating bulls would have facilitated an ancient hybridization, and the genetic input of *B. bison* bulls in wisent herds is in accordance with the fossil record (Flerov, 1979; Harington, 1996; Kurtén, 1968;

McDonald, 1980; Pucek, 1986, 1991; Skinner & Kaisen, 1947; Soubrier et al., 2016; Verkaar et al., 2004). For an interpretation of the data based on incomplete lineage sorting, see Wang et al. (2018). A new term for a specific kind of speciation was introduced, transpatry, which is a phenomenon unique for species living in herds with female philopatry, and few dominating males (Verkaar et al., 2004). Although still hypothetical, it is probably also present in the evolution of deer (Cathey et al., 1998), macaques (Tosi et al., 2000), and the domestic alpaca (Kadwell et al., 2001).

The reticulating evolutionary histories of hybrids can make it difficult to place them correctly in phylogenetic trees. Therefore, when hybridization may have occurred, such as in the case of wisent and American bison or *R. eldii* /*R. duvaucelii*, phylogenies should always be reconstructed by means of both mtDNA and nDNA analyses.

5.2.3 | Morphology

Elaphurus has traits atypical of cervids, such as a long tail and antlers with reversed orientation (Zhang et al., 2018). It also shows little to no morphological resemblance with *Cervus* and *Rusa* (Wemmer, 1983), which was confirmed by craniometrical analyses (Meijaard & Groves, 2004). The latter study also suggested that *R. eldii* represents a different evolutionary lineage than *R. duvaucelii* and *R. schomburgki*.

Pocock (1943) suggested a closer relationship of *Elaphurus* with *Rucervus* based on the branching of the tree. He provided a detailed phenotypic description of the three *Rucervus* species, highlighting specific and subspecific differences and suggested assigning them to three different genera. Although we agree with his accounts on the morphology, we find the three *Rucervus* species more similar to each other than to any other cervid, particularly concerning dental morphology (Heckeberg, 2017b, 2020), which was not considered by Pocock (1943).

According to Groves and Grubb (1987) *Elaphurus* and *R. eldii* share a more flexed skull, smaller canines and higher-crowned teeth compared with other cervids. Further comparisons by Groves and Grubb (1987) demonstrated that the antlers of *R. eldii* are more similar to those of *A. axis* than *Rusa unicolor*, and that *R. eldii* has a deep lacrimal fossa, similar to *Rusa*, while *R. duvaucelii* has a shallower lacrimal fossa.

Detailed description and comparison of the craniodental morphology of *Elaphurus* and *Rucervus*, including antlers, and subsequent phylogenetic analyses show that *R. duvaucelii* and *R. eldii* share similarities in the M3, p4, lower molars, mandibular characters, proportions of the palate, positions of lacrimal foramina and characters of the

basioccipital (Heckeberg, 2017b, 2020). In phylogenetic trees based on morphological data, the position of *Elaphurus* was often nested within a clade including also *Rucervus* and *Rusa* that was diagnosed predominantly by dental and some cranial characters. Ghazanfarullah et al. (2021) stated that the morphological similarities between the three *Rucervus* species possibly represent convergence rather than phylogenetic relatedness.

As discussed, *Elaphurus* has a unique antler morphology (Figures 4 and 6), different from any other cervid, which is also not intermediate between that of its supposed parent species, a phenomenon called transgressive segregation (Groves, 2014; Lydekker, 1898). Similarities of the antlers of *Elaphurus* and *Rucervus eldii*, which were claimed to exist by Samejima and Matsuoka (2020), are not supported by comparative morphology (Heckeberg, 2017b, 2020; Pocock, 1943). The antler morphologies of *R. eldii* and *R. duvaucelii* are similar, and especially more similar to each other than to *E. davidianus* (Figure 6). For these reasons, we consider it inappropriate to classify *R. eldii* in a separate genus (*Panolia*) as is often suggested (Ghazanfarullah et al., 2021; Groves & Grubb, 2011; Kumar et al., 2021; Samejima & Matsuoka, 2020; Turvey et al., 2017; Wong et al., 2021).

6 | PERSPECTIVES AND CONCLUSIONS

The homology of antler structures, based on the scheme proposed by Pocock (1933), has gained wide acceptance and we encourage the use of this scheme. Some remaining unsolved problems and controversies in antler tine homology concern the presence of a brow tine in certain species (e.g., *Capreolus*, *Odocoileus*), the classification of adult spike antlers, and the homology of antler structures in *Elaphurus* and *Odocoileus* with those of other deer species. Decoding the genetic basis of the species-specific antler bauplan may shed more light on this topic in the future. It would also be interesting to test how much phylogenetic signal is contained in the visualizations of the antler branching patterns proposed by Samejima and Matsuoka (2020).

Based on quantitative and qualitative analyses of the systematic relationships of *R. eldii* and *E. davidianus* and considering that the latter species may have originated from an ancient hybridization event, we conclude that *R. eldii* is more closely related to its congeners than to any other deer species, resulting in a monophyletic genus *Rucervus*. The correct systematic position of *Elaphurus* remains a challenge; the taxon exhibits molecular characters of *Cervus* and *Rucervus* and therefore, will often be placed close to one of them in phylogenetic analyses. However, its position would logically be as a separate lineage between a clade including *Cervus* and another one including *Rucervus*.

In general, conflicting systematic hypotheses and discrepancies between two or more topologies and datasets need to be accounted for, especially if they are chosen as the basis of a study design. Just including more data of the same type (e.g., more mtDNA sequences) will then not provide a solution but only tend to confirm previous biased (non-independent) results. Integration and evaluation of the different and potentially conflicting results from molecular and morphological studies are indispensable when investigating and interpreting systematic relationships and evolutionary histories.

AUTHOR CONTRIBUTIONS

Nicola S. Heckeberg: Conceptualization (equal); investigation (equal); project administration (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Frank E. Zachos:** Conceptualization (equal); investigation (equal); writing – original draft (supporting); writing – review and editing (equal). **Uwe Kierdorf:** Conceptualization (equal); investigation (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

ACKNOWLEDGMENTS

We thank K. McKay and A. Hartstone-Rose for handling our submission and three anonymous reviewers for their constructive comments on the manuscript. We are grateful to L. Costeur (NMB Basel), J. Lesur (MNHN Paris), A. Kitchener (NMS Edinburgh), R. Portela Miguez (NHM London), F. Mayer, Christiane Funk (MfN Berlin), and M. Hiermeier (ZSM Munich) for providing access to the investigated specimens. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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How to cite this article: Heckeberg, N. S., Zachos, F. E., & Kierdorf, U. (2023). Antler tine homologies and cervid systematics: A review of past and present controversies with special emphasis on *Elaphurus davidianus*. *The Anatomical Record*, *306*(1), 5–28. <https://doi.org/10.1002/ar.24956>