

Spontaneous Article

Proposal of the colour pattern reconstruction of basal cervids

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ABSTRACT: Methodologies that analyse the colouration and external appearance of extant species are very useful tools when facing one of the greatest challenges in the palaeoartistic reconstructions of extinct fauna: inferring the colour patterns. Earlier works have applied this methodology, for example, in the reconstruction of the Miocene bovid *Tethytragus*, proving that the maximum likelihood (ML) analysis to infer ancestral states has promising potential. This study offers a proposal for the reconstruction of the external appearance of *Heteroprox moralesi* Azanza 1989, an early cervid of the Middle Miocene present in several fossil sites of Central Spain. For the reconstruction of the external appearance, the colour patterns of all the extant species of the family Cervidae were studied with the method of ML analysis, as well as recent works about their phylogeny. The results show the most probable basal colour pattern of the cervids: dark shades on the limbs, dorsal section, and head of the animal, and, in contrast, lighter colours on the neck and perianal region. This basal pattern can be used as a basis for reconstructing colouration and to hypothesise about the external appearance of extinct taxa. Furthermore, the inferred forest habitat of *H. moralesi* has been taken into consideration in order to adjust the colour pattern, comparing the final results of the analysis performed in this study with that of the pattern observed in extant forest deer as well as with previous works employing this methodology.



KEY WORDS: Cervidae, colour patterns, mammalia, palaeoart, phylogeny.

Palaeoart is considered a discipline that can provide valuable information, combining graphic arts and science in order to create images of the reconstruction of extinct animals and their environments with scientific rigour. The methodology currently used for the reconstruction of fossil vertebrates is based on the sequential anatomical reconstruction proposed by Antón & Sánchez (2004). It can be divided into different stages: the identification of the osteological correlations imprinted by soft tissue; the anatomically accurate reconstruction of the bones using comparative anatomy; the inference of muscle insertions – and other soft tissues such as fat, cartilage and tendons – from the basis of the previous osteological reconstruction; and the proposal of the external appearance, such as the skin, colour pattern and, in the case of extinct mammals, hair. Therefore, comparative anatomy becomes an extremely useful tool that allows to infer the live appearance of a fossil taxon.

As could be expected, certain characters that are rarely preserved, and leave little to no evidence of how they would appear in the living organism, present some constraints for their reconstruction. Such as is the case for the trait analysed in this study: the colour pattern in extinct mammals.

Colour pattern is a character that is influenced by an extensive array of variables, such as natural or sexual selection (sometimes both), climate, habitat, behaviour, phylogenetic relationships, body size of the animals or pigment economy, among other factors (Bortolotti 2006; Pérez González *et al.* 2009; Brown *et al.* 2017; Negro *et al.* 2018), and therefore, whose analysis is complex. In the vast majority of fossils, physiological characters, for example, melanosome and carotenoid concentrations, structural colour, and molecular signals (Vinther *et al.* 2010; McNamara *et al.* 2011, 2012, 2018; Li *et al.* 2012; Brown *et al.* 2017; Negro *et al.* 2018; Pan *et al.* 2022), that might indicate

the colouration of the taxon, are not preserved. This is further the case in fossil mammals, in which environmental and organic degradation make it very difficult for structures such as hair or skin to be well preserved (Tridico 2015). In particular, the colouration of the latter characters provides information on the behaviour of the animal, how it related intraspecifically and interspecifically, or how it interacted with its environment. As mentioned in Pérez González *et al.* (2009, and references therein), although climate and habitat have certain influence in the colouration of mammals, another determining factor is the phylogeny of the studied taxon, where the phylogenetic signal responsible for observed patterns of colouration might serve as a reliable source that allows to reconstruct the external appearance of select extinct taxa.

Therefore, phylogenetic information, from an actualist approach, when applied to palaeoartistic reconstructions, can provide to be a very useful frame of reference for making well supported inferences. Specifically, phylogenetically close taxa – current and extinct – give valuable information on the appearance or morphology of anatomical features that would otherwise not be evident nor preserved in the fossil record (Byrant & Russell 1992; Witmer 1995).

Previous works have shown that phylogenetic analyses performed to study coloration patterns are a successful tool, often leading to either palaeoartistic reconstructions, or to understanding the coat pattern evolution within the studied groups. Some examples of such works, which focused on the colour pattern of mammals, include carnivorans (Ortolani & Caro 1996; Werdelin & Olsson 1997; Ortolani 1999; Mattern & McLennan 2000; Werdelin *et al.* 2010), lagomorphs (Stoner *et al.* 2003a), rodents (Lai *et al.* 2008; Ancillotto & Mori 2017) and artiodactyls (Stoner *et al.* 2003b; Caro *et al.* 2004; Pérez González *et al.* 2009).

For the scope of this study, we focus on the order Artiodactyla, specifically the family Cervidae, a group of small to large herbivore mammals that includes 54 extant species (Burgin *et al.* 2020). In particular, Cervidae present a complicated case study for the determination of coat pattern, since there are extensive factors that contribute to the observed phenotypes. One of the influencing factors to consider is intraspecific variation which is present in many other mammalian groups. Additionally, the ontogeny of the individual is involved, as in other artiodactyls, although it is highly noticeable in this group (Fig. 1a). Furthermore, the colour arrangement in specimens varies considerably between different populations of the same species (Fig. 1b). Finally, the colour variations occurring between winter and summer coats are extreme in many cervids (Fig. 1c), unlike in other artiodactyls, although not all genera experience a significantly noticeable change between these two seasons. Conversely, differences in colour pattern as a result of sexual dimorphism are not as marked in this group as they are in, for example, some genera of bovids.

However, despite these limitations, the large number of species and the relatively well resolved phylogenetic relationships within Cervidae (Heckeberg 2020), makes this family an ideal group for the aim of this work, offering a good framework to test the evolution and phylogenetic signal of their colour patterns.

The taxon used to test the inference of the colour pattern in an extinct cervid is *Heteroprox moralesi* Azanza 1989, a basal deer from the Middle Miocene of Central Spain. Its phylogenetic position close to the base of the family Cervidae makes it ideal to be the subject of an analysis of the basal coloration of this group (Heckeberg 2020).

Heteroprox comprises four Eurasian species of medium-sized cervids characterised by the presence of small proto-antlers with 2–3 ramifications, elongated extracranial, supraorbital pedicles, with a relatively smooth surface, and with an ornamentation

consisting of fine striae. Males had well-developed canines (Azanza 1989; Rössner 2010; Heckeberg 2017), as occurs in other species of Cervidae, in either extinct (such as *Procervulus*) or extant groups (such as *Muntiacus* or *Elaphodus*).

Further classification of the genus *Heteroprox* placed it within the subfamily Procervulinae, together with the cervid *Procervulus*, and considered it as basalmost in regards to its phylogenetic relationships within family Cervidae, as is suggested by various authors (Vislobokova 1983; Azanza 1989, 1993; Rössner 1995; Gentry *et al.* 1999; Mennecart *et al.* 2016, 2017). However, other works classify *Heteroprox* as belonging to the Dicrocerini tribe, as they find it to have a greater resemblance to the genus *Dicrocerus* (Bubenik & Bubenik 1990; Grubb 2000). The phylogenetic analysis done by Heckeberg (2020) also places *Heteroprox* close to both *Procervulus* and *Dicrocerus*, in a position close to the Muntiacini tribe, which would place them close to the crown group of extant cervids.

In this study, for the purpose of estimating the phylogenetic position of *Heteroprox*, we choose to follow the criteria of considering *Heteroprox* a member of Procervulinae to estimate its phylogenetic position since, of the two, this proposal is the most agreed upon classification and has been extensively supported. In this context, we perform a character trace analysis using the well understood phylogeny of the family Cervidae, relating extinct species with extant ones; the latter for which colouration pattern information is available. From this analysis, the objective of the present work is to produce a tentative reconstruction of the coat colour pattern of basal cervids, such as *Heteroprox* and its closely related taxa.

1. Materials and methods

The methodology used in this work largely follows the one proposed by Pérez González *et al.* (2009) for the colour pattern reconstruction of the Middle Miocene bovid *Tethytragus*, which is recorded in association in some fossil sites to *Heteroprox*. The analysis employed to infer the ancestral states was the maximum likelihood (ML) (Maddison & Maddison 1989), using software Mesquite version 3.61 (Maddison & Maddison 2021), an analysis which assumes the least number of changes in the character (in this case, the colours) to explain the distribution of states of that character in the taxa that can be observed at the extreme points of the phylogenetic tree (Pérez González *et al.* 2009). ML analysis, combined with Markov algorithms, takes into account the length of the phylogenetic tree branches, in order to infer which character or characters of the studied taxa emerged from a specific ancestor. The most probable percentages of each character in a node between two phylogenetic branches are shown.

The ancestor of all the extant cervids, referenced in this study as the hypothetical ancestor, was used as the most closely related taxon to *Heteroprox* and to other Miocene cervids. These basal cervids were more closely related between them than with the extant cervids, as the work of Heckeberg (2020) shows. This makes it necessary to have an accurate phylogenetic tree of the extant cervids. We followed Heckeberg (2020) as the main source of information; Meijaard & Groves (2004) for the genus *Axis*; Świsłocka *et al.* (2020) for the genus *Alces*; and Zhang *et al.* (2021) for the genus *Muntiacus*.

A total of 51 species of cervids belonging to the two extant subfamilies, Cervinae and Capreolinae, were analysed in order to create a thorough coat colouration database. To follow a same criterion, only images of fully grown adult males were used, to treat the data homogeneously. Also, only the colour pattern for the summer coat of the taxa was considered, since *H. moralesi* is associated with warm environments (López-Martínez *et al.* 2000), and most likely experienced little

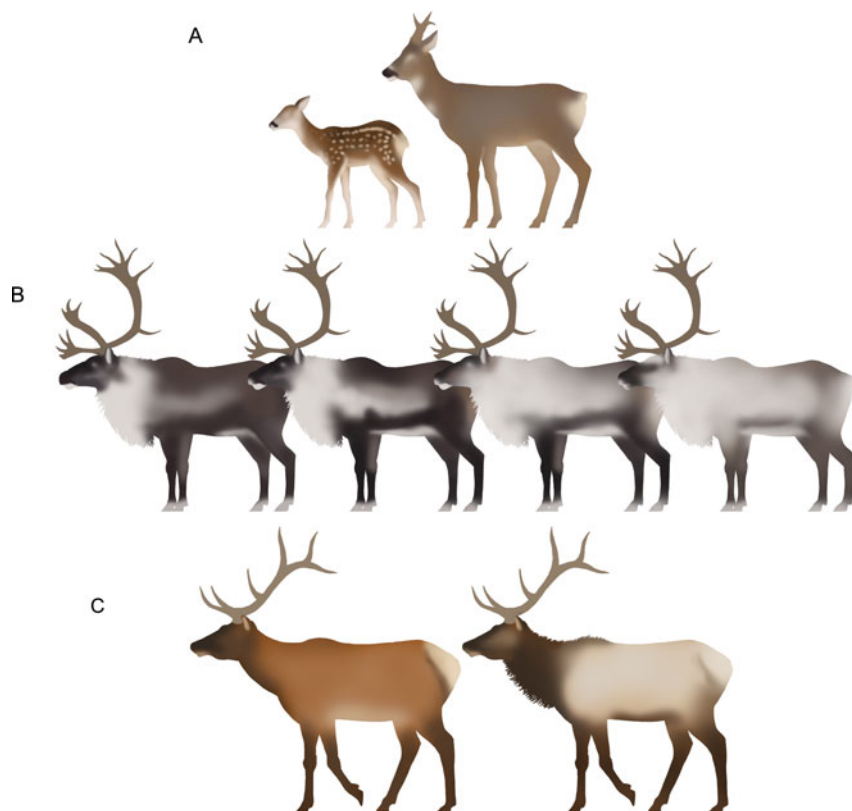


Figure 1. Different colour pattern variations in Cervidae. (a) Ontogeny (*Capreolus capreolus*, fawn, left, and adult, right). (b) Different populations and/or subspecies of the same species (winter coat of *Rangifer tarandus*, from left to right, *Rangifer tarandus caribou*, *Rangifer tarandus groenlandicus*, *Rangifer tarandus tarandus* and *Rangifer tarandus platyrhynchus*). (c) Seasons of the year (*Cervus canadensis*, summer coat, left, and winter coat, right). Not to scale. Illustrations by Jesús Gamarra.

to no discernible changes of coat during the winter. Moreover, the colouration patterns of the summer coat were selectively used because they are present during the season in which male individuals are at their maximum sexual maturation stage and where the expression of characters (e.g., antlers, colourful coats, etc.) is most conspicuous in preparation for the breeding season.

Several images were retrieved for each of the different species, obtained from Google Images. Quality profile photographs were selected with comparable light conditions, except for those of *Mazama chunyi*, *Muntiacus malabaricus*, *Muntiacus putaonensis* and *Muntiacus truongsoneensis*, for which case the illustrations as shown in Burgin *et al.* (2020) were consulted, since quality images with discernible colour pattern for these taxa were not available.

Some species were discarded in this analysis: *Mazama bricenii* as it is possibly a junior synonym of *Mazama rufina* (Heckeberg 2020, and references therein); *Muntiacus rooseveltorum* as it is considered a junior synonym of *Muntiacus feae* (Heckeberg 2020, and references therein); *Muntiacus puhoatensis* since no studies have been found that clarify its systematics; and *Rucervus schomburgki* as it is extinct and no adequate images of its fur could be found, since taxidermy specimens lose their original colouration over time.

To study the colour variations occurring in the same specimen, a schematic template of a general cervid was made (Fig. 2) based on the bovid template created by Pérez González *et al.* (2009) with some modifications. This template sectors the different parts of the body of a cervid where the most common colour changes observed in cervid colour pattern are placed, 26 in total. This template was coloured for each species studied, painting it in flat colours without considering the volume (i.e., lights and shadows) so that the colour pattern was studied uniformly and without alterations.

Once the template of a species was coloured, saturation was reduced to the minimum to obtain a grey scale drawing (Fig. 3b). Using grey scales allow to evaluate the same criteria in the study for each sector in the different species. As each shade in a grey scale can be attributed to a specific and unique colour code, the Adobe Photoshop dropper tool was used to identify the colour code (value) for each shade. The average colour of each sector was then selected and compared with a reference grey scale table (Fig. 3a), which allowed for a more objective determination, rather than just a visual assessment.

The reference grey scale table used is divided into five shades, which represent a range of values: white; light; neutral; dark; and black. The shade values obtained from the image sampling of individuals, were then assigned to one of the five shade categories within the reference greyscale table. The results were then added to the database, a value was assigned to each shade, obtaining a total of 10 values: white (1); light (2); neutral (3); dark (4); black (5); contrasted (6); spotted light (7); spotted neutral (8); spotted dark (9); and spotted black (10). The values of the first five shades were taken from the template of the species *Axis axis* (Fig. 3b), as it has all the grey shades in its colour pattern, from pure white to deep black.

Once the database was completed with all the species, a ML analysis of ancestral states was performed.

2. Results

In Table 1, the results are shown as the most likely percentage for each shade of each sector to appear in the basal node for all extant Cervidae, and further represent the probability of the hypothetical basal cervid ancestor having that colouration.

To follow a criterion, the sectors considered to have significant values are those with at least twice or more the value than the

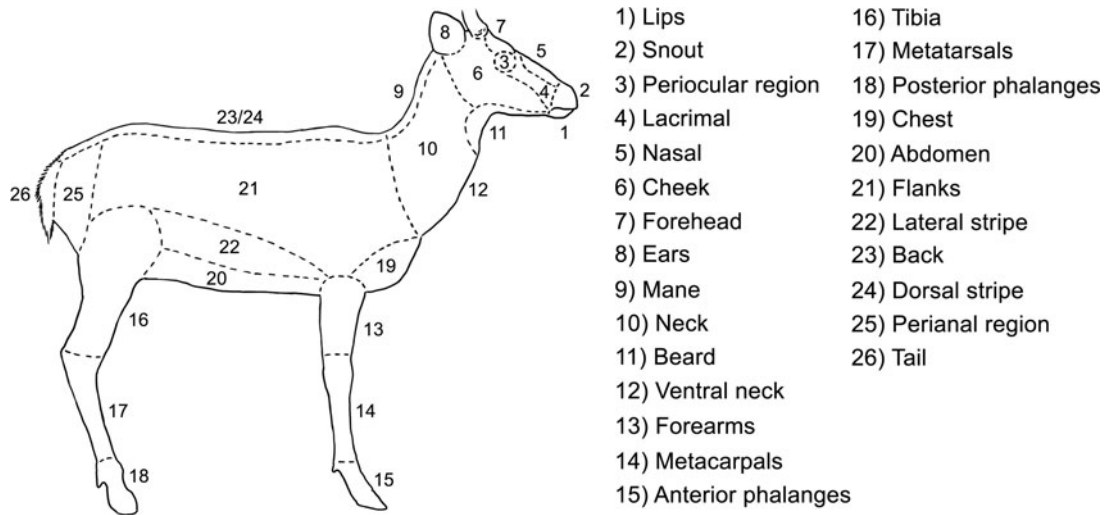


Figure 2. Body sectorisation of a generic cervid used in this work. Based on Pérez González *et al.* (2009).

next highest value (which represents the next most likely shade), and were considered as the final results for that sector. These sectors are shown as in Fig. 4a. Sectors not showing significant values (as the cases aforementioned) were studied separately, and appear in white (see Fig. 4a). In the analysis, these sectors were: 7, forehead; 10, neck; 11, beard; 12, dewlap; 13, forearm; 14, metacarpals; 16, tibia; 17, metatarsals; 20, abdomen; 22, side stripe; 24, dorsal stripe; and 26, tail.

Therefore, to assess the shades of sectors with ambiguous results, and complement the results which did show significant values, further information was needed. Consequently, additional factors affecting colour pattern in *H. moralesi*, such as its inferred habitat, were evaluated.

Heteroprox, as most cervids, inhabited forested areas (López-Martínez *et al.* 2000). While the other Eurasian *Heteroprox* species were known to live in humid forests, the conditions during the Middle Miocene in much of the Central Iberian Peninsula were significantly arid or even semi-desertic (Fesharaki 2016; Menéndez *et al.* 2017). Therefore, the habitats of *H. moralesi* were most likely forest patches near savannas and arid environments. Some current biomes that resemble *Heteroprox* habitats are savannas, deciduous tropical forests and Mediterranean forests.

Taking this into consideration, we should expect to see some similarity to *H. moralesi* in the assortment of shades in extant deer species inhabiting the three types of biomes. We then selected shade values (colour code) of several extant deer species

that live within those biomes, in order to infer which colouration *Heteroprox* was most likely to have in these problematic sectors based on its habitat. Species habitat information was obtained from Myers *et al.* (2022): those living in savanna are *Axis axis*, *Axis porcinus*, *Blastocercus dichotomus*, *Dama dama*, *Dama mesopotamica*, *Mazama americana*, *Mazama gouazoubira*, *Muntiacus muntjak*, *Rucervus duvaucelii*, *Odocoileus hemionus* and *Odocoileus virginianus*; in deciduous tropical forests, *A. axis*, *A. porcinus*, *Blastocercus dichotomus*, *Hydropotes inermis*, *M. americana*, *M. gouazoubira*, *Muntiacus muntjak*, *Muntiacus reevesi*, *Rucervus duvaucelii*, *Rucervus eldii*, *Rusa timorensis*, *Rusa unicorn* and *O. virginianus*; and in Mediterranean forests, *Capreolus capreolus*, *Cervus elaphus*, *D. dama*, *D. mesopotamica* and *Odocoileus hemionus*.

For each one of the biomes, we selected the most common colouration for each ambiguous sector (refer to Table 2) most frequently observed among the different species. The results showed that the predominant shades for the sectors evaluated were similar across all selected biomes. Based on the shades of the compared extant cervids for these arid habitats, new supporting data was obtained which was compared to the previous results (the shades showing similar values, or no significant values; see Table 1), which allowed us to determine the final colour pattern proposed for the ambiguous sectors.

The results for the ambiguous sectors were as follows: 7, forehead, dark to black; 10, neck, neutral; 11, beard, white; 12, dewlap, light; 13, forearm, dark; 14, metacarpals, dark to black; 16,

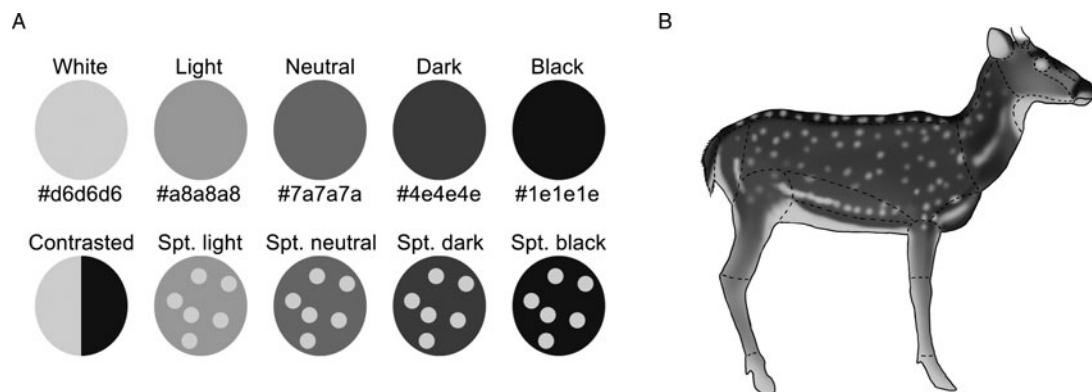


Figure 3. Grey scales used in this work. (a) Grey shades used in this work. Under the top five are their colour codes. Contrasted is where, in a same sector, abrupt changes from light to dark shades can be found. (b) Example of a grey coloured template (in this case, the species is *Axis axis*). Abbreviation: Spt. = spotted.

Table 1. Sectors with the probabilities of appearance of each grey shade in the basal node of the family Cervidae, where *Heteroprox* would be found.

Sectors/shades	Wh	Li	Ne	Da	Bl	Co	Sp. Li	Sp. Ne	Sp. Da	Sp. Bl
1) Lips	0.554	0.108	0.045	0.043	0.094	0.156	–	–	–	–
2) Snout	0.026	0.028	0.028	0.030	0.044	0.845	–	–	–	–
3) Periocular region	0.029	0.678	0.151	0.086	0.029	0.030	–	–	–	–
4) Lacrimal	–	0.100	0.140	0.600	0.171	–	–	–	–	–
5) Nasal	–	–	0.040	0.809	0.109	0.042	–	–	–	–
6) Cheek	–	0.017	0.739	0.200	0.028	0.016	–	–	–	–
7) Forehead	–	–	0.175	0.350	0.307	0.168	–	–	–	–
8) Ear	0.403	0.200	0.152	0.098	0.148	–	–	–	–	–
9) Mane	–	–	0.194	0.550	0.257	–	–	–	–	–
10) Neck	–	0.073	0.121	0.450	0.062	0.230	0.064	–	–	–
11) Beard	0.237	0.313	0.163	0.114	0.113	0.055	–	–	–	–
12) Dewlap	0.214	0.230	0.157	0.201	0.198	–	–	–	–	–
13) Forearm	–	–	0.190	0.245	0.368	0.197	–	–	–	–
14) Metacarpals	0.075	0.190	0.090	0.179	–	0.154	–	–	–	–
15) Anterior phalanges	0.067	0.120	0.055	0.621	0.086	–	–	–	–	–
16) Tibia	–	–	0.088	0.546	0.256	0.043	–	0.067	–	–
17) Metatarsal	0.084	0.154	0.099	0.231	0.296	0.136	–	–	–	–
18) Posterior phalanges	0.057	0.107	0.043	0.038	0.692	0.067	–	–	–	–
19) Chest	0.113	0.123	0.137	0.103	0.433	0.091	–	–	–	–
20) Abdomen	0.158	0.357	0.125	0.201	0.159	–	–	–	–	–
21) Flanks	–	–	0.042	0.725	0.070	–	–	0.029	0.107	0.027
22) Side stripe	–	–	0.281	0.183	0.466	–	0.017	0.018	0.017	0.016
23) Back	–	–	0.043	0.709	0.102	0.102	–	–	0.060	0.087
24) Dorsal stripe	–	–	0.087	0.530	0.382	–	–	–	–	–
25) Perianal region	0.036	0.087	0.050	0.114	0.088	0.625	–	–	–	–
26) Tail	0.030	0.210	0.029	0.028	0.116	0.588	–	–	–	–

Values and sectors in boldface type are those that are highly significant. To reduce the table size, values were rounded to the third decimal place. Abbreviations: Wh = white; Li = light; Ne = neutral; Da = dark; Bl = black; Co = contrasted; Sp. Li = spotted light; Sp. Ne = spotted neutral; Sp. Da = spotted dark; Sp. = black.

tibia, dark; 17, metatarsals, dark to black; 20, abdomen, light; 22, side stripe, neutral; 24, dorsal stripe, black; and 26, tail, contrasted.

The result for *Heteroprox* general colouration shows an animal with a slight general countershading dorsoventrally, as is usual in most cervid species and appears in many other animals. This type of colouration is very common in the animal kingdom since, as mentioned by Cott (1940), it is the basis of camouflage in both predators and prey.

Nonetheless, the results of the countershading in this work indicate further variation, also varying anteroposteriorly, with the neck and the head presenting neutral tones – to the exception

of the upper part of the neck – while the rest of the body would appear darker in tone. This may be due to the fact that, much like the countershading of the abdomen, a slightly lighter colouration on the anteroventral sector of the neck would have been more favourable for blending in, as it would counteract the effect of the shadow – usually produced in areas at an angle less exposed to the sunlight – making it less noticeable by reducing its contrast against the rest of the body (Stoner *et al.* 2003b; Rowland 2009). As seen from the results in Table 2, the beard (11) and dewlap (12) sectors are usually light in the more frequent phenotype of the species from the two most open environments, the savanna and Mediterranean forest, in

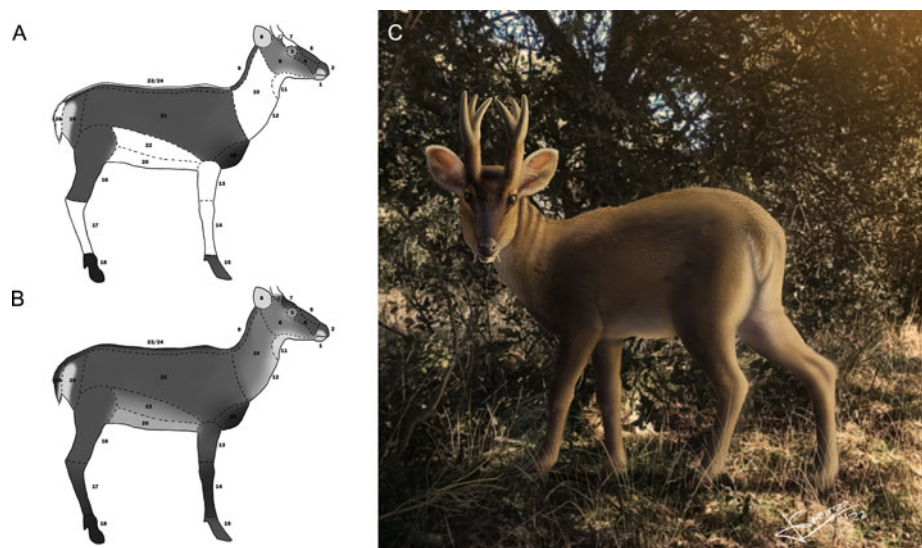


Figure 4. Results of the analysis shown in the template. (a) Sectors with the significant values (coloured) with the problematic sectors (in white). (b) Final result in the template. (c) Palaeoartistic reconstruction of *Heteroprox moralesi* with the results of this study. Illustration by Jesús Gamarra.

Table 2. Results of the problematic sectors analysis according to the habitat.

Biomes	Sectors/shades	Wh	Li	Ne	Da	Bl	Co	Sp. Li	Sp. Ne	Sp. Da	Sp. Bl
Savanna	7) Forehead	–	–	0.18	0.37	0.36	0.09	–	–	–	–
	10) Neck	–	–	0.64	–	–	0.27	0.09	–	–	–
	11) Beard	0.64	0.36	–	–	–	–	–	–	–	–
	12) Dewlap	0.27	0.37	0.36	–	–	–	–	–	–	–
	13) Forearm	–	–	0.37	0.36	0.18	0.09	–	–	–	–
	14) Metacarpals	0.09	0.27	0.27	–	0.37	–	–	–	–	–
	16) Tibia	–	–	0.18	0.55	–	–	–	0.27	–	–
	17) Metatarsal	0.18	0.18	0.18	0.18	0.28	–	–	–	–	–
	20) Abdomen	0.37	0.27	0.27	0.09	–	–	–	–	–	–
	22) Side stripe	–	–	0.55	0.09	–	–	0.09	0.09	0.18	0.09
24) Dorsal stripe	–	–	0.27	0.27	0.46	–	–	–	–	–	
26) Tail	0.18	–	–	0.09	0.09	0.64	–	–	–	–	
Deciduous tropical forest	7) Forehead	–	–	0.15	0.31	0.39	0.15	–	–	–	–
	10) Neck	–	0.08	0.61	0.15	–	0.08	0.08	–	–	–
	11) Beard	0.46	0.46	–	–	0.08	–	–	–	–	–
	12) Dewlap	0.08	0.46	0.34	–	0.08	–	–	–	–	–
	13) Forearm	–	–	0.39	0.38	0.23	–	–	–	–	–
	14) Metacarpals	–	0.23	0.23	0.15	0.39	–	–	–	–	–
	16) Tibia	–	–	0.31	0.54	0.07	–	–	–	–	–
	17) Metatarsal	–	0.23	0.15	0.31	0.31	–	–	–	–	–
	20) Abdomen	0.31	0.38	0.15	0.08	0.08	–	–	–	–	–
	22) Side stripe	–	–	0.54	0.15	–	–	0.08	0.15	0.08	–
24) Dorsal stripe	–	–	0.23	0.31	0.46	–	–	–	–	–	
26) Tail	0.07	0.08	0.08	0.08	0.23	0.46	–	–	–	–	
Mediterranean forest	7) Forehead	–	–	0.20	0.40	0.40	–	–	–	–	–
	10) Neck	–	–	0.60	–	–	0.40	–	–	–	–
	11) Beard	0.60	0.40	–	–	–	–	–	–	–	–
	12) Dewlap	0.40	0.40	0.20	–	–	–	–	–	–	–
	13) Forearm	–	–	0.40	0.40	–	0.20	–	–	–	–
	14) Metacarpals	0.20	0.20	0.40	0.20	–	–	–	–	–	–
	16) Tibia	–	–	0.40	0.20	–	–	–	0.40	–	–
	17) Metatarsal	0.40	0.40	0.20	–	–	–	–	–	–	–
	20) Abdomen	0.40	0.20	0.40	–	–	–	–	–	–	–
	22) Side stripe	–	–	0.40	0.20	–	–	0.20	0.20	–	–
24) Dorsal stripe	–	–	0.60	–	0.40	–	–	–	–	–	
26) Tail	0.40	–	–	–	–	0.60	–	–	–	–	

Colour abbreviations are the same as in Table 1. Values in boldface type are the chosen ones when certainly significant compared to the other values of the likelihood analysis.

comparison to those of the more closed and denser deciduous tropical forest. The shade values of the former (i.e., species from the savanna and Mediterranean forest) were then given preference as a source of reference and were, consequently, used to fill the gaps in the ambiguous-resulting sectors for the reconstruction of *Heteroprox*. The lighter shades in these sectors would suggest that the colouration patterns in *Heteroprox* were more transitional at the head and at the neck, and thus less conspicuous to potential predators, an advantageous morphological trait in the more exposed areas of open vegetation.

The results for *Heteroprox* also suggest that some sectors were darker in comparison to the rest of the general body colour, more distinctively the extremities, dorsal parts of the head and neck, and the dorsal stripe on the back. Darker limbs, which serve in extant cervids as a form of disruptive colouration, are associated with large social groups, open environments and desert habitats (Stoner *et al.* 2003b) and might have aided *Heteroprox* in intra-specific communication. The results for the perianal region and tail sectors further produce a more evident contrast, and result in a conspicuous colouration pattern. Many extant cervids have these strongly contrasted areas, or are directly white (either only on the inner part or on the entire tail). In some species such as *O. virginianus*, for example, this colouration serves for communication when a predator is detected (Blindstein 1983). It may be that in *Heteroprox*, if it had any gregarious nature, that could have served to make other individuals aware of its presence, or to warn of a nearby danger.

Thus, the final colour pattern reconstruction is obtained from the results, as shown in the Fig. 4b template. Overall, *Heteroprox* had a pelage with darker tones and countershading yet some areas in which the colour patterns were more conspicuous. This darker colouration might have served *Heteroprox* and, therefore, basal cervids to go unnoticed among the foliage of the forests where they lived. The countershading could have aided with camouflage, blending its colouration among the warm forest patches near a semiarid savanna (Fig. 4c).

3. Conclusion

The ML analysis to infer ancestral states proved to be an excellent tool that allows to obtain reliable results, with phylogenetic support, when choosing which colour pattern to apply to represent an extinct taxon, whenever extant relatives are available. This is considerably one of the most significant, conditioning factors of the methodology: the need to have a great diversity of extant species from which to obtain the data. Accordingly, in order to have stronger and more reliable results, the methodology should be restricted to groups with a great number of extant species.

Also, as referenced in the work of Pérez González *et al.* (2009), the colouration patterns proposed from this methodology are not definitive, but rather supported by a solid framework meant to provide the palaeoartist, through valuable phylogenetic data, a starting point to reconstruct extinct animals.

This work represents the first time that the colour patterns of the family Cervidae have been analysed using ML analysis, having studied the shades of the vast majority of extant cervid species with the objective of obtaining a basal colouration pattern for the entire family. In this way, the results from this study yield valuable insight on the colouration patterns of basal cervids most likely expressed, a key morphological trait with potential to enhance our understanding of their behaviour, life strategies and interactions with its environment.

The final reconstruction scheme, based on the results, suggest that *H. moralesi* had an overall dark shade, dorsoventral counter-shading both in the abdomen and in the neck, distinctively dark limbs, a dorsal stripe of the back, and a conspicuously white tail and perianal region, the latter two which contrasted the rest of its body. The set of colouration and patterns would have served *Heteroprox* in concealment, to camouflage its silhouette against the background where it inhabited among the warm forest vegetation, and when crossing the savanna from one patch of vegetation to the next. Moreover, the more conspicuous patterns such as the white tail and the much darker limbs would have most likely served *Heteroprox* for intraspecific communication.

4. Supplementary material

Supplementary material is available online at <https://doi.org/10.1017/S1755691023000026>.

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7. Competing interest

No.

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