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RESEARCH ARTICLE

A potential link between lateral semicircular canal orientation, head posture, and dietary habits in extant rhinos (Perissodactyla, Rhinocerotidae)

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Abstract

Extant rhinoceroses share the characteristic nasal horn, although the number and size of horns varies among the five species. Although all species are herbivores, their dietary preferences, occipital shapes, and common head postures vary. Traditionally, to predict the "usual" head posture (the most used head posture of animals during normal unstressed activities, i.e., standing) of rhinos, the occipital shape was used. While a backward inclined occiput implies a downward hanging head (often found in grazers), a forward inclined occiput is related to the horizontal head posture in browsing rhinos. In this study, the lateral semicircular canal (LSC) of the bony labyrinth was virtually reconstructed from μCT-images in order to investigate a possible link between LSC orientation and head posture in extant rhinoceroses. The usual head posture was formerly reconstructed for several non-rhinoceros taxa with the assumption that the LSC of the inner ear is held horizontal (parallel to the ground) during normal activity of the living animal. The current analysis of the LSC orientation resulted in a downward inclined usual head posture for the grazing white rhinoceros and a nearly horizontal head posture in the browsing Javan rhinoceros. The other three browsing or mixed feeding species show subhorizontal (closer to horizontal than a downgrade inclination) head postures. The results show that anatomical and behavioral aspects, like occipital shape, presence and size of horns/tusk-like lower incisors, as well as feeding and feeding height preferences influence the usual head posture. Because quantitative behavioral data are lacking for the usual head postures of the extant rhinos, the here described relationship between the LSC orientation and the resulting head posture linked to feeding preferences gives new insights. The results show, that the inner ear provides additional information to interpret usual head postures linked to feeding preferences that can easily be adapted to fossil rhinoceroses.

KEYWORDS
bony labyrinth, feeding preferences, inner ear, Javan rhinoceros, white rhinoceros

1 | INTRODUCTION

First appearing in the Eocene and flourishing in the Oligocene (Dinerstein, 2011), the rhinoceros diversity is reduced to only five species today, two African and three Asiatic (Harley, de Waal, Murray, & O'Ryan, 2016; IUCN, 2016). The presence and number of horns is traditionally important for systematics, biological significance, or wildlife protection of rhino populations (Dinerstein, 2011). Extant rhinoceroses [i.e., two African species, the white rhinoceros (*Ceratotherium simum*) and the black rhinoceros (*Diceros bicornis*), and three Asiatic species, the Indian rhinoceros (*Rhinoceros unicornis*), the Javan rhinoceros (*Rhinoceros sondaicus*), and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*)] are all herbivores with differences in tooth morphology, tooth formula, and preferred diet (see Supporting Information Table S1 and references therein). Past studies focusing on extant and fossil rhinoceros head postures used to test the combination of different features like the presence and size of horns, the shape of the occiput, the morphology of the cheek teeth, the presence of incisors, or the weight of the mandible and feeding habits [e.g., see Bales (1996), and Zeuner (1934), and references therein] for predicting head posture. The

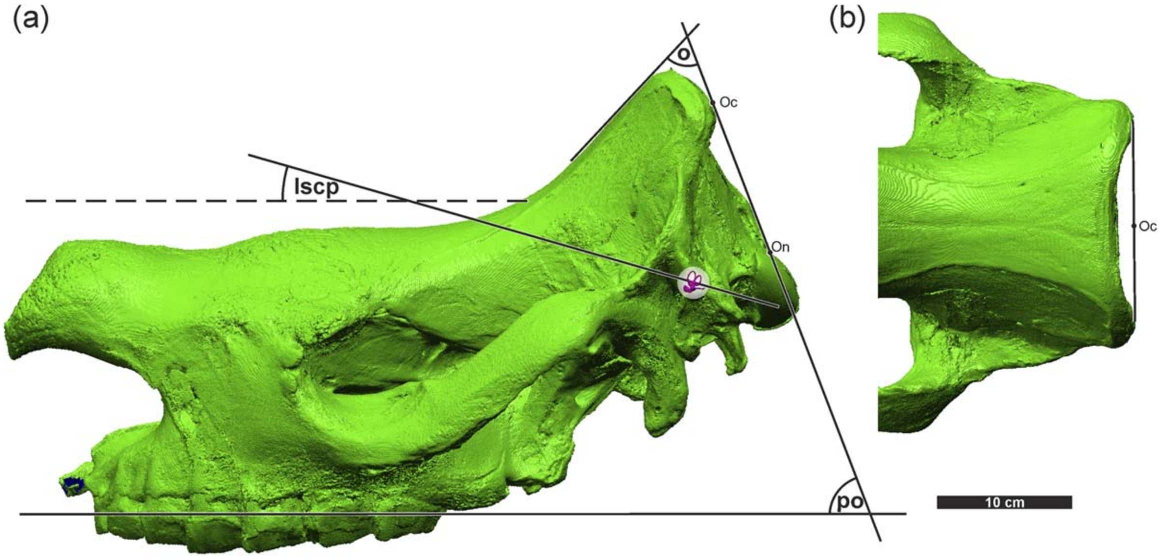

FIGURE 1 Polygonal surface model of a black rhinoceros skull (*Diceros bicornis*, MNHN.ZM-AC 1996.2520) with measured angles. (a) skull in lateral aspect, (b) occiput in dorsorostral aspect; *lscp* – angle between plane spanned between the lateral semicircular canals (LSCs) of both inner ears and the palatal plane; *o* – angle of the occipital crest between the occipital plane and the parietal plane; *po* – angle between occipital plane and palatal plane; Oc – Opisthocranion; On – Opisthion [angles *o* and *po* following Zeuner (1934)]

relation between occiput shape and head posture has long been recognized [see historical reviews in Zeuner (1934) and Bales (1996)]. Zeuner (1934) was the first who investigated the occipital shape quantitatively (angles *o* and *po* in Figure 1). He found that the angle *o* (between parietal plane and occipital plane) is small in grazing rhinos like the white rhinoceros, while this angle is much larger in browsing species like the Javan rhinoceros (Zeuner, 1934). A small angle *o* means a posteriorly elongated occipital crest, which implies a downward oriented skull.

The inner ear of mammals is housed in the bony labyrinth of the petrosal bone and provides sensory input for: (1) hearing with the sound receptive nerve cells of the cochlea and (2) balance using the sensory fields of three semicircular canals (anterior, posterior, and lateral) and the vestibule detecting changes in acceleration (Ekdale, 2016). The term “canals” refers to the semicircular structures of the bony labyrinth (e.g., used to reconstruct inner ear structures of fossil skulls), and the term “duct” refers to the membranous channels of the inner ear in the living animal (Ekdale, 2016). The ducts are immersed in perilymphatic fluid and filled with endolymphatic fluid (Rabbitt, Damiano, & Grant, 2004) with an enlarged sac (the ampulla) at one end containing sensory hair cells (Highstein, Rabbitt, Holstein, & Boyle, 2005). Rotation of the head produces relative motion of the endolymphatic fluid which affects the terminations of the afferent nerves in the ampulla of each canal (Brown, 1874). Therefore, the semicircular canals are the primary system to sense angular acceleration of the head (Rabbitt et al., 2004). The lateral semicircular canal (LSC) of the inner ear, also often called horizontal semicircular canal (or exterior canal in Brown, 1874), is supposedly held horizontally during usual head posture in many tetrapod species (Hullar, 2006); though this relationship remains debated and needs further research (Marugán-Lobón, Chiappe, & Farke, 2013; Taylor, Wedel, & Naish, 2009). The reconstructed head posture resulting from horizontal oriented LSCs has also been related to binocular vision in flying sauropsids (Witmer, Chatterjee, Franzosa, & Rowe, 2003) and predators (Araújo, Fernandez, Polcyn, Fröbisch, & Martins, 2017). A slightly upward oriented LSC in the resting animal, or the relation between the LSC orientation and the “alert”-posture has also been discussed in the literature [see e.g., Hullar (2006) and Witmer et al. (2003)]. Potential correlations between the LSC orientation and head posture(s), and their usage to reconstruct behavior and locomotion of extant and extinct animals were broadly investigated and discussed for different mammals, therapsids, and dinosaurs [e.g., xenarthrans (Coutier, Hautier, Cornette, Amson, & Billet, 2017); rodents, carnivores, marsupials, etc. (Berlin, Kirk, & Rowe, 2013); dinocephalians (Benoit, Manger, Norton, Fernandez, & Rubidge, 2017); gorgonopsians (Araújo et al., 2017); mammals, birds, and sauropods, (Sereno et al., 2007; Taylor et al., 2009)].

This study aims to investigate the validity of the link of LSC orientation and usual head posture in extant rhinos, and explores the potential of this approach for the reconstruction of usual head postures in the rich diversity of extinct Rhinocerotoidea with more than 50 valid fossil genera and several hundred species (Rookmaaker, 2013). Therefore, skulls of all five extant rhinoceros species were scanned using microcomputed tomography (μCT) to segment inner ear endocasts for the analysis of the head postures. The results were compared to existing behavioral data, which document head postures in the living animals (see Supporting Information Table S1). The main focus lies on the interpretation of the possible relationship between LSC orientation and usual head posture in the light of diet, incisor presence, and occipital shape. Although the bony labyrinth of rhinoceroses was the focus of a study by Hyrtl (1873), the current study is, to the author's knowledge, the first study that tests a potential link between LSC orientation and the usual head posture in extant rhinoceroses.

TABLE 1 Here investigated specimens with additional information of μCT-scans and measured angles

Species	Coll. no.	Res. μCT (voxel size)	LSC-palate (*lscp*)	Occipital crest (*o*)	Palate-occiput (*po*)
Ceratotherium simum (Burchell, 1817) (white rhinoceros)	MNHN.ZM-AC 1928.310	126 μm	39°	47°	114°
Ceratotherium simum (Burchell, 1817) (white rhinoceros)	MNHN.ZM-AC 2005.297	272 μm	37°	40°	112°
Ceratotherium simum (Burchell, 1817) (white rhinoceros)	WitmerLab OUVC 9754	999 μm (medical CT)	43°	42°	115°
Dicerorhinus sumatrensis (Fischer, 1814) (Sumatran rhinoceros)	ZMB-MAM-83228	246 μm	14°	72°	75°
Diceros bicornis (Linnaeus, 1758) (black rhinoceros)	MNHN.ZM-AC 1961.195	263 μm	15°	68°	68°
Diceros bicornis (Linnaeus, 1758) (black rhinoceros)	MNHN.ZM-AC 1996.2520	309 μm	16°	64°	69°
Rhinoceros sondaicus Desmarest, 1822 (Javan rhinoceros)	MNHN.ZM-AC 2009.400	259 μm	11°	88°	54°
Rhinoceros sondaicus Desmarest, 1822 (Javan rhinoceros)	MNHN.ZM-AC A7971	294 μm	11°	95°	49°
Rhinoceros unicornis Linnaeus, 1758 (Indian rhinoceros)	MNHN.ZM-AC 1960.59	258 μm	21°	76°	65°
Rhinoceros unicornis Linnaeus, 1758 (Indian rhinoceros)	ZFMK 1988.16	246 μm	21°	79°	55°

For definition of angles see Figure 1 and material and methods section.

2 | MATERIAL AND METHODS

2.1 | Specimens and data acquisition

Nine extant rhinoceros specimens (Table 1) were scanned by high resolution computed tomography (μCT). All specimens were adult indicated by the presence of a fully erupted third upper molar. Seven specimens (see MNHN-numbers in Table 1) are housed in the Muséum national d'Histoire naturelle, Paris, France (MNHN) and were scanned on the MNHN AST-RX platform (GE phoenix|x-ray v|tome|x 240 L; http://www.ums2700.mnhn.fr/ast-rx/ressources) owned by the museum. Specimen ZFMK 1988.16 is housed in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK), and the occipital region was scanned in the Steinmann-Institut, Paläontologie, Bonn (STIPB) using the GE phoenix|x-ray v|tome|x 240s scanner. Specimen ZFMK 1988.16 is only half a skull, and was additionally surface scanned at the STIPB using a BREUCKMANN optoTOP-HE to acquire the skull dimensions [see Figure 2d: surface scan in blue, μCT scan in green (colors in online version)]. Specimen ZMB-MAM-83228, housed in the Museum für Naturkunde Berlin (ZMB), was scanned using the STIPB μCT. Occipital and rostral region were acquired in two separate scans and the polygonal surface models were virtually combined afterwards (Figure 2e). The CT-scan data of the tenth specimen (not acquired in the present study) was downloaded from the web openly accessible under http://www.ohio.edu/people/witmerl/3D_rhino.htm (obtained by a medical CT, Data in DICOM format, resolution 999 μm) (WitmerLab, 2012). This 41-year-old male white rhino is housed at the Ohio University Vertebrate Collection, Athens, OH, USA (OUVC), and contributed to a study on rhino horns (Hieronymus, Witmer, & Ridgely, 2006). Unfortunately, the low resolution of the DICOM dataset compared to the data of the μCTs (e.g., see Hoffmann et al. (2014) for review of different scanning devices and methods) made it impossible to segment the lateral canals of the inner ears of this specimen. Therefore, both anterior and posterior canals of the inner ears were aligned with the completely segmented inner ears of the white rhino specimens to estimate the resulting head posture (Figure 2j). The OUVC-skull (Figure 2j) was the basis to measure the angles *o* and *po* of the μCT-scanned white rhinoceros specimens (MNHN.ZM-AC 2005.297 and MNHN.ZM-AC 1928.310; Figure 2h,i), because both scans lack the occipital crest, which is needed to create the occipital plane. The bony labyrinth endocast within the petrosal bone was segmented using AVIZO 6.3.1 (Visualization Sciences Group).

2.2 | Description of angles and measurement

For characterizing the occipital cranium shape and LSC orientation three different angles were measured (Figure 1), two (*o* and *po*) are according to Zeuner (1934, 1945). Angle *o* is the angle of the occipital crest, also described as the occipital transverse ridge. The angle spans between the dorsal plane connecting the medial portions of both parietals, and the plane connecting the Opisthion (On in Figure 1) to the Opisthocranion (Oc in Figure 1) perpendicular to the sagittal plane. The Opisthion describes the most dorsal point of the foramen magnum, the Opisthocranion is the most caudal point of the occipital transverse ridge. Occasionally the transverse ridge can have lateral wings, which

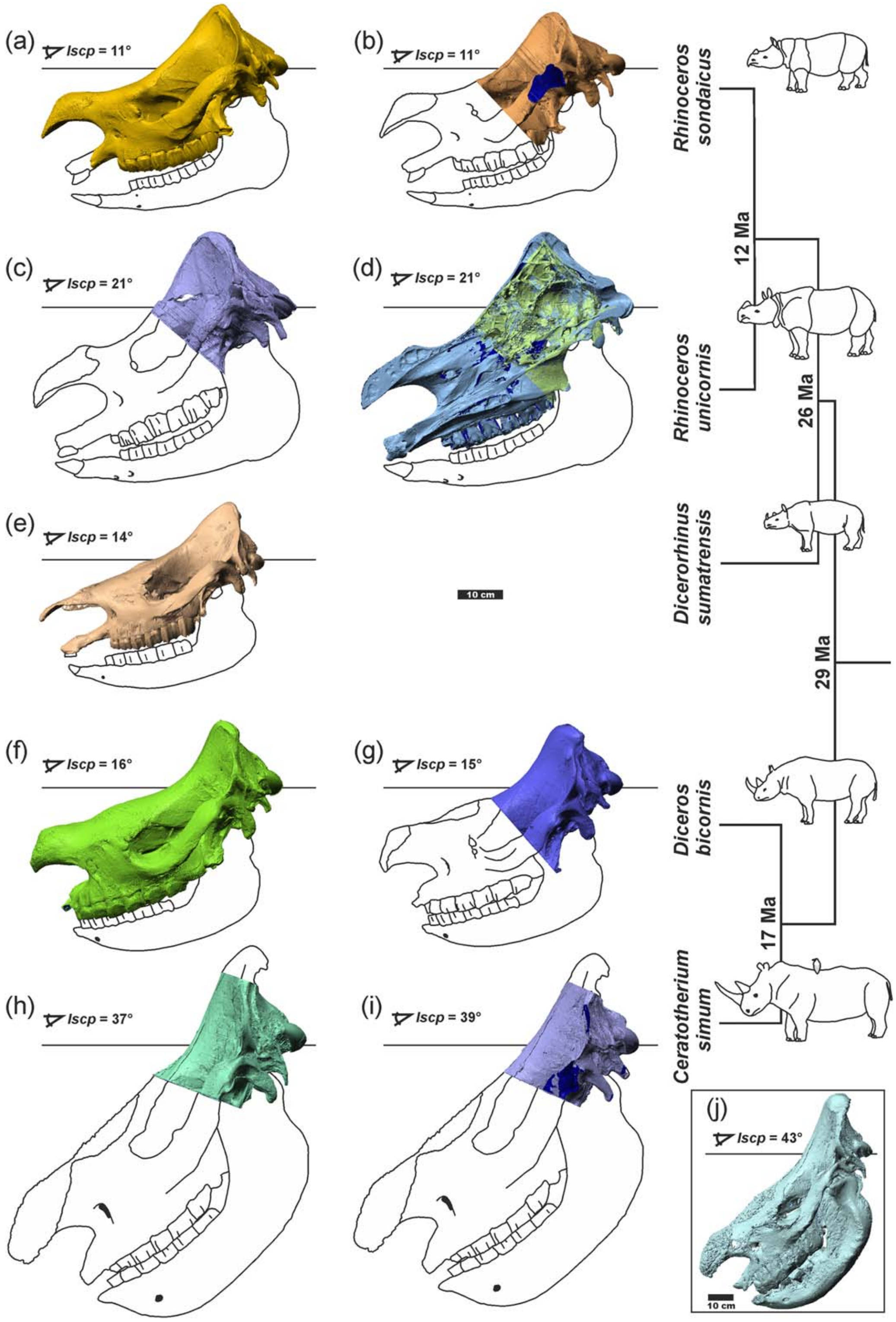

FIGURE 2 Polygonal models of the investigated specimens with horizontally oriented LSCs of the inner ears and resulting head postures. The plane of the LSCs of each skull is indicated by a horizontal line. The phylogeny is based on Tougard, Delefosse, Hänni, and Montgelard (2001), the rhinoceros sketches are redrawn after Sody (1959) and Zeuner (1934). (a, b) Javan rhinoceros (*Rhinoceros sondaicus*; (a) MNHN. ZM-AC 2009.400; (b) MNHN.ZM-AC A7971); (c, d) Indian rhinoceros (*Rhinoceros unicornis*; (c) MNHN.ZM-AC 1960.59; (d) ZFMK 1988.16); (d) Sumatran rhinoceros (*Dicerorhinus sumatrensis*; ZMB-MAM-83228); (f, g) black rhinoceros (*Diceros bicornis*; (f) MNHN.ZM-AC 1996.2520; (g) MNHN.ZM-AC 1961.195); (h, i, j) white rhinoceros (*Ceratotherium simum*; (h) MNHN.ZM-AC 2005.297; (i) MNHN.ZM-AC 1928.310; (j) OUVC 9754)

extent more caudally than the most caudal point of the sagittal plane (von den Driesch, 1976: fig. 12a). In this case, the point of the Opisthocranion is located on the medial point of a virtual line connecting the caudal extremities of the lateral wings (Figure 1b). Angle *po* spans between the plane connecting the Opisthocranion and Opisthion perpendicular to the sagittal section and the palatal plane. The palatal plane is the plane of the hard palate formed by the ventral portions of the palatines and the maxillaries (see also position of palatal plane in lateral view in Figure 1a). The angle *lscp* spans between the plane connecting the LSCs of both inner ears and the palatal plane. The plane of the LSCs is anchored to at least 25 points on the surface models following the inner perimeter of each LSC. The points were picked on both LSC models between the ampulla and the confluence to the posterior semicircular canal, a secondary crus commune between LSC and the posterior semicircular canal is not present in the investigated rhinoceros specimens. The LSC plane was then created as a best fit plane of these 50 or more points (see Supporting Information Figure S1). Some investigated rhino specimens showed LSCs slightly tilted up laterally meaning no complete coplanarity of left and right LSC, what is documented in many mammalian species (Berlin et al., 2013). Specimens deviating from coplanarity are not problematic, because the LSC plane is created as a best fit plane between the picked points on the left LSC and the right LSC. The angles were virtually measured using the software PolyWorks 11.0.5 (InnovMetric Software Inc.). The same software was used to virtually create planes and points on the surface of the polygonal models. If a specimen lacks the palate a complete specimen of the same species is used instead and both surface models were virtually combined. The surfaces were virtually aligned using the characteristic structures in the same position.

2.3 | Definition of the "usual" head posture

Following Zeuner (1934) the usual head posture of an animal is the normal position of the head while the animal is lethargic standing or walking. This head posture has been described for extant rhinos (see Supporting Information for habitual and behavioral head postures in extant rhinos). Within the perissodactyl anatomy, during this relaxed position of the animal the skull is held by the nuchal ligament and no neck muscle should be contracted, neither to lift the head, nor to lower it. This is in accordance with Alexander and Player (1965), who found that in the lowered head posture of the white rhinoceros the elevator muscles for the head (mainly Musculus semispinalis capitis and Musculus rectus capitis) are relaxed. In rhinos, this lowered and relaxed head posture is clearly different from the position during an alert state, which was described by de Beer (1947) as having a more subhorizontal position of the LSCs. However, because rhinos significantly lift their head when alerted (Schenkel & Schenkel-Hulliger, 1969), I primarily focus my observations of usual head postures on standing resting and slowly moving rhino individuals. To define the usual head posture for the rhinos investigated here, I collected information from current literature (Supporting Information Table S1) and observations from videos and pictures available online on public archiving platforms and websites (see Supporting Information: the usual head posture was estimated in screenshots using the deviation of the horizontal plane for the ground and the palatal plane for each species). These behavioral data were discussed in the light of the LSC orientations measured from the CT-scanned rhino specimens.

2.4 | Statistical analyses

Although a small sample size, statistical tests were conducted in IBM SPSS Statistics (Version 24). The measured values for angles *o*, *po*, and *lscp* were tested for normal distribution with the one-sample Kolmogorov–Smirnov test. The three angles showed significances larger than .05 (meaning normal distributed values in the samples) what allowed to use the independent-samples *T*-Test to check for significant differences between two groups. One group is formed by the white rhinoceros (*Ceratotherium simum*), and the other group is formed by the four other extant rhino species [Javan rhino (*R. sondaicus*), Indian rhino (*R. unicornis*), Sumatran rhino (*D. sumatrensis*), and black rhino (*D. bicornis*)]. The procedure was done twice, in one case with the three white rhino specimens (including the OUVC 9754 specimen) in the white rhino group, and in another case with just the two MNHN white rhino specimens (MNHN.ZM-AC 2005.297, MNHN.ZM-AC 1928.310) in the white rhino group. In the latter case, the OUVC 9754 specimen was excluded from the statistical tests because of the issues in segmenting the complete inner ear resulting from the low resolution of the DICOM dataset as stated above.

3 | RESULTS

In the Javan rhinoceros (*Rhinoceros sondaicus*), the skull (i.e., the palatal plane) is oriented nearly horizontal (Figure 2a,b) when the LSCs are aligned horizontally (Figure 2). In comparison, the rostrum and the palatal plane of the Indian rhinoceros (*Rhinoceros unicornis*; Figure 2c,d), are slightly more pointing downward toward the ground when the LSCs are aligned horizontal. This is also found to a lesser extent in the Sumatran rhinoceros (*Dicerorhinus sumatrensis*; Figure 2e) and the black rhinoceros (*Diceros bicornis*; Figure 2f,g). Among the extant species the white rhinoceros (*Ceratotherium simum*; Figure 2h,i; see also Supporting Information Figure S2) has the most downward oriented head posture when the LSCs are placed horizontally. The high *lscp* value supports the result of a downward oriented head posture in the white rhinoceros. The Javan rhinoceros shows the smallest *lscp* angles (Table 1). The black rhinoceros, the Sumatran rhinoceros, and the Indian rhinoceros all show intermediate values, though they are slightly higher in the latter species. However, these intermediate *lscp* values are closer to the Javan rhinoceros *lscp* values than to the values of the white rhinoceros.

The values of the angles *o* and *po* show a similar distribution pattern within the extant rhinoceros species (Table 1). A lower value for angle *o* means a more posterior extended occipital crest and possibly related to that a downward oriented skull. For the angle *po* the relationships are the opposite, a higher value indicates a more posterior extended occipital crest also indicating a downward oriented skull. In the white rhinoceros (*C. simum*), the value for *o* is the lowest and for *po*

TABLE 2 Summary of Zeuner's (1934) ranges of angular measurements (min-median-max) for the here investigated rhinoceros species with his characterizations for habitat, diet, and head posture

Species	Common name	Habitat	Diet	Head posture	Occipital crest angle (*o*)	Palate-occiput angle (*po*)
Ceratotherium simum	white rhinoceros	savannah	grass	strongly downgrade	59°-64°-71°	80°-88°-103°
Dicerorhinus sumatrensis	Sumatran rhinoceros	sub-/tropical rainforest	leaves	horizontal	80°-88°-100°	55°-64°-73°
Diceros bicornis	black rhinoceros	shrubland	leaves + grass	downgrade	57°-70°-79°	56°-67°-88°
Rhinoceros sondaicus	Javan rhinoceros	sub-/tropical rainforest	leaves	horizontal	78°-94°-103°	40°-45°-70°
Rhinoceros unicornis	Indian rhinoceros	sub-/tropical rainforest	leaves + grass	horizontal	73°-82°-94°	41°-48.5°-58°

See also Figure 1 for description of angles and results of the present study in Table 1.

the highest of all samples (Table 1), suggesting a strongly downward oriented skull. In comparison, the Javan rhinoceros (*R. sondaicus*) shows the highest value for *o* and the lowest for *po*, indicating a horizontal head posture. The black rhinoceros (*D. bicornis*), the Sumatran rhinoceros (*D. sumatrensis*), and the Indian rhinoceros (*R. unicornis*) show intermediate values for the *lscp*, although considerably closer to the *lscp* values of the Javan rhinoceros than to those of the white rhinoceros.

The angles *o* and *po* depicting the posterior skull shape (Table 1) show an intraspecific variation of 10° at maximum in the sample. The intraspecific variation of the angle *lscp* is smaller with 0°–1° in most species, and about 6° in the three specimens of the white rhinoceros (*C. simum*; Figure 2h–j, Table 1), 2° without the OUVC white rhino specimen (WitmerLab, 2012) (Figure 2j).

According to the different head postures between the white rhino individuals (downgrade usual head posture) and the four other species of extant rhinos (horizontal to subhorizontal head posture) resulting from horizontal LSCs (Figure 2 and Supporting Information Figure S2), it was tested if there is a significant difference between the values for the measured angles (*o*, *po*, *lscp*) between both groups. The conducted independent-samples *T*-Tests showed highly significant differences ($p \leq .000$ for *lscp* and *po*, $p \leq .001$ for *o*) between the white rhinoceros specimens and the individuals of the four other species for all three measured angles (LSC orientation angle *lscp*, and occipital shape angles *o* and *po*). In the *T*-Tests without the OUVC specimen in the white rhino group the results also show a highly significant ($p \leq .000$) difference between white rhinos and the others for *lscp* and *po*, and a high significant ($\leq .005$) difference for angle *o* between both groups.

4 | DISCUSSION

Extant rhinoceroses share similarities like the presence of a nasal horn and the general herbivore diet. However, the five extant species vary not only in anatomical appearance and head posture but also in the number of horns, and the composition of the herbivorous diet content. According to literature (e.g., Becker, Bürgin, Oberli, & Scherler, 2009; Kurtén, 1968; Zeuner, 1934) and pictures from the wild, the white rhinoceros (*Ceratotherium simum*) has the most downward inclined usual head posture, while for Javan rhinoceros (*Rhinoceros sondaicus*) and Indian rhinoceros (*R. unicornis*) a horizontal or even slightly upward tilted head posture is commonly reported. The Sumatran (*Dicerorhinus sumatrensis*) and black rhinoceroses (*Diceros bicornis*) are inconsistently observed with a horizontal or intermediate lowered head. The existing relation between the shape of the occiput (angles *o* and *po* in this study) and the usual head posture in rhinoceroses has a long tradition. Osborn (1898), for example, noted the different occipital shapes of the extant rhinoceroses, and also reported different preferred diets, but did not explicitly state about different head postures. Zeuner (1934) was the first to present quantitative data linking the occipital shape to head posture and feeding preferences in extant rhinoceroses.

4.1 | LSC orientation, usual head posture, and feeding habits

While much is known about the behavioral habits and lifestyles of extant rhinoceroses (Dinerstein, 2011), quantitative data on head postures during various behavioral sequences are rather rare (see Supporting Information). However, Becker et al. [2009, following Bales (1996)] recently took the approach to reconstruct the head position of Oligocene, Miocene and extant rhinoceroses during feeding behaviors based on measurements of the occipital crest. Other studies by Heissig (1989) and Zeuner (1934) reveal interesting relations between occipital shape, head holding positions and feeding habits among rhino species.

In accordance with previous studies, the strongly oblique LSC relative to the palate of the white rhino (*C. simum*) shows the most downward oriented usual head posture in this study ($lscp = 37°\text{-}43°$). This can be supported by pictures from wild white rhinos in feeding or resting poses (see Supporting Information). In comparison, the Javan rhinoceros (*R. sondaicus*) has a more horizontal usual head posture (Becker et al., 2009; Zeuner, 1934), which is in accordance with their less oblique LSC within the skull ($lscp = 11°$). However, the Indian rhinoceros (*R. unicornis*), reported to have a similar usual head posture to the Javan rhino (Becker et al., 2009; Zeuner, 1934), has a slightly more oblique LSC according to the measured values presented here. The same is true for the Sumatran rhinoceros (*D. sumatrensis*) whose subhorizontal (somewhat intermediate) LSC orientation does not agree with Zeuner (1934) (Table 2). Zeuner (1934) postulates a horizontal head posture, although an intermediate head posture during feeding was mentioned by Becker et al. (2009). The limited qualitative behavioral data provide in fact only a very rough picture of usual head

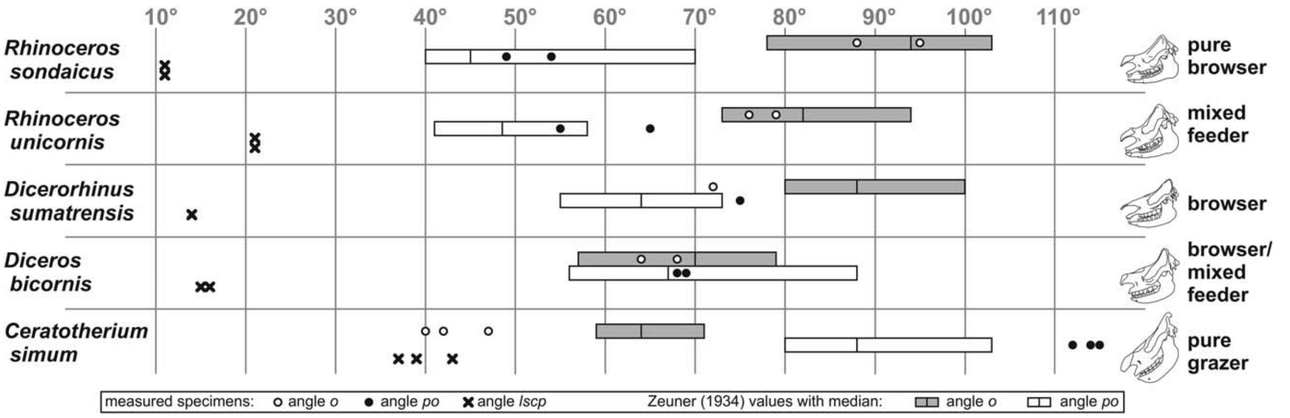

FIGURE 3 Comparison of the measurements of the here investigated specimens (circles, filled circles, crosses; for values see Table 1) in comparison to Zeuner's (1934) ranges of angular measurements (bars with median; see also Table 2), and the resulting head postures according to the present study (see also Figure 2) linked to the feeding type of each species [after Becker et al. (2009) and Zeuner (1934); see also Supporting Information Table S1]. (Skulls are not to scale. See Figure 1 for description of angles.)

postures in rhinos and caution is required for the interpretation until more quantitative data are available.

The orientations of the LSCs within the skulls and the resulting usual head postures, show a clear difference between the white rhinoceros (*Ceratotherium simum*) and the other extant species (see Figure 3), what is also supported by the *T*-Test results. This matches well with the different feeding habits among the extant species. The black rhinoceros (*Diceros bicornis*) and the Indian rhinoceros (*Rhinoceros unicornis*) showing LSCs suggesting a subhorizontal to slightly downgrade head posture in this analysis, have a diet consisting of leaves and grass (Zeuner, 1934). According to Owen-Smith (1988) and several others (Becker et al., 2009; Kaiser et al., 2013; Mendoza & Palmqvist, 2008) the black rhinoceros is considered a browsing species with only a little amount of grass in the diet [less than 25% after Palmqvist, Gröcke, Arribas and Fariña (2003)]. Therefore, a head posture more horizontal than that of the Indian rhinoceros with 50% to 75% grass in the diet (Palmqvist et al., 2003) seems reasonable for foraging mostly leaves of bushes and trees. This assumption is supported by the different values for the *lscp* angle of the black and the Indian rhinoceros (see Figure 2 and Table 1). Though it is known that extant rhinoceros species are all herbivores, the plant diet in reality is so varying that it is hard to categorize their food preferences with limited terms like "browser," "grazer," and "mixed feeder" (see Supporting Information Table S1 and references therein). Palmqvist et al. (2003) specified the feeding categories of rhinos by adding the dietary percentage of grass, and their study is not restricted to rhinoceroses only, they also provide dietary data for example for bovids as well.

The Indian rhinoceros is widely considered a mixed feeder, but according to Owen-Smith (1988) it also favors tall grasses (species of *Saccharum*) as part of their diet. The white rhinoceros, on the other hand, is a strict grazer and favors short grass (Owen-Smith, 1988). The black rhinoceros is often cited as a browser that favors herbaceous plants and forbs (Owen-Smith, 1988). Some authors consider them as mixed feeders with a diet also containing grasses and leaves (Kurtén, 1968; Zeuner, 1934). The Javan and Sumatran rhinoceroses are reported to be browsing species (Owen-Smith, 1988). The differently reported diets imply different feeding height preferences. The grazing species, such as the white rhino, forage closer to the ground and browsing species, such as the Javan and Sumatran rhinos, feed on bushes not close to the ground. The same is true for mixed feeding species with tall-grasses in their diet like the Indian rhino. Because feeding is a large part in an herbivorous animal's life the different heights of plants very likely influence the different usual head postures. Such a link between feeding habits, occipital shape and head posture in rhinos has been previously considered. After Kurtén (1968) browsing rhinos habitually have a slightly tilted upward head posture and the occipital plane is inclined forward. The grass and leaf eating black rhino carries its head horizontally, while the pure grazing white rhino habitually has a strongly nose-down head posture (Kurtén, 1968). Thus, the here presented results support the assumption that feeding habits (as a large part of an herbivorous animal's life) can seemingly influence anatomical differences, for example the inclination of the LSC within the skull relative to the palatal plane. Such anatomical differences can also be noticed in the length of the skull of the white rhinoceros (*Ceratotherium simum*) which is an adaptation to the grass diet (Owen-Smith, 2013). Among the extant rhino species the white rhinoceros has the longest skull (compare skull length in Figure 2) and one could argue that the downgrade head posture is a size effect of the much larger skull. However, as stated by Zeuner (1934), the total body mass is also much larger in the white rhino with much stronger ligaments and muscles and the center of gravity of the white rhino skull is also different compared to the other extant rhino species.

The linkage of the usual head posture to feeding habits has been tested in other vertebrates. For example, the head posture of the sauropod *Nigersaurus* was determined using the LSC orientation among other characters (Sereno et al., 2007). The orientation of the LSC within the skull led to the assumption that the muzzle is rotated downward for ground-level browsing, which was confirmed by labial (external) abrasion facets on the teeth (Sereno et al., 2007). Others agreed with this feeding posture but doubt this being the normal head posture when not feeding (Taylor et al., 2009). As mentioned before, in large herbivore animals like sauropods and rhinoceroses foraging and feeding occupy a large part of lifetime and, therefore, may influence the usual head posture. Owen-Smith (1988) reported an occupation of 49% of daylight hours and 50% of the night for foraging in the white rhinoceros (*Ceratotherium simum*), which is in agreement with the importance of the feeding activity during the rhinos' life.

It was also previously discussed that animals may hold their heads with horizontally placed LSCs in the "alert" posture when their senses are heightened (Witmer, Ridgely, Dufeau, & Semones, 2008; see also Witmer et al. (2003) and Hullar (2006) and references therein). This seems to be true for many mammalian species (de Beer, 1947) but according to behavioral observations for rhinos the alert head posture is mainly an uplifted snout (Owen-Smith, 1973), which is the opposite of the feeding posture. Owen-Smith (1973) reports a "head up" alert posture in the white rhinoceros without any quantitative value, which seems to be slightly higher than that indicated by the LSC suggested head posture. The feeding posture is most likely lower. As noted above, quantitative data on head postures during various behaviors are limited and more are needed to investigate these hypotheses in further detail.

4.2 | LSC-orientation and occipital shape

Because quantitative behavioral data on usual head postures in extant rhinos are limited, the comparison of the LSC orientation within the skull in relation to other variables may be more insightful. Zeuner (1934) was the first to link the usual head posture and feeding preferences to the occipital shape in rhinos. In comparison, the results for angles *o* and *po* (Table 1) fall in Zeuner's (1934) range (Table 2), except for the white rhinoceros, the Sumatran rhinoceros, and one value of the Indian rhinoceros (see also Figure 3). The investigated specimens of the white rhinoceros (*Ceratotherium simum*) in this study show lower values for the angle *o* and higher values for the angle *po* than measured by Zeuner (1934) (Table 2 and Figure 3). The same is true for the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) specimen. Either all four specimens (three white rhinos and one Sumatran rhino) share an extremely backward inclined occipital plane for their species compared to the specimens available to Zeuner (1934), or the measuring processes are slightly different between the studies. Both, Zeuner (1934) and Groves (1982), reported zoo specimens of the Indian rhino (*Rhinoceros unicornis*) and Sumatran rhino (*Dicerorhinus sumatrensis*) with unusual occipital shapes, possibly resulting from trough feeding on the floor which may affect the values of angles *o* and *po*. An unusually ground fed individual of an Indian rhino might develop a more posterior inclined occipital plane showing smaller values for *o* and larger values for *po* than individuals from the wild. This phenomenon can theoretically affect the formation of a normal occipital shape in tall-grass mixed feeders, like the Indian rhino, and browsers, like the Sumatran rhino. However, zoo-style ground feeding should not affect the white rhinoceros which is grazing on the ground anyway in the wild and has a backward inclined occipital plane naturally. Because for most of the specimens used here data about their origin are lacking, the possibility exists that a zoo-style fed browser or mixed feeder may be included. The differences between Zeuner's (1934) data and the data presented here might be explained in that Zeuner (1934) measured other subspecies. The collections used here only labeled down to the species level and not the subspecies level. For example, of white rhinoceroses two subspecies exist: the southern (*C. s. simum*) and the northern subspecies (*C. s. cottoni*) with a reported higher usual head posture (Owen-Smith, 2013), which very likely results in different occipital shapes. Two subspecies are also (or were) existing for the Sumatran rhinoceros (*D. s. sumatrensis*, *D. s. harrissoni*) (Dinerstein, 2011).

Although small discrepancies between the measurements of Zeuner (1934) and the ones presented here exist, the values for the angles *o* and *po* still show a similar distribution pattern in extant rhinos: *po* is the highest (suggestive for a downgrade usual head posture) in the white rhinoceroses, and the lowest (suggestive for a more horizontal usual head posture) in the Javan rhinos, while it is the opposite pattern for the angle *o* (a small value is suggestive for a downgrade head posture and a large value is suggestive for a more horizontal head posture). In fact, these patterns are supported by that of the *lscp*, with the white rhinoceros showing values suggestive for a strongly downgrade head posture and the Javan rhinoceros for a more horizontal one, and the other three species having somewhat intermediate values in between suggesting a subhorizontal head posture (Figure 3). Such a consistency or trend between these three potential indicators (*lscp*, *o*, and *po*) of a usual head posture in extant rhinos is striking, and it may argue for a potential relationship, what is also supported by the results of the conducted *T*-Tests (see results section; note that the sample size is small and the statistical power very low, and a more conservative threshold (e.g., $p \leq .0001$) should be used to prove significant differences, which would affect the results for angle *o*, and therefore, the statistical support should be handled with caution). However, whether this represents a direct relationship between each of these indicators and the usual head posture, or it is rather the sign of architectural links between the LSC orientation and the shape of the occipital cranium, has still to be determined. It has to be emphasized (and it is very obvious in Figure 3), that the values of the angles *o* and *po* measured by Zeuner (1934) show a large overlap in their ranges. None of the species clearly separates from another by, neither their values of *o* nor of *po*. Zeuner (1934), therefore, provided the median of each of his ranges to show the trend for the different species. In descriptive statistics, the median (compared to the mean) is more stable against outliers (extremely small or extremely large individuals) in a sample.

4.3 | LSC-orientation, horn size, and second lower incisor presence in extant and fossil rhinoceroses

In addition to the different usual head postures, extant rhinos show differences in horn size and incisor presence (e.g., Groves, 1972; Groves & Kurt, 1972; Groves & Leslie, 2011; Hillman-Smith & Groves, 1994; Laurie, Lang, & Groves, 1983) (see also Supporting Information). For example, the two extant African species (*C. simum*, *D. bicornis*) show two massive horns but lack front teeth, while the extant Asiatic species have tusk-like lower second incisors in combination with either one small nasal horn (*R. sondaicus*, *R. unicornis*), or a small nasal and a small frontal horn (*D. sumatrensis*). Following the considerations of Gaudry (1878) and Matthew (1931), Geist (1966) and Heissig (1972) noted an inverse relation between the size of horns and the size of the lower second incisors in two different groups of fossil rhinos from the late Tertiary. Heissig (1972, 1989), reported that the Rhinocerotinae [Rhinocerotini according to current systematics, e.g., Antoine et al. (2010)] had strong horns but weak or no lower second incisors, while the Aceratheriinae [Aceratheriini according to current systematics, e.g., Antoine et al. (2010)] had strong tusk-like lower second incisors but just one small or no horn (Heissig, 1972, 1989). Although the presence/absence of large horns or the presence/absence of large tusks is a trend within different rhinoceros subfamilies and tribes (Heissig, 1973), the horn formation itself is different within these clades and this character is, thus, regarded as convergent/parallel. Same is true for the loss of the incisors (Heissig, 1981, 1989). As illustrated and measured by using the angle *lscp* (Table 1), the here investigated extant rhinoceros species show different LSC orientations within their skulls (Figure 2). Cranial measurements (angle *o* and *po*) and the hypothesis of the correlation of the LSC-orientation with resting and/or alert behaviors (e.g., de Beer, 1947; Duijm, 1951; Hullar, 2006) indicate that the grazing white rhinoceros (*Ceratotherium simum*) has the most downward oriented skull as usual head posture, while the browsing Javan rhinoceros (*Rhinoceros sondaicus*) has an almost horizontal usual head posture. For these two species, the results support the hypothesis that rhinos with dominant horns but lacking incisors have a downward oriented skull (like in the white rhinoceros). Moreover, the results also support the hypothesis that rhinos with large lower second incisors but one small nasal horn (like in the Javan rhinoceros) have a horizontal head posture. Heissig (1972, 1989) proposed that fossil rhinos with strong lower tusks used them as weapons against predators as extant Asiatic rhinos do, based on the well-documented usage of tusks in fighting in the extant *Rhinoceros unicornis* and *Rhinoceros sondaicus* (Owen-Smith, 1988). In comparison, extant African species showing fully reduced incisors use their massive horns for fighting (Dinerstein, 2011). Dinerstein (2011) also cautiously correlated these behavioral aspects to usual head posture by noting that rhinos with strong lower tusks may have a rather horizontal head posture allowing the usage of the tusks as weapons. A nose-down head posture is only shown in extant and fossil rhinos with massive horns that lost their lower second incisors (Heissig, 1973). The results presented here support the view that the presence of lower incisors seem to influence the usual head posture in extant rhinoceroses. Although the lower jaws have not been part of the 3D measurements, it is necessary to show the outlines here (Figure 2), which are based on photographs in lateral aspect. The tusk bearing lower jaws of the Asiatic rhinos (Figure 2a–e) show a more triangular shape narrowing towards the incisors. The ventral margins of the mandibles are oriented nearly horizontal which results in a position with the lower tusk tip pointing forward. In comparison, the African rhinos that lack the incisors show different mandible shapes and orientations (Figure 2f–j). The subhorizontal or somewhat intermediate downgrade head posture in the Indian and Sumatran rhinoceros enables the lower jaw tusks being used during fighting similar to the condition found in the Javan rhinoceros (Figure 2).

It has been suggested that the development of two massive horns results in a lowered skull in order to use these, and the lowered muzzle, therefore, could be used for grazing (Heissig, 1989). A massive horn and lost incisors with a downgrade head posture are present in the grazing white rhinoceros (*Ceratotherium simum*) and the results presented here shed light on the black rhinoceros (*Diceros bicornis*; Figure 2f,g), that has a much higher usual head posture (subhorizontal) but also lacks incisors and has two massive horns. Geraads (2005) suggested a mixed feeding common ancestor for both the grazing *Ceratotherium* and browsing *Diceros* lineages in the early Pliocene. According to molecular data, the divergence time for the split of the lineages occurred in the Miocene, between 12 million years ago (Tougard, et al., 2001) (Figure 2) and 15.1 to 15.9 million years ago (Willerslev et al., 2009). It is very likely that this common ancestor already lost the incisors or at least was in the process of reducing them. This is supported by Pliocene rhinoceros material from Africa which is described as belonging to *Ceratotherium praecox* and considered closely related to *Diceros* (Hooijer & Patterson, 1972). The material was later assigned to *Diceros praecox* (Geraads, 2005, 2010), and further studies (Hernesniemi, Giaourtsakis, Evans, & Fortelius, 2011) identified some of the material to belong to the black rhino (*Diceros bicornis*). Apart from the discussion about the taxonomic attribution, the material, assigned to be closely related to the extant black rhinoceros, shows that the black rhino mainly developed a browsing habit in contrast to the proposed ancestral mixed feeder (Geraads, 2005). This finding supports a relation between the usual head posture and feeding habit. The hypothetical mixed feeding ancestor with reduced incisors very likely had a more lowered usual head posture, than the subhorizontal one in the extant browsing black rhinoceros, supported by the *lscp* results.

4.4 | Phylogenetic relationships of extant rhinos and the influence on lateral semicirclar canal orientation

The extant rhinoceros fauna comprises five species with a critically endangered status on the IUCN red list of threatened species for most of them (IUCN, 2016). The introduction of a sixth extant species was suggested earlier, by treating the two subspecies of the white rhinoceros (*Ceratotherium simum*) as two different species (Groves, Fernando, & Robovský, 2010). But it seems to be more applicable to designate subspecies of the northern and southern white rhinoceros according to the comparison of their mitochondrial genome sequences (Harley et al., 2016). Harley et al. (2016) were able to show a close relationship of black (*D. bicornis*) and white rhinoceros forming a sister group to Indian (*R. unicornis*) and Javan rhinoceros (*R. sondaicus*), with the Sumatran rhinoceros (*D. sumatrensis*) as basal to all extant rhinos. They also report a possible placement of the Sumatran rhino as the sister taxon to the African rhinos (Harley et al., 2016). Both Sumatran rhino placements as basal or sister to African rhinoceroses are in contrast to Tougard et al. (2001) (also depicted in Figure 2). In the Tougard et al. (2001) study, the African rhinoceroses are the sister group to all three Asiatic rhinos with the Sumatran rhinoceros as the basal Asiatic rhino. In some phylogenetic studies, where the white rhinoceros is excluded, the Sumatran rhino results as the direct sister taxon to the black rhino (Antoine, 2003; Becker, Antoine, & Maridet, 2013). Thus, the phylogenetic position of the Sumatran rhino is still under debate, but there is consensus that Indian (*Rhinoceros unicornis*) and Javan rhinoceros (*Rhinoceros sondaicus*) are closely related sister taxa, so are the white (*Ceratotherium simum*) and black rhinoceroses (*Diceros bicornis*) (e.g., Antoine, 2002; Guérin, 1980; Orlando et al., 2003; Willerslev et al., 2009). Interestingly, the inclusion of the Pleistocene woolly rhinoceros (*Coelodonta antiquitatis*) in phylogenetic analyses put this taxon in close relationship to the extant Sumatran rhinoceros (Orlando et al., 2003; Willerslev et al., 2009). The woolly rhinoceros is also considered a grazer with a low usual head posture (e.g., Kurtén, 1968; Zeuner, 1934). Preliminary studies using the LSCs of the woolly rhinoceros suggest that the resulting head posture is comparable to the downward oriented head in the extant white rhinoceros (Schellhorn, 2014, 2015a, 2015b). It is important to note here that the grazing woolly rhinoceros is phylogenetically closely related to the browsing Sumatran rhinoceros, and the grazing white rhinoceros is closely related to the browsing black rhinoceros. According to the results presented here, woolly and white rhinoceros show a downward inclined usual head posture, while Sumatran and black rhinoceros show a more horizontal usual head posture. It seems that the phylogenetic relationships are not primarily affecting the estimated usual head postures resulting from the here presented approach.

5 | CONCLUSION

The results show the diversity of anatomically different LSC-orientations in the skulls of the five extant rhinoceros species. Whether or not the LSC-orientation is indicative of the usual head postures or reflect other behavioral head positions (i.e., during resting, locomoting, or feeding) in each species cannot be fully answered, because quantitative behavioral data are lacking. However, the review of preferred diet and preferred feeding height in the extant rhinoceroses seem to support that a relationship exists between the LSC-orientations, the occipital shape, and the feeding strategies. The link between the LSC-orientation and occipital shape is interesting and needs further investigation.

COMPETING INTERESTS

There are no competing interests.

AUTHORS' CONTRIBUTIONS

RS designed the study, analyzed the data, drafted the manuscript, and gave final approval for publication.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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