



Morphology of Metapodiophalangeal Joints and Mobility of Finger and Toe in Bovids

Authors: Takeda, Sei-ichiro, Oshida, Tatsuo, Motokawa, Masaharu, Kawada, Shin-ichiro, and Endo, Hideki

Source: Mammal Study, 48(3) : 145-157

Published By: Mammal Society of Japan

URL: <https://doi.org/10.3106/ms2022-0049>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Morphology of metapodiophalangeal joints and mobility of finger and toe in bovids

Sei-ichiro Takeda^{1,2,*}, Tatsuo Oshida³, Masaharu Motokawa⁴, Shin-ichiro Kawada⁵ and Hideki Endo¹

¹ The University Museum, The University of Tokyo 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0032, Japan

² Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1, Yayoi, Bunkyo-ku, Tokyo 113-0032, Japan

³ Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro 080-8555, Japan

⁴ The Kyoto University Museum, Kyoto University, Kyoto 606-8501, Japan

⁵ Department of Zoology, National Museum of Nature and Science, 4-1-1, Amakubo, Tsukuba, Ibaraki 305-0005, Japan

Published online 8 May, 2023; Print publication July 31, 2023

Abstract. Bovid morphologies differ depending on body size and habitat. We hypothesized that bovids also vary their mobility of fingers and toes depending on body size and habitat. In this study, we compared the shape of the distal ends of the metapodial bones and the proximal facet of the proximal phalanges to examine the metapodiophalangeal joint gaps and simulated the three-dimensional motion of the bovid metapodiophalangeal joints during the opening and closing states through CT scans to investigate whether the mobility of the finger and toe is affected by body size and habitat. The results showed that species with gaps in the metapodiophalangeal joints had higher mobility and that species living in mountains had larger gaps. This suggests that bovids living in unstable terrains can move better on unstable substrates due to their increased mobility of digit. Similarly, our results indicate that smaller bovids are more likely to display variations in the mobility of digits than larger-sized bovids since greater body size reduces the range of mobility to avoid dislocation risk. Our results show that bovids have been able to be flexible to a range of body sizes and habitats by varying the size of their metapodiophalangeal joint gaps.

Key words: joint gap, metapodials, osteology, proximal phalanges, three-dimensional image analysis.

Bovids are diverse in both body size and habitat (Nowak 1999; Wilson et al. 2011) due to anatomical, morphological, and behavioral adaptations that allow them to thrive on a variety of food resources in many different locations (Wilson et al. 2011). These adaptations include the shape of the weight-bearing bones found in their limbs (Biewener 1989; Christiansen 1999). For example, the long limb bones of heavier species have wider articular surfaces and strongly enhanced, robust muscle attachment sites involved in weight-bearing and propulsion (Etienne et al. 2021). Since the habitat strongly influences bone shape in addition to the body size and phylogenetic constraint (Kappelman 1988; Polly 2008; Curran 2012; Dunn 2018), the limb bones of the bovids are also considered to be adapted to the environment in which they live. For example, open-habitat

species escape from predators by running on flat ground, whereas closed-habitat species tend to rely on camouflage to evade predators, which requires them to move over complex substrates when running (Kappelman 1988; Kappelman et al. 1997; Plummer et al. 2008). Like closed-habitat species, mountainous species take advantage of the complex substrates to escape from their predators and do not need to gallop as often (Kappelman 1988; Wilson et al. 2011; Rozzi and Palombo 2013a; Etienne et al. 2021). Thus, open-habitat species show adaptations for cursoriality, whereas closed-habitat and mountainous species for joint mobility (Kappelman 1988; Rozzi and Palombo 2013a; Barr 2014; Etienne et al. 2021).

The body size and habitat diversity of bovids suggest that their limb extremities which support the body

*To whom correspondence should be addressed. E-mail: seiichiro.takeda@um.u-tokyo.ac.jp

weight in each various environment are also diverse. Similarly, pad stiffness varies in animals with padded feet depending on their body size and habitat (Dagg 1974; Alexander et al. 1986; Bennett 1999; Lammers and Bikenvicius 2004; Chi and Roth 2010). Larger animals use pads to distribute pressure across their feet (Benz et al. 2005; Panagiotopoulou et al. 2012, 2016, 2019; Clemente et al. 2020). It has also been reported that the foot contact areas of bovids and other mammals are strongly correlated with body size, regardless of habitat (Cumming and Cumming 2003; Michilsens et al. 2009; Clemente et al. 2020). It could thus be argued that the foot morphology of animals is flexible depending on their habitats and body size. Although bovids do not possess a pad-like cushion and support their weight only with hooves (Nowak 1999; Wilson et al. 2011), it is expected that their bone morphology reflects variations in body size and substrate rather than soft tissue structure.

The distal ends of the bovid metapodials, one of the bones found in the extremities, possess a trochlear keel (Janis and Scott 1987; Clifford 2010). The metapodial keels prevent the metapodiophalangeal joints from spreading by fitting into the groove in the proximal facets of the proximal phalanges (Cope 1889; Wortman 1893). It was hypothesized in previous studies that open-habitat bovid species would possess higher metapodial keels to prevent joint disarticulation and to run faster on flat ground and that the metapodial of closed-habitat bovid species would possess lower keels to better spread the fingers and toes when moving over complex substrates (Köhler 1993; Scott and Barr 2014); however, the height of the distal ends of the metapodial keels did not differ by the habitat (Klein et al. 2010; Scott and Barr 2014). Several studies have investigated the relationship between habitat and the morphology of bovid phalanges including proximal phalanges and mentioned the mobility of the metapodiophalangeal joints (DeGusta and Vrba 2005; Louys et al. 2013; Rozzi and Palombo 2013b; Rossouw 2022). The metapodiophalangeal joints are composed of the metapodial bones and the proximal phalanges (König and Liebich 2007). Thus, we considered it necessary to examine the distal ends of the metapodials and the proximal facet of the proximal phalanges to verify the mobility of the metapodiophalangeal joints. If the mobility of digits varies by habitat and body size, bovids that can spread the fingers and toes widely would possess gaps in the metapodiophalangeal joints. Furthermore, we expected that the correlation between mobility and morphology would be more

compelling when combining osteometric analyses and three-dimensional simulations.

In this study, we used a CT scanner to simulate the three-dimensional motion of the bovid metapodiophalangeal joints during the opening and closing states, and then compared the shape of the distal ends of the metapodial bones and the proximal facet of the proximal phalanges that form the metapodiophalangeal joints. We hypothesized that closed-habitat and mountainous species possess gaps on the metapodiophalangeal joints to better spread the fingers and toes. By combining the results of the three-dimensional simulations and osteometric analyses, we aimed to clarify differences in metapodiophalangeal joint morphology by habitat and body size. This will help to elucidate how bovids have been able to expand and adapt to such diverse environments.

Materials and methods

Three-dimensional simulation

Budorcas taxicolor, *Capra falconeri*, *C. hircus*, *Oryx leucoryx*, *Ovis canadensis*, and *Pseudois nayaur* carcasses that had been donated to the University Museum, the University of Tokyo (UMUT) were used (Table 1). These species were selected since they are found in different habitats: *B. taxicolor*, *C. falconeri*, *O. canadensis* and *P. nayaur* in rocky or mountainous terrain; *O. leucoryx* in open terrain; and *C. hircus* as a domesticated species (Nowak 1999; Scott and Barr 2014; Etienne et al. 2021).

We referred to Endo et al. (2019) for CT scanning and angle measurement methods from 3D images. Briefly, a CT scanner (Asteion PREMIUM 4 EDITION, Toshiba Medical Systems, Tokyo, Japan) was used to serially section the extremities of the limbs from the parallel distal to the proximal planes at a 0.5 mm thickness, without a gap. The current and voltage were 100 mA and 120 kV, respectively. The left forefoot and hindfoot were scanned in all individuals. The phalanges were positioned to simulate the opening and closing movements during CT scanning. During the opening state, the phalanges were opened to their furthest extent, whereas the phalanges and metacarpals or metatarsals were closed to their closest extent during the closing state. The obtained series of CT images were then used to reconstruct 3D images of the forefoot and hindfoot. We measured the angle and distance between the third and fourth phalanges. The angle and distance of the phalanges were examined using a 3D image analyzing system (Amira 2021.1: Visage Imaging GmbH, Berlin,

Table 1. Species and number of individuals used in this study

Tribe	Species	Abbreviation	Habitat	<i>n</i>
Alcelaphini	<i>Connochaetes taurinus</i>	<i>Ct</i>	Open	1
Alcelaphini	<i>Damaliscus pygargus</i>	<i>Dp</i>	Open	1
Antilopini	<i>Antilope cervicapra</i>	<i>Ac</i>	Open	2
Bovini	<i>Bison bison</i>	<i>Bib</i>	Open	3
Bovini	<i>Bos gaurus</i>	<i>Bg</i>	Heavy cover	2
Bovini	<i>Bos taurus</i>	<i>Bot</i>	Domesticated	4
Bovini	<i>Bubalus bubalis</i>	<i>Bub</i>	Domesticated	6
Bovini	<i>Bubalus depressicornis</i>	<i>Bd</i>	Forest	1
Caprini	<i>Ammotragus lervia</i>	<i>Al</i>	Mountain	2
Caprini	<i>Budorcas taxicolor</i>	<i>But</i>	Mountain	3 (1)
Caprini	<i>Capra falconeri</i>	<i>Cf</i>	Mountain	4 (1)
Caprini	<i>Capra hircus</i>	<i>Ch</i>	Domesticated	4 (1)
Caprini	<i>Capricornis crispus</i>	<i>Cc</i>	Mountain	9
Caprini	<i>Hemitragus jemlahicus</i>	<i>Hj</i>	Mountain	3
Caprini	<i>Naemorhaedus goral</i>	<i>Ng</i>	Mountain	1
Caprini	<i>Oreamnos americanus</i>	<i>Oa</i>	Mountain	3
Caprini	<i>Ovibos moschatus</i>	<i>Om</i>	Open	2
Caprini	<i>Ovis canadensis</i>	<i>Oc</i>	Mountain	4 (1)
Caprini	<i>Ovis gmelini</i>	<i>Og</i>	Mountain	5
Caprini	<i>Pseudois nayaur</i>	<i>Pn</i>	Mountain	4 (1)
Caprini	<i>Rupicapra rupicapra</i>	<i>Rr</i>	Mountain	4
Hippotragini	<i>Addax nasomaculatus</i>	<i>An</i>	Open	1
Hippotragini	<i>Oryx dammah</i>	<i>Od</i>	Open	4
Hippotragini	<i>Oryx leucoryx</i>	<i>Ol</i>	Open	2 (1)
Tragelaphini	<i>Tragelaphus eurycerus</i>	<i>Te</i>	Forest	1
Tragelaphini	<i>Tragelaphus spekii</i>	<i>Ts</i>	Heavy cover	4

n is the number of individuals used in the osteometrical analysis, and species used in the three-dimensional simulation are indicated by the number of individuals in parentheses.

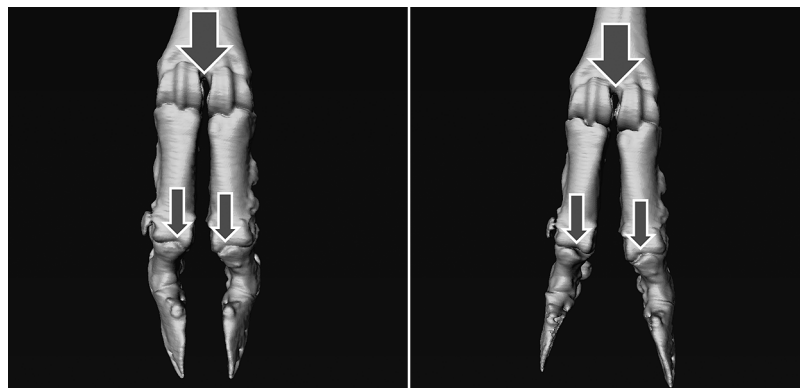


Fig. 1. Landmarks used in the 3D-reconstructed image osteometry (A fore limb of *Ovis canadensis*: left, closing state; right, opening state). Large arrows (the most proximal point of the attachment line between the medial and lateral trochleae) indicate the proximal point to measure the angles between the proximal phalanges. Small arrows indicate the dorsodistal point of the proximal phalanges to measure the angles and distances between the proximal phalanges. Landmarks were referred to Endo et al. (2019).

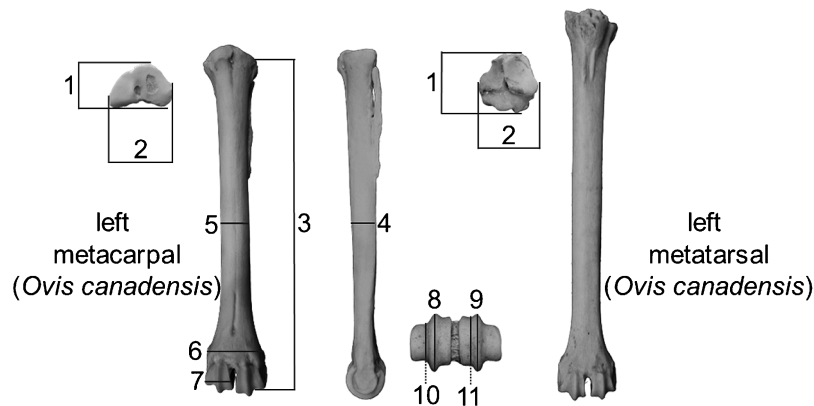


Fig. 2. The measurements used to calculate the size variable (SV). 1: anteroposterior diameter of the proximal articulation; 2: mediolateral diameter of the proximal articulation; 3: functional length; 4: anteroposterior diameter of the midshaft; 5: mediolateral diameter of the midshaft; 6: mediolateral diameter of the distal diaphysis; 7: mediolateral diameter of the medial trochlea; 8: anteroposterior diameter of the medial verticilli; 9: anteroposterior diameter of the lateral verticilli; 10: minimum anteroposterior diameter of the medial trochlea; 11: maximum anteroposterior diameter of the lateral trochlea. The geometric mean of the total 22 metacarpal and metatarsal measurements was used as SV.

Germany) to quantitatively clarify the opening and closing movements of the foot bones. The angle/distance between phalanges in the opening and closing states were measured respectively, and the difference between the two states was considered as the angle/distance change. The landmarks used to measure angles and distances in the reconstructed images are shown in Fig. 1.

Osteometrical analysis

The metacarpals, metatarsals, and proximal phalanges of 67 individuals from 26 bovid species were used in this study (Table 1 and Supplementary Table S1). The specimens are stored in UMUT, the National Museum of Nature and Science (NMNS), and the Mie Prefectural Museum (MPM). Specimens with fused metacarpal and metatarsal epiphyses and no noticeable lesions were selected. The species used in this study display a broad range of body sizes and inhabit a variety of habitats. Habitat attribution follows the categories proposed by Etienne et al. (2021). We used the species assignments to habitat categories of Kovarovic and Andrews (2007), Scott and Barr (2014), and Etienne et al. (2021). When a species of our sample had not been assigned to a habitat category by any of them, we assigned the species to a habitat category by ourselves based on Wilson et al. (2011). Eight species were classified as open-habitat species, two as forest species, two as heavy cover species, 11 as mountainous species, and three as domesticated species (Table 1).

We measured 15 characters of the metacarpals and metatarsals and two characters of the proximal phalanges

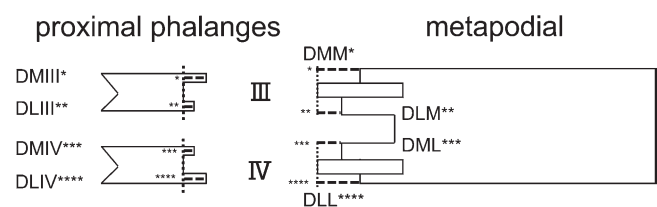


Fig. 3. The measurements used to examine the gap of metapodiophalangeal joints. DMM: maximum depth of medial facet of medial trochlea; DLM: minimum depth of lateral facet of medial trochlea; DML: minimum depth of medial facet of lateral trochlea; DLL: maximum depth of lateral facet of lateral trochlea; DMIII: maximum depth of proximal medial facet of third proximal phalanx; DLIII: minimum depth of proximal lateral facet of third proximal phalanx; DMIV: minimum depth of proximal medial facet of fourth proximal phalanx; DLIV: maximum depth of proximal lateral facet of fourth proximal phalanx. The measurements indicated by the same number of asterisks in metapodial and proximal phalanges are the sites articulated at metapodiophalangeal joints. Therefore, the gap of metapodiophalangeal joints was defined as the difference in relative length between metapodial and proximal phalanges of the same number of asterisks.

using digital calipers (Mitsutoyo Corp, Kanagawa, Japan) (Figs. 2 and 3). The 11 metacarpal and metatarsal measurements shown in Fig. 2 were taken by Eisenmann et al. (1988), Klein et al. (2010), and Scott and Barr (2014). The geometric mean of the 22 metacarpal and metatarsal measurements was used as a proxy for size (SV; see Scott and Barr 2014). Eight measurements of metapodiophalangeal joints (Fig. 3), namely, the maximum depth of medial trochlea (DMM), the minimum depth of lateral facet of medial trochlea (DLM), the minimum depth of medial facet of lateral trochlea (DML), the maximum depth of lateral facet of lateral

trochlea (DLL), the maximum depth of proximal medial facet of third proximal phalanx (DMIII), the minimum depth of proximal lateral facet of third proximal phalanx (DLIII), the minimum depth of proximal medial facet of fourth proximal phalanx (DMIV), and the maximum depth of proximal lateral facet of fourth proximal phalanx (DLIV), were obtained. The difference in the lengths between the metapodials and proximal phalanges at the corresponding sites was calculated as the gap of metapodiophalangeal joints (e.g., gap of medial third metapodiophalangeal joint = DMIII – DMM).

A phylogenetic generalized least squares (PGLS) was performed in R using the caper package (Orme et al. 2013) for each of the gaps of metapodiophalangeal joints in absolute values to test the influence of size (SV) and habitat in a phylogenetic framework. Size and habitat were included as independent variables in each model. We incorporated species relationships in the models using the species-level phylogeny of Cetartiodactyla (Zurano et al. 2019). Pairwise comparisons between habitat means were made for each variable if there was a significant habitat effect found. As mountainous species could be further classified into two categories (Kovarovic and Andrews 2007), it is expected that gaps vary among them. To supplement PGLS, an analysis of variance (ANOVA) was performed for each of the gaps of mountainous species. For ANOVA tests, the measurements of metapodiophalangeal joints were divided by SV to remove the effect of size (e.g., relative DMM = DMM/SV). The gaps of metapodiophalangeal joints were also expressed in relative length (i.e., divided by SV). Data from species for which only one individual was measured

were excluded from ANOVA. The normality assumption was checked by analyzing the ANOVA model residuals using quartile-quartile (Q-Q) plots, and all data points were arranged approximately along the reference line. Holm–Bonferroni methods were conducted to identify the specific pairwise comparisons that differed significantly from one another. To test whether gap size correlated with the angle measured in this study, the simple/multiple regression analyses were performed with angle as the objective variable and gap as the explanatory variable. The angle change measured in this study corresponded to the gaps of the same species for which the angle was measured. Eight distinct combinations of gaps (gap of medial third metapodiophalangeal joint; gap of lateral third metapodiophalangeal joint; gap of medial fourth metapodiophalangeal joint; gap of lateral fourth metapodiophalangeal joint, gap of medial third metapodiophalangeal joint + gap of lateral fourth metapodiophalangeal joint; gap of lateral third metapodiophalangeal joint + gap of medial fourth metapodiophalangeal joint; all four gaps) served as explanatory variables. ANOVA and simple/multiple regression analyses were performed using EZR (Kanda 2013).

Results

Three-dimensional simulation

In the forelimb, the difference in angle between the opening and closing states of mountainous species *B. taxicolor*, *C. falconeri*, *O. canadensis*, and *P. nayaur* was 4.3, 7.7, 5.9, and 5.1 degrees, respectively. The angle change was only 2.5 degrees in *C. hircus* (domesti-

Table 2. Three-dimensional data in the metacarpophalangeal joints

Species	State	Angle (degree)	Distance (mm)	Angle change (degree)	Distance change (mm)
<i>Budorcas taxicolor</i>	Closing	32.7	34.22		
	Opening	37.0	38.71	4.3	4.49
<i>Capra falconeri</i>	Closing	23.5	22.47		
	Opening	31.2	29.91	7.7	7.44
<i>Capra hircus</i>	Closing	21.7	17.16		
	Opening	24.2	19.62	2.5	2.46
<i>Ovis canadensis</i>	Closing	17.0	16.10		
	Opening	22.9	22.06	5.9	5.96
<i>Pseudois nayaur</i>	Closing	20.3	16.18		
	Opening	25.4	20.26	5.1	4.08
<i>Oryx leucoryx</i>	Closing	19.1	18.50		
	Opening	21.0	20.61	1.9	2.11

Table 3. Three-dimensional data in the metatarsophalangeal joints

Species	State	Angle (degree)	Distance (mm)	Angle change (degree)	Distance change (mm)
<i>B. taxicolor</i>	Closing	24.4	25.54		
	Opening	26.1	27.76	1.7	2.22
<i>C. falconeri</i>	Closing	18.6	13.94		
	Opening	25.2	24.38	6.6	10.44
<i>C. hircus</i>	Closing	18.2	14.50		
	Opening	20.6	16.65	2.4	2.15
<i>O. canadensis</i>	Closing	16.9	15.86		
	Opening	19.0	18.17	2.1	2.31
<i>P. nayaur</i>	Closing	16.9	14.66		
	Opening	21.4	18.01	4.5	3.35
<i>O. leucoryx</i>	Closing	18.0	16.86		
	Opening	18.6	18.36	0.6	1.50

cated) and 1.9 degrees in *O. leucoryx* (open) (Table 2). The proximal phalanges exhibited large medial and lateral movement during the opening and closing states in *B. taxicolor*, *C. falconeri*, *O. canadensis*, and *P. nayaur*. *C. hircus* and *O. leucoryx* showed little change between the abduction and adduction of the metacarpophalangeal joints.

In the hindlimb, the difference in angle of *C. falconeri*, *C. hircus*, and *P. nayaur* was slightly small compared to the forelimb at 6.6, 2.4, and 4.5 degrees, respectively, whereas the difference in angle of *B. taxicolor*, *O. canadensis*, and *O. leucoryx* were smaller than that of the forelimb at 1.7, 2.1, and 0.6 degrees, respectively (Table 3).

Osteometrical analysis

PGLS results showed that the gaps of the medial third and lateral fourth metapodiophalangeal joints were significantly correlated with size, but all had low coefficients of determination (0.16–0.33) (Table 4). In contrast, habitat was significantly correlated with the gaps of the lateral third metapodiophalangeal joints, medial fourth metapodiophalangeal joints, and lateral fourth metacarpophalangeal joints, with moderate coefficients of determination for the gaps of the lateral third, medial fourth, and lateral fourth metatarsophalangeal joints at around 0.5 and large coefficients of determination for the gaps of the lateral third and medial fourth metacarpophalangeal joints at over 0.8 (Table 4).

The species-specific differences in the metacarpophalangeal joint gaps are shown in Fig. 4. The gaps of the medial third and lateral fourth metacarpophalangeal

Table 4. Results of the phylogenetic generalized least squares regressions

	SV		Habitat	
	<i>P</i>	<i>R</i> ²	<i>P</i>	<i>R</i> ²
Gap of medial third MCP joint	*	0.16	ns	0.24
Gap of lateral third MCP joint	ns	0.12	***	0.87
Gap of medial fourth MCP joint	ns	0.09	***	0.83
Gap of lateral fourth MCP joint	**	0.26	**	0.53
Gap of medial third MTP joint	*	0.24	ns	0.12
Gap of lateral third MTP joint	ns	0.06	*	0.42
Gap of medial fourth MTP joint	ns	0.05	**	0.48
Gap of lateral fourth MTP joint	**	0.33	ns	0.21

* : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$; ns: nonsignificant.

joints were small in the species found in Fig. 4a and d. The mountainous species showed a large gap on the lateral third and medial fourth metacarpophalangeal joints, which was not seen in other bovids (Fig. 4b and c; Table 5). All mountainous species used in this study were Caprini (Table 1), but two Caprini species (*C. hircus* and *Ovibos moschatus*) lacked the gap (Fig. 4b and c). In forest species, the gaps of the lateral third and medial fourth metacarpophalangeal joints differed significantly from those in other habitats (Table 5). However, the gaps of the lateral third and medial fourth metacarpophalangeal joints of the forest species had similar values to those of the open-habitat species (Fig. 4b and c).

Gap differences in the metatarsophalangeal joints are provided by species in Fig. 5. The gaps of all four meta-

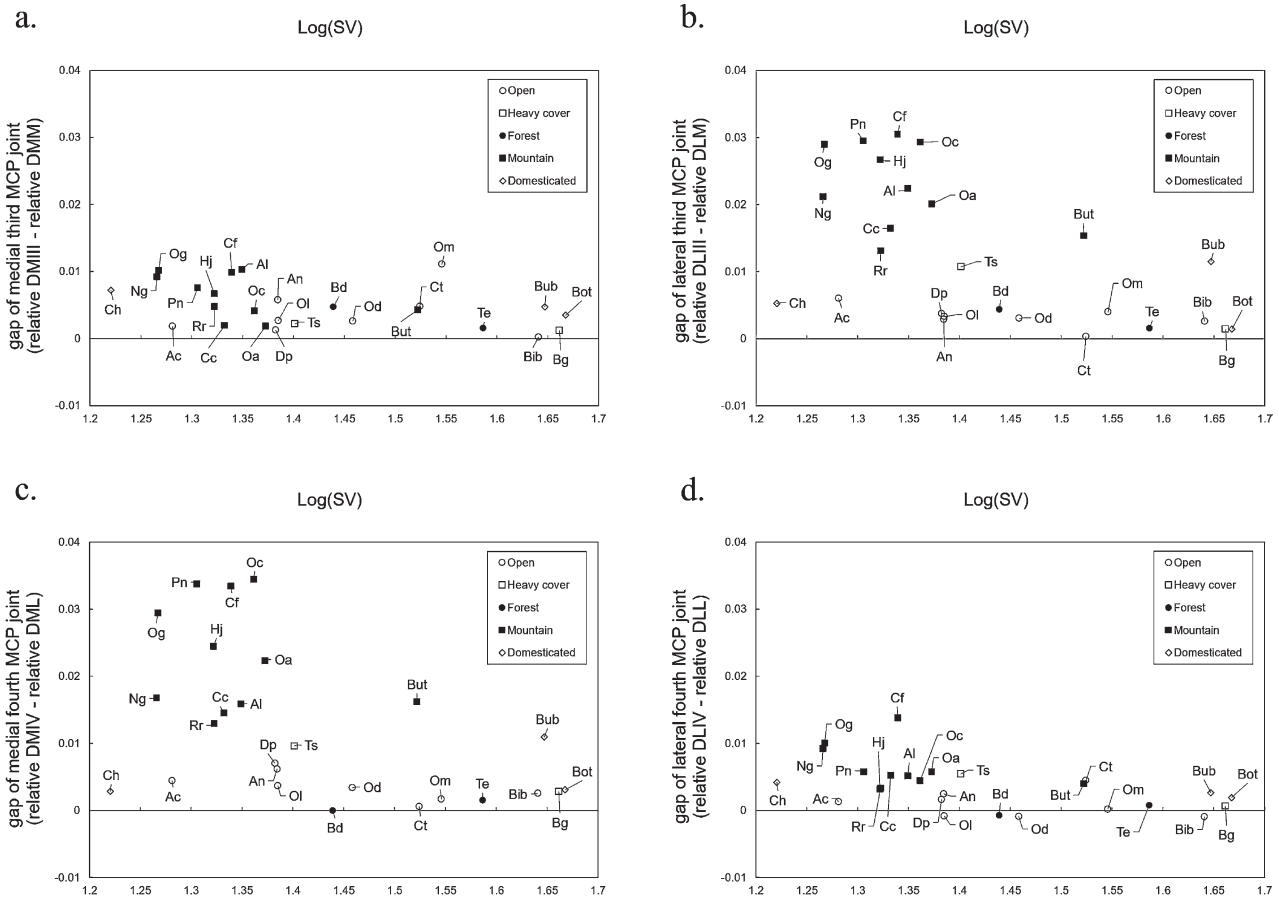


Fig. 4. Scatterplot showing the size of the gap by interspecies in the metacarpophalangeal joint. (a) Medial third metacarpophalangeal joint. (b) Lateral third metacarpophalangeal joint. (c) Medial fourth metacarpophalangeal joint. (d) Lateral fourth metacarpophalangeal joint. The vertical axis shows the relative metacarpophalangeal joint gap size, and the horizontal axis is body size (Log (SV)). The plotted values are mean values for each species. The species' abbreviations are shown in Table 1.

Table 5. Pairwise comparison of the gap of metacarpophalangeal joints between habitat groups by PGLS

Gap of lateral third MCP joint	Open	Heavy cover	Forest	Mountain	Domesticated
Open					
Heavy cover	ns				
Forest	**	**			
Mountain	***	***	***		
Domesticated	ns	ns	**	***	
Gap of medial fourth MCP joint	Open	Heavy cover	Forest	Mountain	Domesticated
Open					
Heavy cover	ns				
Forest	**	*			
Mountain	***	***	***		
Domesticated	ns	ns	**	***	
Gap of lateral fourth MCP joint	Open	Heavy cover	Forest	Mountain	Domesticated
Open					
Heavy cover	ns				
Forest	ns	ns			
Mountain	***	ns	**		
Domesticated	ns	ns	ns	ns	

* : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$; ns: nonsignificant.

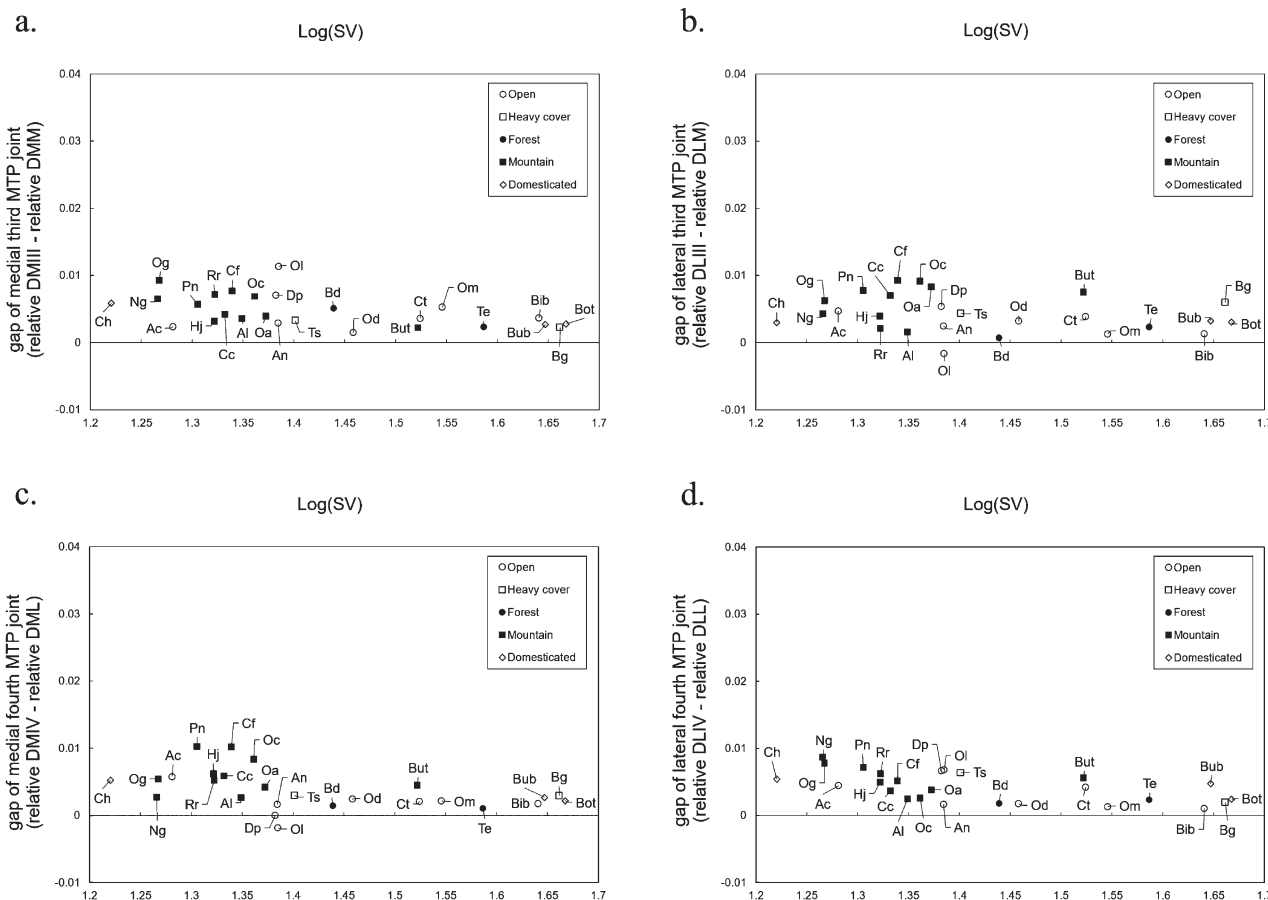


Fig. 5. Scatterplot showing the size of the gap by interspecies in the metatarsophalangeal joint. (a) Medial third metatarsophalangeal joint. (b) Lateral third metatarsophalangeal joint. (c) Medial fourth metatarsophalangeal joint. (d) Lateral fourth metatarsophalangeal joint. The vertical axis shows the relative metatarsophalangeal joint gap size, and the horizontal axis is body size (Log (SV)). The plotted values are mean values for each species. The species' abbreviations are shown in Table 1.

Table 6. Pairwise comparison of the gap of metatarsophalangeal joints between habitat groups by PGLS

Gap of lateral third MTP joint	Open	Heavy cover	Forest	Mountain	Domesticated
Open					
Heavy cover	ns				
Forest	ns	ns			
Mountain	**	ns	*		
Domesticated	ns	ns	ns	ns	
Gap of medial fourth MTP joint	Open	Heavy cover	Forest	Mountain	Domesticated
Open					
Heavy cover	ns				
Forest	ns	ns			
Mountain	***	ns	*		
Domesticated	ns	ns	ns	ns	

* : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$; ns: nonsignificant.

tarsophalangeal joints were small, which was like the gaps of the medial third and lateral fourth metacarpophalangeal joints. The gaps of the lateral third and medial fourth metatarsophalangeal joints of the moun-

tainous species were significantly different from those of the open-habitat and forest species (Table 6), although the differences were not as pronounced as those observed in the lateral third and medial fourth meta-

Table 7. Results of ANOVA for mountainous species

	<i>P</i>
Gap of medial third MCP joint	**
Gap of lateral third MCP joint	***
Gap of medial fourth MCP joint	***
Gap of lateral fourth MCP joint	ns
Gap of medial third MTP joint	ns
Gap of lateral third MTP joint	ns
Gap of medial fourth MTP joint	ns
Gap of lateral fourth MTP joint	ns

** : $P < 0.01$; *** : $P < 0.001$; ns: nonsignificant.

carpophalangeal joints (Fig. 4b and c and Fig. 5b and c).

The results of ANOVA for the mountainous species showed significant differences between species in the gaps of the medial third, lateral third, and medial fourth metacarpophalangeal joints (Table 7). A significant difference was observed in the gap of the medial third metacarpophalangeal joint only in the combination of *Capricornis crispus* and *O. gmelini* (Fig. 4a; Table 8). In the gap of the lateral third metacarpophalangeal joint, *C. crispus* and *Rupicapra rupicapra* demonstrated a smaller gap, while *C. falconeri*, *O. canadensis*, *O. gmelini*, and *P. nayaur* exhibited a larger gap (Fig. 4b; Table 8). Similarly, a smaller gap was observed in *Ammotragus lervia*, *B. taxicolor*, *C. crispus*, and *R. rupicapra* in the gap of the medial fourth metacarpophalangeal joint, while *C. falconeri*, *O. canadensis*, *O. gmelini*, and *P. nayaur* exhibited a larger gap (Fig. 4c; Table 8). No significant differences were detected among any species combination in the metatarsophalangeal joints (Table 7).

Regression analyses showed that the gap of lateral third metapodiophalangeal joint, the gap of medial fourth metapodiophalangeal joint, and the gap of lateral third metapodiophalangeal joint + the gap of medial fourth metapodiophalangeal joint were correlated with the angle change, while the other explanatory variables did not demonstrate any correlation with the angle change. The determination coefficients for the explanatory variables that demonstrated significant differences were all approximately 0.6, which is deemed a certain level of precision (Table 9).

Discussion

Budorcas taxicolor, *C. falconeri*, *O. canadensis*, and *P. nayaur*, whose angle of the metacarpophalangeal

joints changed significantly between opening and closing states in the three-dimensional simulation, possessed gaps on the lateral third and medial fourth metacarpophalangeal joints. In contrast, *C. hircus* and *O. leucoryx*, whose angle of the metacarpophalangeal joints hardly changed, had no gaps in the metacarpophalangeal joints. Thus, the gaps of the lateral third and medial fourth metacarpophalangeal joints allow for mobility in the abduction and adduction of the metacarpophalangeal joints. *C. hircus* and *O. leucoryx* had no gap in the metacarpophalangeal joints, which eliminated the space to move in the medial and lateral directions and prevented the proximal phalanges from moving in the medial and lateral directions. *Budorcas taxicolor*, *C. falconeri*, *O. canadensis*, and *P. nayaur* possessed gaps on the lateral third and medial fourth metacarpophalangeal joints, which allowed the proximal phalanges to move in the medial and lateral directions. The metatarsophalangeal joints showed less change in angles than the metacarpophalangeal joints, possibly, because the metatarsophalangeal joints had no gaps. The reason why gaps were observed in the metacarpophalangeal joints but not in the metatarsophalangeal joints is assumed to be due to the functional differences between the forelimb and hindlimb. Specifically, the forelimb has a stronger weight-bearing function and can easily support its weight by increasing finger mobility, whereas the hindlimb has a stronger propulsive function, so that suppressing toe mobility prevents force dispersion and generates a greater propulsive force (McGuigan and Wilson 2003; Hanot et al. 2017).

Of the species used in this study, all Caprini (except *C. hircus* and *O. moschatus*) live in mountainous terrain (Scott and Barr 2014; Etienne et al. 2021) and displayed gaps in the lateral third and medial fourth metacarpophalangeal joints (Fig. 3b and c). This increased finger mobility may be an adaptation to better maintain balance on the sloping footholds found in mountainous terrain. Bovids from rugged-mountainous areas and some island species tend to minimize lateral bending at the femur, radius, metacarpal, metatarsal, and phalangeal bones by evolving relatively robust and short lower limb bones (Scott 1985; Rozzi and Palombo 2013a, 2013b; Higgins 2014; Rozzi and Palombo 2014; Rozzi et al. 2020) whereas a few mountainous Antilopinae, such as *C. crispus* and *R. pyrenaica ornata*, exhibit relatively long and slender metapodials (Rozzi and Palombo 2013b, 2014; Rozzi et al. 2020; Etienne et al. 2021). Among the mountainous species used in this study,

Table 8. Pairwise comparison of the gap of metacarpophalangeal joints between the mountainous species

	<i>A. lervia</i>	<i>B. taxicolor</i>	<i>C. falconeri</i>	<i>C. crispus</i>	<i>H. jemlahicus</i>	<i>O. americanus</i>	<i>O. canadensis</i>	<i>O. gmelini</i>	<i>P. nayaur</i>	<i>R. rupicapra</i>
Gap of medial third MCP joint										
<i>A. lervia</i>										
<i>B. taxicolor</i>	ns									
<i>C. falconeri</i>	ns	ns								
<i>C. crispus</i>	ns	ns	ns							
<i>H. jemlahicus</i>	ns	ns	ns	ns						
<i>O. americanus</i>	ns	ns	ns	ns	ns					
<i>O. canadensis</i>	ns	ns	ns	ns	ns	ns				
<i>O. gmelini</i>	ns	ns	ns	*	ns	ns	ns			
<i>P. nayaur</i>	ns	ns	ns	ns	ns	ns	ns	ns		
<i>R. rupicapra</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Gap of lateral third MCP joint										
<i>A. lervia</i>										
<i>B. taxicolor</i>	ns									
<i>C. falconeri</i>	ns	ns								
<i>C. crispus</i>	ns	ns	*							
<i>H. jemlahicus</i>	ns	ns	ns	ns						
<i>O. americanus</i>	ns	ns	ns	ns	ns					
<i>O. canadensis</i>	ns	ns	ns	*	ns	ns				
<i>O. gmelini</i>	ns	ns	ns	*	ns	ns	ns			
<i>P. nayaur</i>	ns	ns	ns	*	ns	ns	ns	ns		
<i>R. rupicapra</i>	ns	ns	**	ns	ns	ns	*	**	*	
Gap of medial fourth MCP joint										
<i>A. lervia</i>										
<i>B. taxicolor</i>	ns									
<i>C. falconeri</i>	*	*								
<i>C. crispus</i>	ns	ns	***							
<i>H. jemlahicus</i>	ns	ns	ns	ns						
<i>O. americanus</i>	ns	ns	ns	ns	ns					
<i>O. canadensis</i>	*	**	ns	***	ns	ns				
<i>O. gmelini</i>	ns	ns	ns	**	ns	ns	ns			
<i>P. nayaur</i>	*	*	ns	***	ns	ns	ns	ns	ns	
<i>R. rupicapra</i>	ns	ns	***	ns	ns	ns	***	**	***	*

* : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$; ns: nonsignificant.

Table 9. Results of the simple/multiple regression analyses

Explanatory variable	<i>P</i>	<i>R</i> ²
Gap of medial third MCP/MTP joint	ns	0.03
Gap of lateral third MCP/MTP joint	**	0.62
Gap of medial fourth MCP/MTP joint	**	0.64
Gap of lateral fourth MCP/MTP joint	ns	0.28
Gap of medial third MCP/MTP joint +	ns	0.32
Gap of lateral fourth MCP/MTP joint		
Gap of lateral third MCP/MTP joint +	**	0.65
Gap of medial fourth MCP/MTP joint		
All gaps	ns	0.69

** : $P < 0.01$; ns: nonsignificant.

dependence on mountain terrain varies, with *C. falconeri*, *O. canadensis*, *O. gmelini*, and *P. nayaur* being more dependent on mountainous terrain, *B. taxicolor*, *C. crispus*, and *R. rupicapra* using high elevation forests, and *A. lervia* inhabiting high-elevation arid terrain (Wilson et al. 2011). The former group (*C. falconeri*, *O. canadensis*, *O. gmelini*, and *P. nayaur*) had even greater gaps compared to the latter (*A. lervia*, *B. taxicolor*, *C. crispus*, and *R. rupicapra*) (Fig. 3b and c; Table 8), suggesting that the joint gaps of the mountainous species can change based on their dependence on mountainous terrain as well as the length of limb bones. The distal phalanges of springboks exhibit variation in morphological traits among subspecies from distinct habitats (Rossouw 2022). As some bovids, such as *C. crispus*, exhibit regional variation in habitat elevation and terrain (Wilson et al. 2011), intraspecific variation in morphological characteristics within such species could contribute to the discussion on the relationship between morphological traits and habitat. *O. moschatus*, unlike other Caprini, was not equipped with gaps of the metacarpophalangeal joints, which may be because *O. moschatus* lives in plains rather than in mountainous terrain (Etienne et al. 2021). Eliminating the metacarpophalangeal joint gaps stabilizes the metacarpophalangeal joints and prevents force dispersion when living in the plains. It is assumed that the absence of gaps in the metacarpophalangeal joints of other bovids can also be explained by this reasoning. Like *O. moschatus*, *C. hircus* was not equipped with gaps in the metacarpophalangeal joints, which is presumably because, as a domestic animal, *C. hircus* does not need to survive on unstable footholds and thus does not need high finger

mobility.

Forest species resulted in smaller gaps than other habitats in the gaps of the lateral third and lateral fourth metacarpophalangeal joints when phylogeny was considered. This is likely because the most closely related species to *Tragelaphus eurycerus* and *Bubalus depressicornis*, classified as forest species, are *T. spekii* and *B. bubalis*, respectively, both of which have larger gaps (Fig. 4b and c). Both *B. bubalis* and *T. spekii* are semi-aquatic species (Nowak 1999; Wilson et al. 2011; Scott and Barr 2014; Etienne et al. 2021). Hippopotamuses and tapirs are also hoofed mammals that prefer a permanent water habitat and move their medial and lateral digits during the opening and closing states for their semi-aquatic walking (Endo et al. 2019). Similarly, bovids living in wetlands presumably prevent the sinking of their limbs on soft footholds by spreading their fingers to increase ground contact area. In this study, only two species of heavy cover and two species of forest were used, and no light cover species were included. The Boselaphini, Cephalophini, and Reduncini tribes, which were not used in this study, include a diverse range of species that inhabit light cover, heavy cover, and forest environments (Kovarovic and Andrews 2007; Scott and Barr 2014; Etienne et al. 2021). These species merit consideration in the discussion about the mobility of fingers and toes in closed-habitat species.

Weak or no correlation was observed between the gaps of the metapodiophalangeal joints and body size (Table 4). Conversely, in the lateral third and medial fourth metacarpophalangeal joints, many of the smaller species exhibited larger gaps, while the majority of the larger species displayed smaller gaps (Fig. 4b and c). One possible reason for these results is that Caprini species used in this study had a small to medium body size range and not as large as the body size of bovine species. Most of the bovids that possessed gaps in this study were from Caprini. Thus, the small body size included in Caprini may appear to be equipped with large gaps; however, *Antilope cervicapra* and *O. leucoryx* displayed no gaps despite having body sizes similar to those of the Caprini used in this study. In addition, a functional factor may limit the possible adduction and abduction angles, since a larger body size increases the force exerted on the distal portions of the limb, which increases the risk of dislocation (Cope 1889; Wortman 1893). Conversely, the risk of dislocation in smaller species remains small, even as the angle of adduction and abduction is increased, because the force applied to the

distal portion of the limbs is also small. Thus, it is implied that smaller bovids are more likely to vary in their metacarpophalangeal and metatarsophalangeal joint gaps, which allows them to adapt to mountainous terrain. The largest bovid species that live in mountainous terrain is *B. taxicolor*, which weighs about 300 kg, whereas *B. bubalis*, one of the largest bovid species, weighs over one ton (Jones et al. 2009; Wilson et al. 2011). This may explain why few bovid species living in mountainous terrain are large. Since *C. hircus* was the smallest species in this study, it is hypothesized that additional research on smaller bovids not included in this study, such as dik-diks and duikers, would further reveal the diversity of metacarpophalangeal and metatarsophalangeal joints.

Supplementary data

Supplementary data are available at *Mammal Study* online. **Supplementary Table S1.** Measurements of metapodials and proximal phalanges.

Acknowledgments: We are grateful to Kaori Tamura (Mie Prefectural Museum) for providing access to museum collections of bovids. This study was supported by the Sasakawa Scientific Research Grant from The Japan Science Society, grant number 2021-5001. This study was also financially supported by JSPS KAKENHI Grant Numbers 19H00534, 20H01381 and 22H00013 from Japan Society for the Promotion of Science (JSPS).

References

- Alexander, R. M., Bennett, M. B. and Ker, R. F. 1986. Mechanical properties and function of the paw pads of some mammals. *Journal of Zoology* 209: 405–419.
- Barr, W. A. 2014. Functional morphology of the bovid astragalus in relation to habitat: controlling phylogenetic signal in ecomorphology. *Journal of Morphology* 275: 1201–1216.
- Bennett, M. B. 1999. Foot areas, ground reaction forces and pressures beneath the feet of kangaroos, wallabies and rat-kangaroos (Marsupialia: Macropodoidea). *Journal of Zoology* 247: 365–369.
- Benz, A., Zenker, W., Hildebrandt, T. B., Weissengruber, G. and Geyer, H. 2005. About the macroscopic and microscopic morphology of elephants' hooves (Elephantidae). *Verhandlungsbericht ber Erkrankungen Zootiere* 42: 167–170.
- Biewener, A. A. 1989. Mammalian terrestrial locomotion and size. *Bioscience* 39: 776–783.
- Chi, K. J. and Roth, V. L. 2010. Scaling and mechanics of carnivoran footpads reveal the principles of footpad design. *Journal of the Royal Society Interface* 7: 1145–1155.
- Christiansen, P. 1999. Scaling of mammalian long bones: small and large mammals compared. *Journal of Zoology* 247: 333–348.
- Clemente, C. J., Dick, T. J., Glen, C. L. and Panagiotopoulou, O. 2020. Biomechanical insights into the role of foot pads during locomotion in camelid species. *Scientific Reports* 10: 1–12.
- Clifford, A. B. 2010. The evolution of the unguligrade manus in artiodactyls. *Journal of Vertebrate Paleontology* 30: 1827–1839.
- Cope, E. D. 1889. The Artiodactyla (continued). *The American Naturalist* 23: 111–136.
- Cumming, D. H. and Cumming, G. S. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* 134: 560–568.
- Curran, S. C. 2012. Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science* 39: 1172–1182.
- Dagg, A. I. 1974. The locomotion of the camel (*Camelus dromedarius*). *Journal of Zoology* 174: 67–78.
- DeGusta, D. and Vrba, E. 2005. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science* 32: 1099–1113.
- Dunn, R. H. 2018. Functional morphology of the postcranial skeleton. In (Croft, D., Su, D. and Simpson, F., eds.) *Methods in Paleocology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities*, Vertebrate Paleobiology and Paleoanthropology Series, pp. 23–36. Springer, Cham.
- Eisenmann, V., Alberdi, M. T., de Giuli, C. and Staesche, U. 1988. Volume I: Methodology. In (Woodburne, M. O. and Sondaar, P., eds.) *Studying Fossil Horses*, pp. 1–71. E. J. Brill, Leiden.
- Endo, H., Yoshida, M., Nguyen, T. S., Akiba, Y., Takeda, M. and Kudo, K. 2019. Three-dimensional CT examination of the forefoot and hindfoot of the hippopotamus and tapir during a semiaquatic walking. *Anatomia, Histologia, Embryologia* 48: 3–11.
- Etienne, C., Filippo, A., Cornette, R. and Houssaye, A. 2021. Effect of mass and habitat on the shape of limb long bones: A morpho-functional investigation on Bovidae (Mammalia: Cetartiodactyla). *Journal of Anatomy* 238: 886–904.
- Hanot, P., Guintard, C., Lepetz, S. and Cornette, R. 2017. Identifying domestic horses, donkeys and hybrids from archaeological deposits: a 3D morphological investigation on skeletons. *Journal of Archaeological Science* 78: 88–98.
- Higgins, R. W. 2014. The effects of terrain on long bone robusticity and cross-sectional shape in lower limb bones of bovids, Neandertals, and Upper Paleolithic modern humans. In (Carlson, K. J. and Marchi, D., eds.) *Reconstructing Mobility*, pp. 227–252. Springer, Boston.
- Janis, C. M. and Scott, K. M. 1987. The interrelationship of higher ruminant families: with special emphasis on the member of the Cervoidea. *American Museum Novitates* 2893: 1–85.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology* 90: 2648–2648.
- Kanda, Y. 2013. Investigation of the freely available easy-to-use software 'EZR' for medical statistics. *Bone Marrow Transplantation* 48: 452–458.
- Kappelman, J. 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198: 119–130.
- Kappelman, J., Plummer, T., Bishop, L., Duncan, A. and Appleton, S. 1997. Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* 32: 229–256.
- Klein, R. G., Franciscus, R. G. and Steele, T. E. 2010. Morphometric identification of bovid metapodials to genus and implications for taxon-free habitat reconstruction. *Journal of Archaeological*

- Science 37: 389–401.
- Kovarovic, K. and Andrews, P. 2007. Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. *Journal of Human Evolution* 52: 663–680.
- Köhler, M. 1993. Skeleton and habitat of recent and fossil ruminants. *Munchner Geowissenschaftliche Abhandlungen* 25: 1–88.
- König, H. E. and Liebich, H. G. 2007. *Veterinary Anatomy of Domestic Mammals: Textbook and Colour Atlas*. Schattauer, Verlag, 700 pp.
- Lammers, A. R. and Biknevicius, A. R. 2004. The biodynamics of arboreal locomotion: the effects of substrate diameter on locomotor kinetics in the gray short-tailed opossum (*Monodelphis domestica*). *Journal of Experimental Biology* 207: 4325–4336.
- Louys, J., Montanari, S., Plummer, T., Hertel, F. and Bishop, L. C. 2013. Evolutionary divergence and convergence in shape and size within African antelope proximal phalanges. *Journal of Mammalian Evolution* 20: 239–248.
- McGuigan, M. P. and Wilson, A. M. 2003. The effect of gait and digital flexor muscle activation on limb compliance in the forelimb of the horse *Equus caballus*. *Journal of Experimental Biology* 206: 1325–1336.
- Michilzens, F., Aerts, P., Van Damme, R. and D’Août, K. 2009. Scaling of plantar pressures in mammals. *Journal of Zoology* 279: 236–242.
- Nowak, R. M. 1999. *Walker’s Mammals of the World*, 6th ed. Johns Hopkins University Press, Baltimore, 1936 pp.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. and Pearse, W. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R Package Version 5: 1–36.
- Panagiotopoulou, O., Pataky, T. C., Day, M., Hensman, M. C., Hensman, S., Hutchinson, J. R. and Clemente, C. J. 2016. Foot pressure distributions during walking in African elephants (*Loxodonta africana*). *Royal Society Open Science* 3: 160203.
- Panagiotopoulou, O., Pataky, T. C., Hill, Z. and Hutchinson, J. R. 2012. Statistical parametric mapping of the regional distribution and ontogenetic scaling of foot pressures during walking in Asian elephants (*Elephas maximus*). *Journal of Experimental Biology* 215: 1584–1593.
- Panagiotopoulou, O., Pataky, T. C. and Hutchinson, J. R. 2019. Foot pressure distribution in White Rhinoceroses (*Ceratotherium simum*) during walking. *PeerJ* 7: e6881.
- Plummer, T. W., Bishop, L. C. and Hertel, F. 2008. Habitat preference of extant African bovids based on astragalus morphology: operationalizing ecomorphology for palaeoenvironmental reconstruction. *Journal of Archaeological Science* 35: 3016–3027.
- Polly, D. 2008. Limbs in mammalian evolution. In (Hall, B. K., ed.) *Fins Into Limbs: Evolution, Development, and Transformation*, pp. 245–268. University of Chicago Press, Chicago.
- Rossouw, L. 2022. Morphological variation in the distal phalanges of the springbok, *Antidorcas marsupialis* (Zimmermann, 1780) (Mammalia: Bovidae). *South African Journal of Science* 118: 1–5.
- Rozzi, R. and Palombo, M. R. 2013a. The morphology of femur as palaeohabitat predictor in insular bovids. *Bollettino della Società Paleontologica Italiana* 52: 177–186.
- Rozzi, R. and Palombo, M. R. 2013b. Do methods for predicting paleohabitats apply for mountain and insular fossil bovids? *Integrative Zoology* 8: 244–259.
- Rozzi, R. and Palombo, M. R. 2014. Lights and shadows in the evolutionary patterns of insular bovids. *Integrative Zoology* 9: 213–228.
- Rozzi, R., Varela, S., Bover, P. and Martin, J. M. 2020. Causal explanations for the evolution of ‘low gear’ locomotion in insular ruminants. *Journal of Biogeography* 47: 2274–2285.
- Scott, K. M. 1985. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History* 179: 197–288.
- Scott, R. S. and Barr, W. A. 2014. Ecomorphology and phylogenetic risk: implications for habitat reconstruction using fossil bovids. *Journal of Human Evolution* 73: 47–57.
- Wilson, D. E., Wilson, D. E. and Mittermeier, R. A. 2011. *Handbook of the Mammals of the World, Volume 2: Hoofed Mammals*. Lynx Ediciones, Barcelona, 885 pp.
- Wortman, J. L. 1893. A new theory of the mechanical evolution of the metapodial keels of Diplarthra. *The American Naturalist* 27: 421–434.
- Zurano, J. P., Magalhães, F. M., Asato, A. E., Silva, G., Bidau, C. J., Mesquita, D. O. and Costa, G. C. 2019. Cetartiodactyla: updating a time-calibrated molecular phylogeny. *Molecular Phylogenetics and Evolution* 133: 256–262.

Received 9 October 2022. Accepted 24 February 2023.

Editor was Mugino Kubo.