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DATES:**Received:** 21 Mar. 2021**Revised:** 02 Nov. 2021**Accepted:** 15 Dec. 2021**Published:** 29 Mar. 2022**HOW TO CITE:**

Rossouw L. Morphological variation in the distal phalanges of the springbok, *Antidorcas marsupialis* (Zimmermann, 1780) (Mammalia: Bovidae). S Afr J Sci. 2022;118(3/4), Art. #10452. <https://doi.org/10.17159/sajs.2022/10452>

ARTICLE INCLUDES: Peer review [Supplementary material](#)**DATA AVAILABILITY:** Open data set All data included On request from author(s) Not available Not applicable**EDITORS:**

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KEYWORDS:southern Africa, *Antidorcas marsupialis*, osteometry, osteomorphology**FUNDING:**

National Museum Bloemfontein

Morphological variation in the distal phalanges of the springbok, *Antidorcas marsupialis* (Zimmermann, 1780) (Mammalia: Bovidae)

A comparative study of distal phalanges belonging to adult springbok individuals shows distinctive morphological differences between the subspecies *Antidorcas marsupialis marsupialis* and *Antidorcas marsupialis hofmeyri*, most notably reflected by significant lengthening of the sole of the latter. Results were derived from comparative osteomorphological techniques, using standard anatomical nomenclature for descriptions and parametric statistics for measurements and dimensions. The configuration in *A. m. hofmeyri* proved useful for distinguishing between the two subspecies. The findings suggest that the osteometrical differences observed in the distal phalanges relate to different habitats occupied by the species.

Significance:

Intraspecific morphological variation exhibited by distal phalanges in *Antidorcas marsupialis* is significant. The results lay the groundwork for further testing of relationships between functional morphology of foot bones and substrate in bovids.

Introduction

This study was undertaken after cursory examination revealed observable morphological variation in the distal phalanges of the springbok, *Antidorcas marsupialis*. Springbok are plains-dwelling animals, adapted to arid regions as well as open grasslands; they are confined largely to the inland plateau and the western coastal regions of southern Africa (Figure 1).¹⁻⁴ The species is the sole living representative of the genus *Antidorcas* and the only antelope species found in southern Africa today. It belongs to a group of antelopes that evolved from a single cluster of gazelline-like antelopes that eventually separated from the genus *Gazella* during the Pliocene in East Africa to evolve further in isolation in southern Africa.⁵⁻⁸ A long history of intensive farming activities in South Africa severely depleted wildlife, but following the proclamation of several national parks since the beginning of the last century, ungulates were re-introduced to these reserves in an attempt to approximate the original wildlife composition in those areas.^{9,10} Today, the existing populations of springbok in the Republic of South Africa are commercially managed through introduction into nature reserves and game farms resulting in the reoccupation of most of the springbok's historical range.^{11,12} Although the species is continuously distributed, differences in body size, size of the postcranial skeleton and other external characteristics have been shown to vary according to locality.¹³⁻¹⁵ Body mass was highly correlated with winter dietary protein, demonstrating significant differences between the nominate subspecies *Antidorcas marsupialis marsupialis* and two larger northern groups.¹⁶ Three subspecies are recognised: the nominate subspecies *Antidorcas marsupialis marsupialis* or southern springbok, found in the central interior of South Africa and south of the lower Orange River; *Antidorcas marsupialis angolensis*, a northwestern springbok group confined mainly to the western parts of southern Angola, the Kaokoveld and the northern Namib Desert; and the Kalahari springbok, *Antidorcas marsupialis hofmeyri* (Thomas, 1926), which is generally restricted to southern Namibia, southern and western Botswana, and the adjacent parts of the Northern Cape in South Africa north of the Orange River.^{17,18} Current opinion on the taxonomic status of *A. marsupialis* varies, with recent classifications also raising all three subspecies to species rank.¹⁹ The general taxonomy in this study followed Groves' description of the springbok as a polytypic species, based on the geographical division of three subspecies.²⁰

Materials and methods

Testing variance in size and morphology in the distal phalanx of the subspecies *A. m. marsupialis* and *A. m. hofmeyri* was based on a sample comprising 19 *marsupialis* and 16 *hofmeyri* individuals from both sexes. Measurements for the 19 *marsupialis* individuals were obtained from a comparative osteomorphological study of *Antidorcas marsupialis* and grey rhebok, *Pelea capreolus* (Forster, 1790) published in 1992.¹⁵ The 16 *hofmeyri* individuals come from a single springbok population, culled several years ago in the Kalahari Gemsbok National Park and curated at the Florisbad Quaternary Research Station near Bloemfontein in the Free State Province, South Africa (Supplementary table 1). The *hofmeyri* specimens were measured with a slide caliper to the nearest 0.1 mm. Osteomorphological descriptions follow the nomenclature proposed by the International Committee on Veterinary Gross Anatomical Nomenclature.²¹ Dimensions included greatest diagonal length of the sole (DLS), greatest height in the region of the extensor process (processus extensorius, HP), length of the dorsal surface (Ld) and greatest breadth of the proximal articular surface (facies articularis proximalis, BFp)²² (Figure 2, Supplementary table 2). The dimensions were statistically tested for subspecies and sex-based effects using the parametric Student's *t*-test (Table 1).

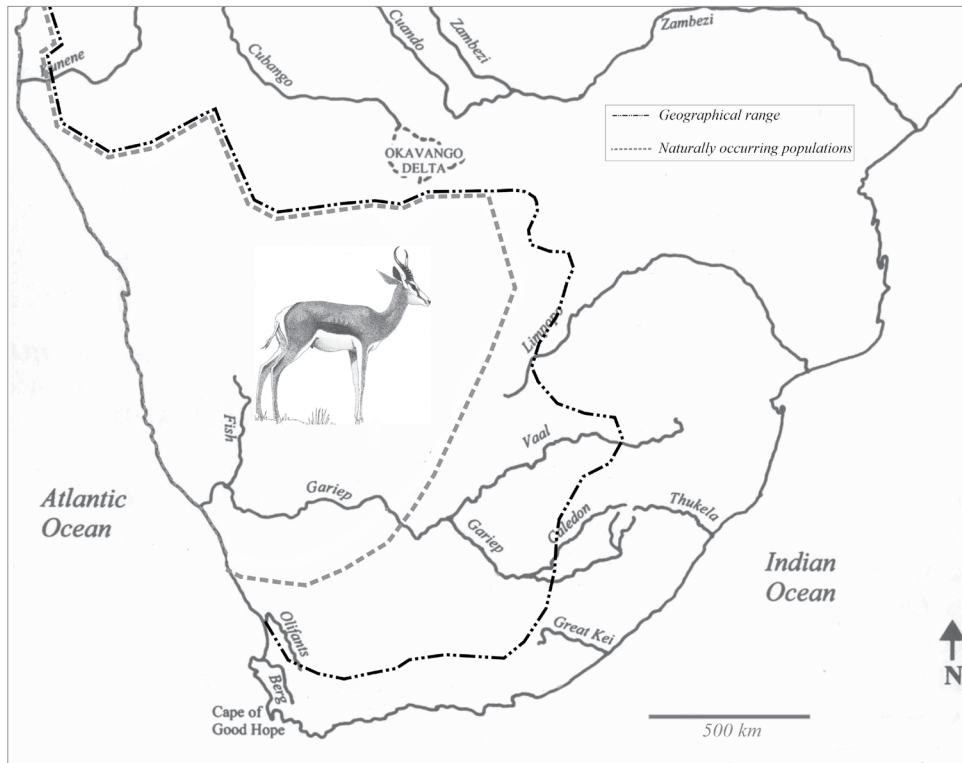
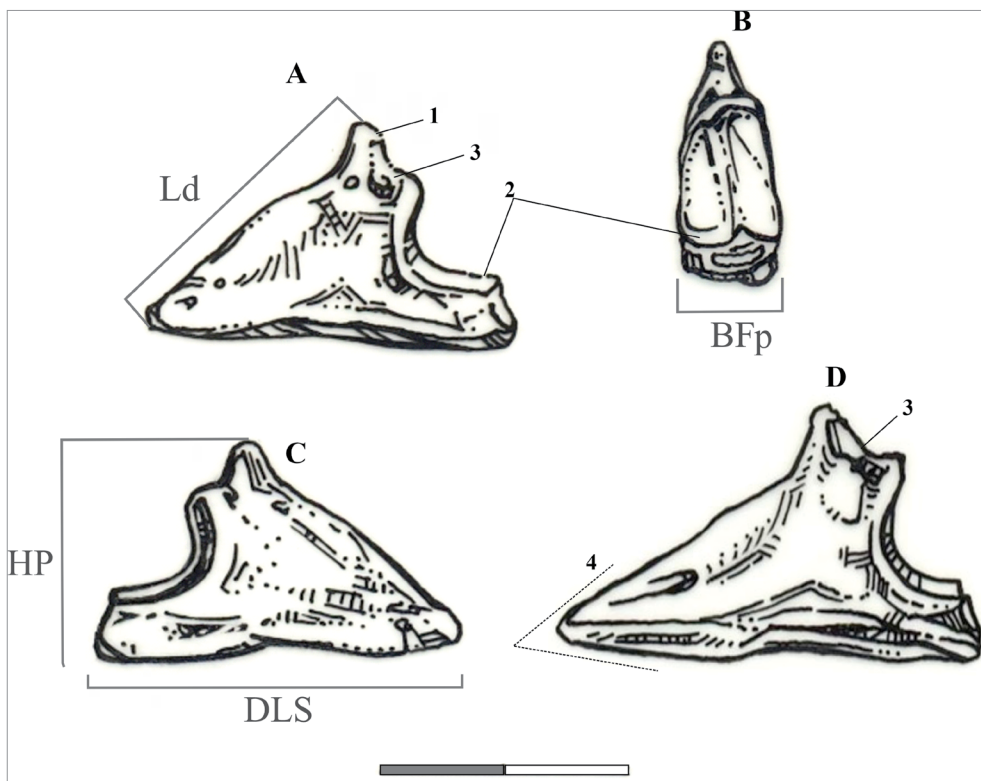


Figure 1: Present-day geographical range and present-day range of naturally occurring populations of *Antidorcas marsupialis* according to Smithers² and Skinner and Louw³.



Illustrations: Estie Rossouw, with the light coming from the top left-hand corner
Scale = each scale bar represents 10 mm

Figure 2: (A) *A. m. marsupialis*, p. distalis manus, axial view; Ld = length of dorsal surface. (B) *A. m. marsupialis*, p. distalis manus, proximal view; BFp = (greatest) breadth of the proximal articular surface. (C) *A. m. marsupialis*, p. distalis manus, abaxial view; HP = height in the region of the extensor process and DLS = (greatest) diagonal length of sole. (D) *A. m. hofmeyri*, p. distalis manus, axial view; 1 = extensor process, 2 = horizontal and posteriorly extended proximal articular surface, 3 = dorsal to palmar (manus) / dorsal to plantar (pedis) angle.

Table 1: Comparison of means between groups for sex-based and subspecies effects using *t*-tests

Variable	Mean <i>marsupialis</i> M	Mean <i>marsupialis</i> F	<i>p</i> -value	<i>n</i> <i>marsupialis</i> F	<i>n</i> <i>marsupialis</i> M	s.d. <i>marsupialis</i> M	s.d. <i>marsupialis</i> F
DLS	28.20	27.39	0.072738	15	22	0.84	1.55
Ld	23.53	22.89	0.081820	15	22	0.72	1.26
HP	17.58	16.65	0.009391	15	22	0.79	1.12
BFp	8.34	7.89	0.027606	15	22	0.41	0.67
	Mean <i>hofmeyri</i> M	Mean <i>hofmeyri</i> F	<i>p</i> -value	<i>n</i> <i>hofmeyri</i> M	<i>n</i> <i>hofmeyri</i> F	s.d. <i>hofmeyri</i> M	s.d. <i>hofmeyri</i> F
DLS	36.24	33.68	0.000000	20	11	1.00	1.03
Ld	31.25	28.36	0.000000	20	11	1.09	1.07
HP	19.82	18.43	0.000062	20	11	0.89	0.55
BFp	9.20	8.86	0.004870	20	11	0.33	0.20
	Mean <i>marsupialis</i>	Mean <i>hofmeyri</i>	<i>p</i> -value	<i>n</i> <i>marsupialis</i>	<i>n</i> <i>hofmeyri</i>	s.d. <i>marsupialis</i>	s.d. <i>hofmeyri</i>
DLS	27.72	35.33	0.000000	37	31	1.36	1.59
Ld	23.15	30.22	0.000000	37	31	1.11	1.76
HP	17.03	19.32	0.000000	37	31	1.09	1.03
BFp	8.07	9.08	0.000000	37	31	0.62	0.33
Ratio DLS/Ld	1.20	1.17	0.000150	37	31	0.03	0.02
Ratio DLS/BFp	1.59	1.62	0.009385	37	31	0.04	0.02
Ratio DLS/HP	1.63	1.83	0.000000	37	31	0.08	0.08

DLS, (greatest) diagonal length of sole; Ld, length of dorsal surface; HP, height in the region of the extensor process; BFp, (greatest) breadth of the proximal articular surface

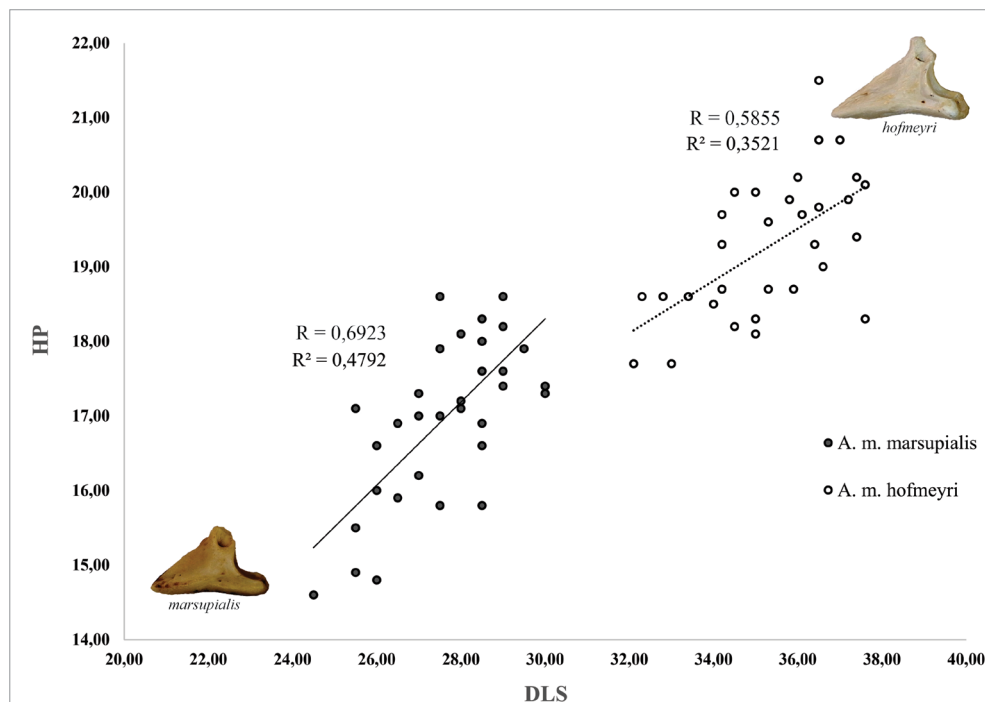
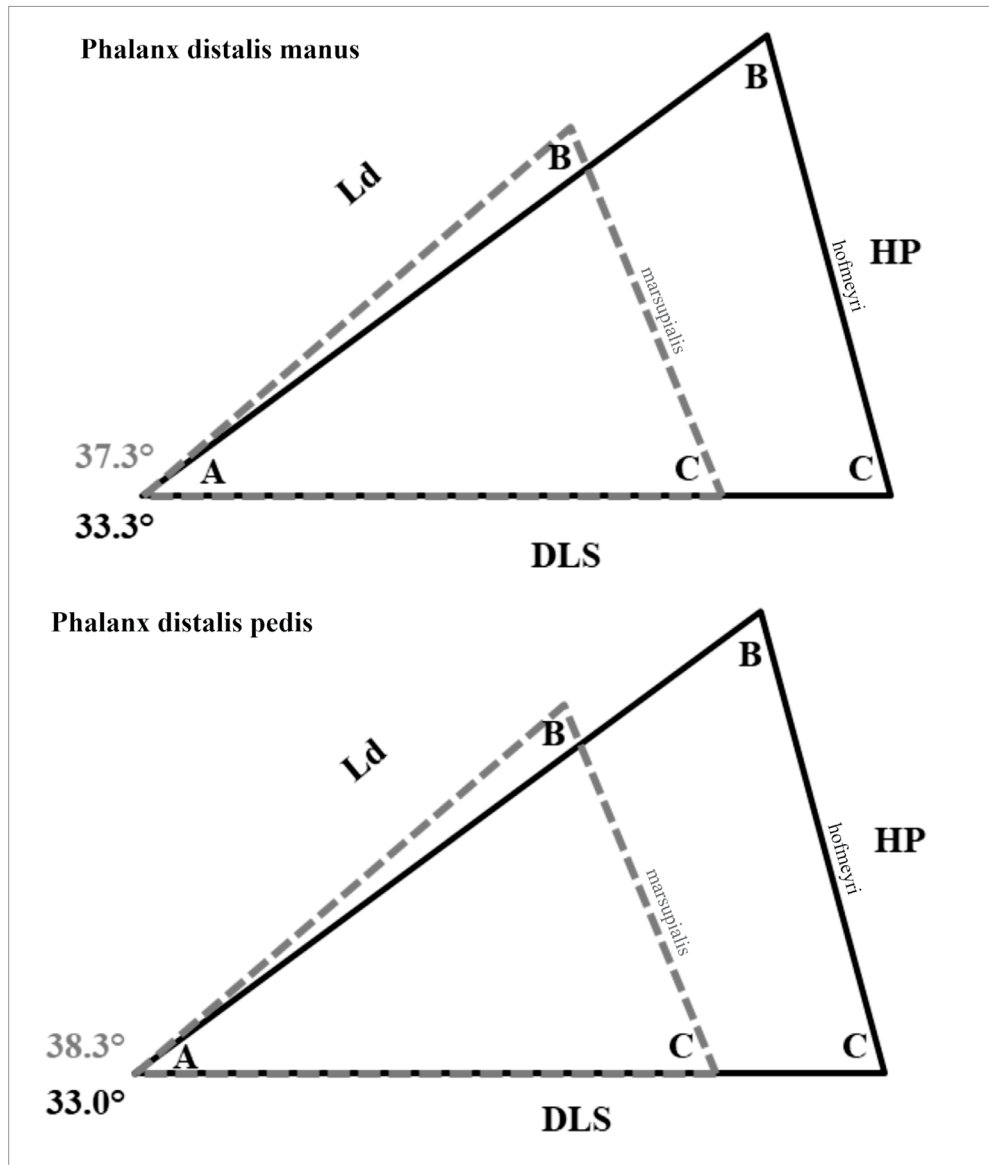


Figure 3: Bivariate plot of variables DLS ((greatest) diagonal length of sole) and HP (height in the region of the extensor process) measured for *Antidorcas marsupialis*. Smaller *A. m. marsupialis* was clearly differentiated from larger *A. m. hofmeyri*, with no overlap in values.



Ld, length of dorsal surface; HP, height in the region of the extensor process; DLS, (greatest) diagonal length of sole

Figure 4: Diagrammatic representation of distal phalanges manus (A) and pedis (B) in both subspecies. Trigonometric formulae for solution of oblique triangles were based on means for DLS, Ld and HP and calculated for dorsal to palmar / plantar surface (AB to AC), dorsal to proximal surface (AB to BC) and the proximal to palmar / plantar surface (BC to BA).

Results

The shape of the distal phalanx in the springbok is typical of the family Bovidae, resembling a triangular-shaped and mediolaterally flattened body (Figure 2). Both subspecies exhibited a prominent extensor process (Figure 2, Attr. 1), situated proximally on the dorsal surface of the body and above a posteriorly extended proximal articular surface that ends in a well-developed flexor tubercle (Figure 2, Attr. 2). The phalanges also revealed a characteristically large nutrient foramen on the axial side at the base of the extensor process (Figure 2, Attr. 3). Compared to *A. m. marsupialis*, the distal phalanx in *A. m. hofmeyri* appeared to be distally elongated, resulting in a comparably more peg-like appearance (Figure 2, Attr. 4). This morphological trait remained noteworthy in overall proportion when compared metrically to that of *A. m. marsupialis*. As expected, variables DLS, Ld, HP and BFP were larger in *A. m. hofmeyri* for both sexes with *A. m. marsupialis* and *A. m. hofmeyri* falling into two discrete and non-overlapping clusters (Figure 3). This also applied to the log-transformed values. Even though sex-based variability varied from significant in *A. m. hofmeyri* to not in *A. m. marsupialis*, it had no effect on subspecies, which were significant in all the dimensions ($n=66$,

$p<0.05$). Disproportionate lengthening along the anteroposterior axis of the corpus was indicated by significantly higher DLS:HP ($p<0.001$) and DLS:BFp ($p=0.009$) ratios for *A.m. hofmeyri* (Supplementary figure 1). The results were supported by simple trigonometrical analysis, based on mean values of dimensions DLS, Ld and HP, showing comparatively lower dorsal to palmar (manus) and dorsal to plantar (pedis) angles in *A. m. hofmeyri* (Figure 4, Supplementary table 3).

Concluding remarks

Findings from this study indicate that configuration of the distal phalanx in *A.m. hofmeyri* is at variance with that of the nominate subspecies and that the measurements, and the indices based on them, proved useful for distinguishing between the distal phalanges of the two subspecies. In this case, a significant increase in the DLS:HP ratio as merely a function of increased body size in *A.m. hofmeyri* is not consistent with the assumption that two subspecies of different size, but sharing a common morphology, will also have the dimensions of their distal phalanges in the same ratio.

Selection pressures that operate within a specific environment have been linked to the functional expression of postcranial characteristics in modern African bovids, e.g. broad-level correlations between bovid postcrania and open or closed habitats.²³⁻²⁶ While *Antidorcas marsupialis* is a plains-living species, the osteometrical differences observed in the distal phalanges relate to the different habitats that the species occupy. Being generally restricted to southern Namibia, southern and western Botswana and the adjacent parts of the Northern Cape Province north of the Orange River, the natural habitat of *A. m. hofmeyri* is underlain by a distinctive and homogeneous substrate, made up of thick surface sands of different ages that were established during periods of widespread aridity.²⁷ Deposits vary from extensive areas covered by linear dunes to gently undulating sand sheets that extend from southern Angola and western Zambia in the north to the Orange River in the south.²⁸⁻³⁰ With the lower Orange River acting as a natural barrier, it is readily perceived that the distinct morphology exhibited by *A. m. hofmeyri*'s distal phalanges, could have resulted from an allopatric isolation event sometime in the past, following continual locomotion on unconsolidated dune and sand sheet accumulations in the region. Further investigations, using a larger, more inclusive data set, will be required to test these assumptions, but for now, it is postulated that in addition to dietary effects¹⁶, abiotic conditions like substrate may also be a driver of morphological alteration within the polytypic springbok.

Acknowledgements

The National Museum in Bloemfontein provided financial support for the project (ethical clearance number NMB ECC 2019/5). The author is indebted to Estie Rossouw (independent graphic designer) for creating the drawings.

Competing interests

I have no competing interests to declare.

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