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The body proportions in *Myotragus balearicus* Bate, 1909

by C.F. Spoor

Institute of Earth Sciences, University of Utrecht, the Netherlands
Present address: Department of Anatomy and Embryology, University of Groningen, Oostersingel 69, 9713 EZ Groningen, the Netherlands

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ABSTRACT

The body proportions in *Myotragus balearicus* are compared with those in recent Caprinae. The relative neck length of *M. balearicus* is comparable to that in the Caprinae. The fore and hind limbs of *M. balearicus* are short due to a short humerus, os femoris, tibia, and short metapodia and phalanges. The intermembral index (fore / hind limb length) of *M. balearicus* is larger than in the recent Caprinae. All limb segments except the radius are more robust (sagittal diameter relative to the length) than those in the Caprinae. The proportions indicate that in *M. balearicus* robustness, stability and the corresponding reduction of speed are combined with basically cursorial propulsion.

INTRODUCTION

Myotragus balearicus Bate, 1909 is an endemic bovid from the Pleistocene of Mallorca and Menorca, and became extinct 5,000 years B.P. (Burleigh and Clutton-Brock, 1980). In addition to *M. balearicus* the Pleistocene mammalian fauna of Mallorca comprises several species of bats, the shrew *Nesiotites* and the dormouse *Hypnomys*.

The skull of *M. balearicus* is characterized by the very hypsodont teeth, a single pair of continuously growing incisors in the lower jaw and the rostrally facing orbita. Although *M. balearicus* is widely known among paleontologists for its short and stout limb bones (e.g. Kurtén, 1968; Sondaar, 1977; Thenius, 1979 and Alcover et al. 1981), no detailed studies on the proportions of the postcranial skeleton have been made. Only some aspects of the proportions of the limb bones were discussed briefly by Andrews (1914) and Alcover et al. (1981).

In this paper the body proportions of *M. balearicus* are analysed and compared with those of recent Caprinae (the subfamily in which *M. balearicus* is currently placed). Some functional aspects of the characteristic body proportions in *M. balearicus* are discussed in relation to the insular isolation.

MATERIAL AND METHODS

The studied material of *M. balearicus* comes from the cave Son Muleta, and is in the collection of the Deia Archaeological Museum, Mallorca. The age of the material, which consists of isolated bones, ranges from 30,000 to 6,000 years B.P. (Waldren, 1982). In addition one complete skeleton from Cova des Corral des Porc (collection of the Sociedad Historia Natural de Baleares, Palma de Mallorca) was studied. The comparative skeletal material of recent species is in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden, the Institute of Earth Sciences, Utrecht, and the British Museum (NH), London.

The body proportions of *M. balearicus* are studied by the analysis of lengths of the limb bones and the cervical spine relative to the length of the thoracolumbar spine, expressed in various indices. The measurements were taken with Vernier callipers to the nearest millimetre, following the method of Duerst (1926).

The length of the limb bones was measured from the proximal to the distal articulation surface. The sagittal midshaft diameter of the long limb bones and the sagittal diameter of the proximal articulation surface of the phalanges were measured. The sagittal midshaft diameter, which is commonly used in studies concerning allometry and biomechanics (McMahon, 1975; Alexander, 1977; Alexander et al., 1979), is indicative of the bone's moment of resistance against

Table 1: Lengths of the cervical spine, limbs and limb bones given as a percentage of the thoracolumbar spine length, and the intermembral index. Numbers in brackets give the thoracolumber spine length in mm.

	cervical spine	fore limb	hind limb	hum.	rad.	m.c.	o.fe.	tib.	m.t.	ph.1	ph.2	inter-membral
Myotragus balearicus												
Son Muleta (357)	46	95	101	31	40	15	34	39	18	5	4	94
C.d. Corral d. Porcs (315)	45	93	99	30	38	15	33	38	17	6	4	94
Ammotragus lervia (550)	55	116	136	35	40	28	45	49	29	8	5	85
Capra caucasica (579)	50	107	131	35	36	25	42	50	26	8	4	82
C. ibex (546)	48	108	130	35	36	24	43	50	24	8	5	82
Capricornis crispus (442)	42	115	135	37	38	26	43	51	28	9	5	85
C. sumatraensis (484)	44	119	140	40	37	27	46	51	28	9	6	84
Hemitragus jemlahicus (458)	51	111	134	34	37	27	42	51	28	8	5	83
Oreamnos americanus (495)	43	113	134	40	39	21	48	51	23	8	5	84
Ovis ammon musimon (364)	51	122	150	35	38	34	45	54	37	9	5	81
O. vignei (434)	56	131	160	36	43	38	47	58	40	9	5	82
Rupicapra rupicapra (457)	49	125	153	37	41	32	45	57	37	9	5	82
Saiga tatarica (454)	46	112	133	29	36	33	39	44	38	9	4	84
Budorcas taxicolar (764)	39	94	109	35	34	15	40	41	18	6	5	87
Ovibos moschatus (751)	35	111	121	37	39	23	45	42	23	8	4	92

bending. The index of the bone diameter and length represents the robustness of the bone. The length of the thoracolumbar spine, which is representative of the body size, was taken as a standard to calculate the relative lengths of the limb bones. The lengths of the intervertebral disks can only be measured accurately in fresh material and they are therefore omitted in the method of measuring the spine length. Hence in the *M. balearicus* skeleton from Cova des Corral des Porc and in the recent species the cervical and thoracolumbar spine length is the sum of the ventral lengths of the vertebral bodies. To compare the mean lengths of the isolated limb bones (for sample size see table 3) in *M. balearicus* from Son Muleta, the mean length of the thoracolumbar spine was calculated. The mean of the ventral lengths of the thoracal and lumbar vertebral bodies (412 specimens) multiplied by 19 (number of thoracolumbar vertebrae) represents the mean thoracolumbar spine length. The mean length of the cervical spine was calculated by adding the mean length of the vertebral bodies of the atlas (47 specimens), the axis (24 specimens) and the cervical vertebrae 3–7 (93 specimens). The length of the fore and hind limb are defined respectively as the lengths of the humerus + radius + metacarpus + phalanges I and II, and the lengths of the os femoris + tibia + metatarsus + phalanges I and II. Since it proved impossible to separate the phalanges of the fore and hind limb in *M. balearicus*, the data of these bones in the recent species represent the mean of the fore and hind limb measurements.

RESULTS

Table 1 gives the indices of the lengths of the cervical spine, limbs and limb segments relative to the length of the thoracolumbar spine as well as the intermembral index (length fore limb / hind limb × 100). Table 2 shows the

Table 2: Lengths of the limb bones given as a percentage of the fore and hind limb length.

	hum	rad	m.c.	ph.1	ph.2	o.fe.	tib.	m.t.	ph.1	ph.2
Myotragus balearicus										
Son Muleta	32	42	16	5	4	34	39	18	5	4
C.d. Corral d.Porcs	32	41	16	6	4	34	39	18	6	4
Ammotragus lervia	31	34	24	7	4	33	36	21	6	4
Capra caucasica	33	33	23	7	4	32	38	20	6	3
C. ibex	32	33	22	7	4	33	38	19	6	4
Capricornis crispus	32	33	23	7	5	31	38	21	6	4
C. sumatraensis	34	31	23	7	5	33	36	20	6	4
Hemitragus jemlahicus	31	33	24	7	4	32	38	21	6	4
Oreamnos americanus	35	35	19	7	4	36	38	17	6	4
Ovis ammon musimon	29	31	28	7	4	30	36	25	6	4
O. vignei	27	33	29	7	4	30	36	25	6	3
Rupicapra rupicapra	30	33	26	7	4	29	37	24	6	4
Saiga tatarica	26	32	29	8	4	29	33	28	7	3
Budorcas taxicolar	37	36	16	6	5	37	37	16	5	4
Ovibos moschatus	33	35	21	7	4	37	34	19	6	4

length of each limb segment as a percentage of the total length of the limb, and table 3 the indices representing the robustness of each limb segment. When the term "Caprinae" is used in the following comparison and discussion, *Budorcas taxicolar* and *Ovibos moschatus* are not included. These two species (both about twice as large as *M. balearicus*) are discussed separately to prevent misinterpretation of the indices due to the allometric effects of differences in body size.

The proportions which were statistically calculated for *M. balearicus* from Son Muleta correspond well to those of the individual from Cova des Corral des Porcs (tables 1 and 2). The indices calculated in the same way for material from the caves Son Maiol and Cova des Moro (both isolated bones of around 25 individuals) reveal the same values. It can be concluded that the method of comparing the means of the limb bone lengths with a calculated mean spine length gives an accurate representation of the body proportions.

The relative necklength in *M. balearicus* is within the range of that in the recent Caprinae. The length of the forelimb of *M. balearicus* is smaller than that of the Caprinae due to the shorter humerus, metacarpus and phalanges. The difference between the hind limb length in *M. balearicus* and the Caprinae is even larger than that for the fore limb. Therefore the intermembral index of *M. balearicus* is considerably larger than that of the Caprinae. All limb segments, especially the metatarsus, contribute to the shortness of the hindlimb. Table 2 shows that the length of the humerus as a percentage of the forelimb length is about the same in *M. balearicus* and the recent Caprinae, since the relatively short metacarpal bone and phalange I in *M. balearicus* are compensated by its relatively long radius. In *M. balearicus* the five limb

Table 3: The index of robustness (definition see Material and Methods.

		hum	rad	m.c.	o.fe.	tib.	m.t.	ph.1	ph.2
Myotragus balearic	*n*	114	70	210	119	124	117	72	76
Son Muleta	X	17	11	22	13	10	21	56	73
	SD	1	8	2	1	1	2	4	6
	range	15–19	8–12	18–27	11–15	9–12	18–25	48–66	61–86
Ammotragus lervia		14	9	10	10	8	10	43	52
Capra caucasica		13	8	10	9	7	10	43	59
C. ibex		14	9	11	9	7	11	34	46
Capricornis crispus		11	9	9	9	6	10	39	42
C. sumatraensis		12	12	9	8	7	9	33	46
Hemitragus jemlahicus		14	9	11	10	8	10	38	59
Oreamnos americanus		14	10	12	9	7	13	37	48
Ovis ammon musimon		12	7	7	8	6	8	39	51
O. vignei		12	7	8	9	6	8	39	54
Rupicapra rupicapra		11	7	7	9	7	8	37	56
Saiga tatarica		12	7	7	8	7	8	31	63
Budorcas taxicolar		14	14	16	11	9	14	50	50
Ovibos moschatus		18	10	13	11	8	16	47	79

segments contribute to the whole length of the hind limb to almost the same extent as they do in Caprinae. Among the Caprinae *Oreamnos americanus* has the relatively shortest metapodia. However, in contrast to *M. balearicus*, this species has normal caprine limb lengths and also the relatively longest stylopodial segments (humerus and os femoris) among the Caprinae.

Table 3 shows that all limb segments, except the radius, are notably more robust in *M. balearicus* than in the Caprinae. One can visualize the robustness as a linear relation between the length and the midshaft diameter by plotting these variables on log-log scales. As an example the length and diameter of 119 specimens of the os femoris in *M. balearicus*, and those of this bone in 84 recent artiodactyl species (after McMahon, 1975) are plotted in fig. 1. The cluster of *M. balearicus* is clearly below that of the recent artiodactyls, and it is directed approximately parallel to the regression line for the recent species. This shows that the robustness of the os femoris in *M. balearicus* is a character which is independent of size.

The limbs, metapodia and phalanges are as short in *Budorcas taxicolor* as

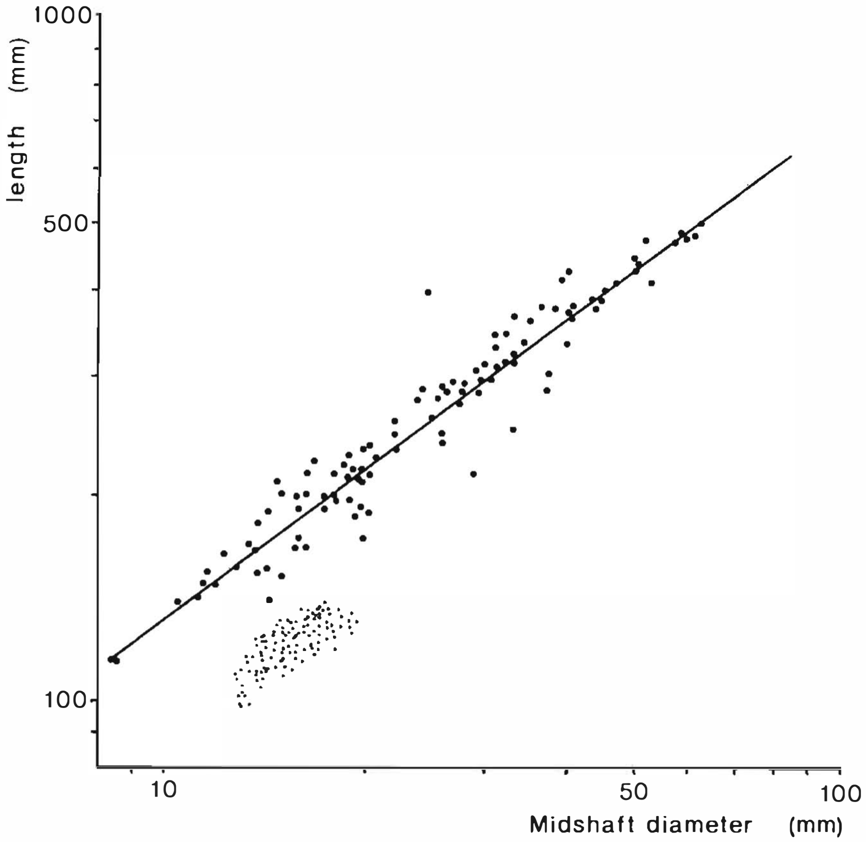

Fig. 1. Length versus sagittal midshaft diameter of the os femoris. The large dots represent 84 species of recent Artiodactyla (after McMahon, 1975), and the small dots represent 119 specimens of *Myotragus balearicus* from Son Muleta.

they are in *M. balearicus*. Like *O. americanus* it differs from *M. balearicus* by its relatively long stylopodial segments and its "normal" intermembral index. The lengths of the limbs and the stylopodial segments in *B. taxicolar* are comparable to those in other equal-sized (large) Bovidae. However, its metapodia are the shortest observed among all recent Bovidae. *Ovibos moschatus* is the only known recent bovid which has an intermembral index as large as that of *M. balearicus*.

DISCUSSION

Shortening of the limbs, especially in the distal region, is a phenomenon which is generally known in many mammals from endemic insular faunas (Sondaar, 1977). It is thought to be related to the particular conditions of the island environment (e.g. the absence of large carnivores and the relatively limited area), which do not require adaptations to fast locomotion. From this point of view the proportions in *M. balearicus* are the consequence of the shortening of all limb segments (except the radius) during its isolated evolution.

In order to study whether the body proportions of *M. balearicus* are the product of a simple shortening process or that additional changes in the midshaft diameters must have occurred, I took the proportions of each of the recent Caprinae as being those of the fictive mainland ancestor of *M. balearicus*. After a theoretical shortening of the caprine limb bones to the relative lengths in *M. balearicus*, new (post-shortening) indices of robustness of the caprine bones were calculated. These new indices of robustness must correspond to those in *M. balearicus* if only shortening marked the changes in proportion from the fictive ancestor to *M. balearicus*. Table 4 gives the post-shortening indices of robustness in each of the caprines together with the real values in *M. balearicus*. The proportions of the humerus, radius, os femoris and tibia in *M. balearicus* can largely be explained by a simple decrease in the length of these bones in any hypothetical caprine-shaped ancestor. The data of the metapodia suggest addi-

Table 4: The expected indices of robustness in recent Caprinae after shortening to the length proportion in *Myotragus balearicus*, and the real values in the latter.

	hum	rad	m.c.	o.fe.	tib.	m.t.	ph.1	ph.2
Myotragus balearicus								
Son Muleta	17	11	22	13	10	21	56	73
Ammotragus lervia	17	9	13	13	11	16	64	62
Capra caucasica	14	7	13	11	9	15	62	64
C. ibex	16	8	14	12	9	15	51	53
Capricornis crispus	13	9	11	11	8	15	63	55
C. sumatraensis	16	11	13	11	9	15	53	65
Hemitragus jemlahicus	16	8	14	12	10	16	56	69
Oreamnos americanus	19	10	15	13	9	16	52	59
Ovis ammon musimon	14	6	11	11	8	17	66	67
O. vignei	14	8	12	12	8	17	66	71
Rupicapra rupicapra	14	8	11	12	9	17	61	74
Saiga tatarica	12	6	8	9	7	16	53	64

tional increase of the midshaft diameter. This increase might have a functional background, in the sense that it renders the bone more robust. However, it might also have been a consequence of the shortening process in the metapodia. If the distance between the epiphyses becomes as small as in the metapodia of *M. balearicus*, the midshaft diameter will tend to approach the diameter of the epiphyses.

Shortening of the limbs also occurred during the domestication process of *Capra* and *Ovis*. However, the intermembral index and length of the limb segments relative to the limb length remained the same as in the wild species. The limbs of certain races of *Ovis aries* are for instances as short as those of *M. balearicus*, but like their wild ancestors, they have relatively long metapodia (fig. 2).

Shortness of the limbs and distal limb bones is characteristic for the proportions in relatively unspecialized (i.e. less-cursorial) artiodactyls like *Tayassu albirostris* and *Hyemoschus aquaticus* (which both have fused metapodia 3 and 4). However, these species differ from *M. balearicus* in having longer stylopodial than zygopodial (radius and tibia) segments (fig. 2), and the same intermembral indices as observed in the recent Caprinae.

The relation between the body proportions and the locomotion pattern of mammals was studied extensively by e.g. Gregory (1912), Howell (1944), Smith and Savage (1956) and Gambaryan (1974). In the light of these studies the short limbs, metapodia and phalanges in *M. balearicus* are typical non-cursorial characters, whereas relatively short stylopodial and long zygopodial segments are usually related to cursorial locomotion. This paradoxical length distribution of the limb segments is also found in some primitive condylarths and perissodactyls which had "high speed tibial and radial ratios and low speed

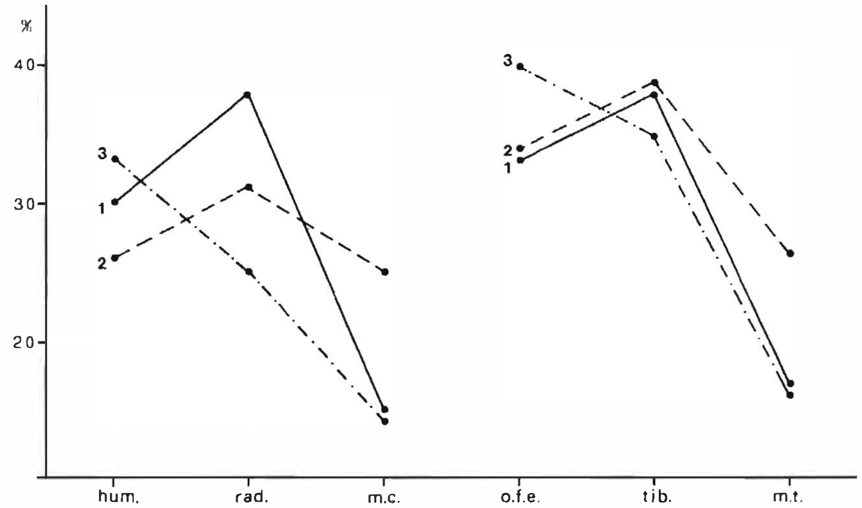

Fig. 2. Length of the long limb bones as percentage of the thoracolumbar spine length in three short-limbed artiodactyls. 1. *Myotragus balearicus*, 2. *Ovis aries*, race from the Netherlands, 3. *Tayassu albirostris*.

metapodial ratios" (Howell, 1944). The short and robust limbs, metapodia and phalanges are clearly related to a gain in stability and a reduction in speed, if compared to other Caprinae. In *M. balearicus* the centre of gravity of the body is closer to the ground, and the lever arms of disarticulating forces working on the distal limb joints are reduced. The protractor and retractor muscles, which are largely responsible for the propulsion, are mainly inserted in the region around the elbow and knee joint. Relatively long stylopodial segments produce more powerful propulsion than short ones which are more related to speed. The stylopodial segments have about the same relative length (to the limb length) in *M. balearicus* as in most of the Caprinae, despite the short metapodia and phalanges in the former. Therefore the various lever arms of the protractors and retractors of the hip and shoulder joint were probably proportionally equal in *M. balearicus* and the Caprinae. From this it might be concluded that the type of the locomotory propulsion in *M. balearicus* was not absolutely different from that in recent Caprinae. In *M. balearicus* robustness, stability and the resulting reduction of speed are combined with basically cursorial propulsion. The absence of carnivores must have been a major condition for the evolution of these proportions.

Since *Budorcas taxicolar* has considerably shorter metapodia than equally sized Bovidae, the proportions in this species and *M. balearicus* might represent analogous adaptations. However, although one can draw conclusions about a generally common stability, very few deductions can be drawn from the available data since the allometric effects due to differences in body size (e.g. large Bovidae tend to have relatively short limbs with long stylopodial and short metapodial segments) are very complex.

The functional implications of the unusual intermembral index (the forelimb which is relatively long in relation to the hind limb) in *M. balearicus* and *Ovibos moschatus* are not understood. According to Kummer (1959) the index has no influence on the distribution of the body weight over the fore and hind limbs. In the case of *M. balearicus* it might be a non-functional consequence of the process of shortening in the limb bones. In the recent Hyaenidae the intermembral index is larger than in the recent Canidae. This difference, which is comparable to that between *M. balearicus* and recent Caprinae, was found to be significantly related to the locomotion pattern (Spoor, 1985; Spoor and Belterman, 1986). Analysis of the fossil footprints of *M. balearicus* (described by Fornos and Pons-Moya, 1982), might give information about its locomotion pattern.

A study of the morphology of the limb bones of *M. balearicus*, especially of the articulation surfaces and the muscle insertions, will supply more information about the relation between the morphology of the skeleton of *M. balearicus* and its mode of life.

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