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Authors' addresses: JOHN P. DUNN, Pennsylvania Game Commission, Rt. 3, Box 61F, Boswell, Penn. 15531, USA; Prof. Dr. JOSEPH A. CHAPMAN, Department of Fisheries and Wildlife, College of Natural Resources, Utah State University, Logan, Utah 84322, USA

Osteological measurements and some remarks on the evolution of the Svalbard reindeer, *Rangifer tarandus platyrhynchus*

By G. F. WILLEMSSEN

Institute of Earth Sciences, Utrecht, The Netherlands

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Abstract

Some measurements of the limb bones of *Rangifer tarandus platyrhynchus* are presented and a comparison with other reindeer subspecies is made. It is pointed out that the Svalbard reindeer shows an interesting parallel with many pleistocene island ruminants. Some remarks on the possible evolution of the Svalbard reindeer are made.

Introduction

The Svalbard reindeer, *Rangifer tarandus platyrhynchus* Vrolik, 1829 is probably the most clearly distinguishable of all subspecies of *Rangifer tarandus* (L., 1758), the reindeer and caribou. The species is highly variable and many different forms can be distinguished. The taxonomy is far from uniform, but there is no doubt about the subspecific rank of *R. t. platyrhynchus*.

The most striking differences with the other subspecies are its small size and its short legs. In this paper I present some measurements on the limb bones of this animal as well as some remarks on its evolution.

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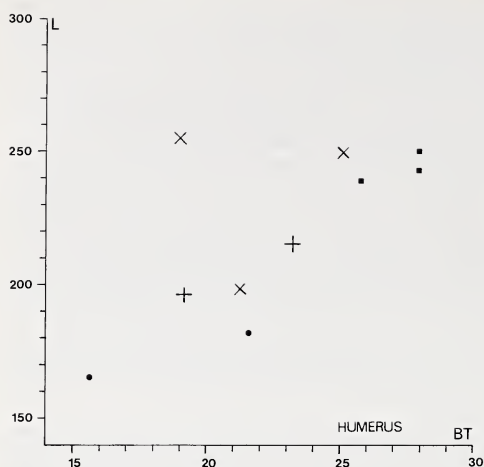


Fig. 1. Length and diaphysal width of the humerus. Fig. 1-6: *Rangifer tarandus* ♦ - *eogroenlandicus*, × - *fennicus*, ■ - *groenlandicus*, ● - *platyrhynchus*, + - *tarandus*, j - juvenile

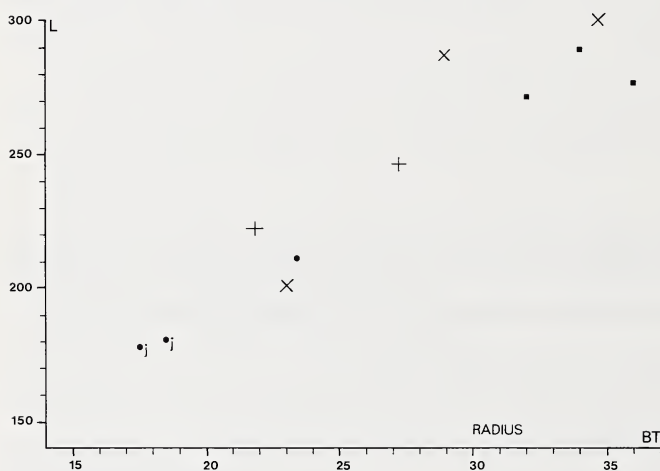


Fig. 2. Length and diaphysal width of the radius

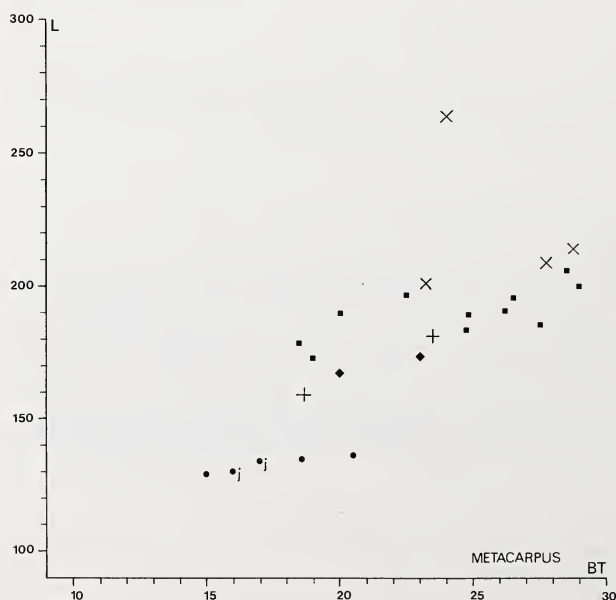


Fig. 3. Length and diaphysal width of the metacarpus

Fig. 4. Length and diaphysal width of the femur

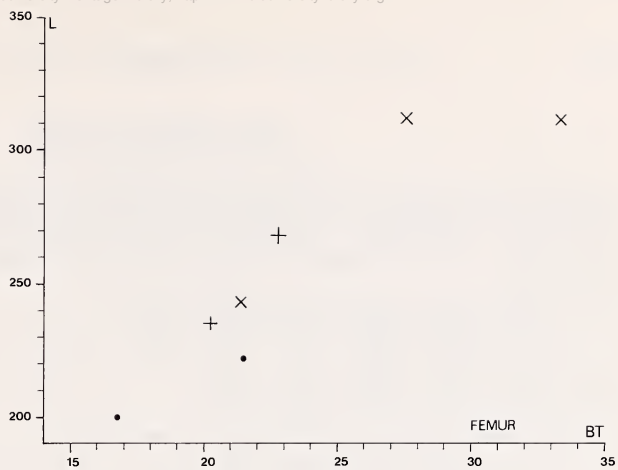


Fig. 5. Length and diaphysal width of the tibia

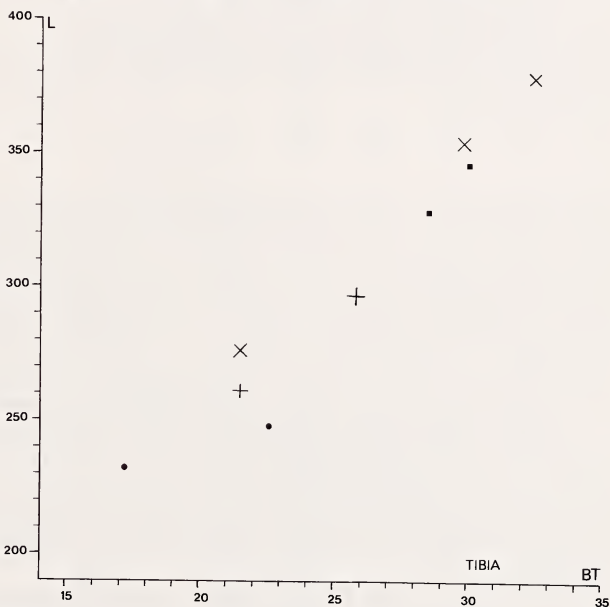
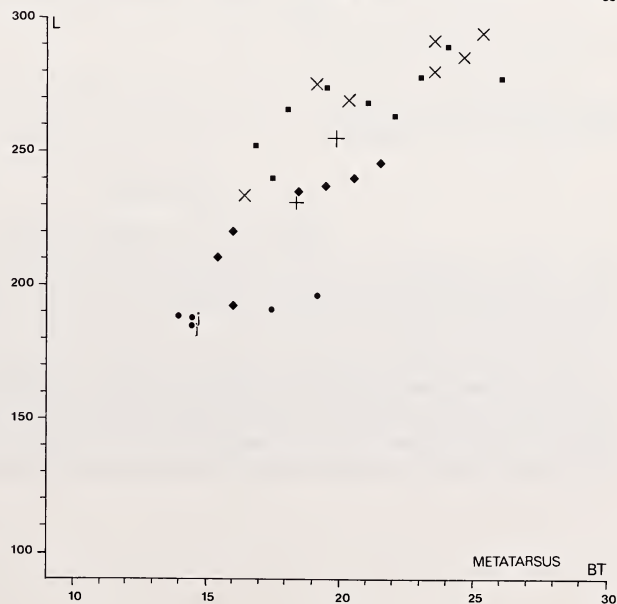


Fig. 6. Length and diaphysal width of the metatarsus



Material and methods

All reindeer specimens of which I present measurements in this paper are in the collection of the Naturhistoriska Riksmuseet in Stockholm. The approximate ages of the juvenile specimens, given in the catalogue of the museum, were checked by the eruption pattern of the teeth (BROMÉE-SKUNCKE 1952). Bones, in which the epiphyses and the diaphysis are fused, are considered to have reached their adult length.

The following measurements were taken:

- L: humerus: length from head to medial epicondyle
- femur: length from head to lateral epicondyle
- other bones: total length

BT: Smallest transversal width of the diaphysis

All measurements are given in millimeters.

The following subspecies have been used for comparison:

R. t. tarandus (L., 1758) from Scandinavia.

R. t. fennicus Lonnberg, 1909 from Scandinavia.

R. t. eogroenlandicus Degerbøl, 1957 from East Greenland.

R. t. groenlandicus (Borowski, 1780) from West Greenland.

Measurements of the latter two subspecies are taken from DEGERBØL (1957). I followed the taxonomy of BANFIELD (1961).

Results

The measurements of the limb bones of the front leg are given in table 1, those of the hind leg in table 2. From the tables and from the figures, it is clear, that all bones are smaller in *R. t. platyrhynchus* than in the other subspecies. In table 3, the length of the humerus, radius and metacarpus and of the femur, tibia and metatarsus are given as a percentage of the total length of humerus, radius and metacarpus, respectively of femur, tibia and metatarsus. It is clear that the metacarpus is relatively shorter in the Svalbard reindeer than in the other subspecies. The metatarsus is relatively somewhat shorter than in the *R. t. tarandus* specimens, but with *R. t. fennicus* there is no difference.

In table 4 some indexes are given, which are calculated by dividing the lengths of the two bones. The metacarpus/humerus and the metacarpus/radius indexes are considerably lower in *R. t. platyrhynchus* than in the other subspecies. This again shows, that the metacarpus is relatively short in this subspecies. The metatarsus is shorter in the Svalbard reindeer in relation to the tibia if compared with *tarandus*, but not if compared with *fennicus*.

The indexes in table 5 show, that in the *fennicus* specimens the radius is shorter in relation to the tibia than in the other subspecies. In *platyrhynchus* the metacarpus is shorter in relation to the metatarsus.

Summarizing the results, we can say that in *platyrhynchus* all limb bones are shorter than in the other subspecies used for comparison. The metacarpal bone is relatively more shortened than other bones.

Discussion

The size of *R. t. platyrhynchus*

The Svalbard reindeer is smaller than the other reindeer subspecies. This is clear from measurements given in WOLLEBAEK (1926), BANFIELD (1961), KROG et al. (1976) and LØNØ (1959, 1968).

KROG et al. (1976) compared Svalbard reindeer with domestic reindeer from Hinnøya, Norway. They found, that the Svalbard reindeer is smaller. They state that "... the dimensions of the Spitsbergen deer are significantly smaller than those of the continental deer they are compared with; an exception to this, however, is the somewhat longer back and larger circumference of the chest. The latter may be due to the thicker pelt and a larger

Table 1
 Measurements of the front leg

		Humerus		Radius		Metacarpus		1st phal.		2nd phal.	
		L	BT	L	BT	L	BT	L	BT	L	BT
<i>platyrhynchus</i>											
NRS 4690	♂ juv.	—	—	181	18.5	133.7	17.0	40.0	12.8	30.2	11.5
NRS 4689	♂ juv.	—	—	178	17.5	130.2	16.0	39.6	12.6	29.4	11.2
NRS 8326	♂ ad.	182	21.6	211	23.4	136	20.5	39.0	14.2	31	13.0
NRS 8318	ad.	165	15.6	—	—	129.8	15.0	—	—	—	—
NRS 4700	♀ ad.	—	—	—	—	134.7	18.6	38.9	11.5	29.5	11.7
<i>tarandus</i>											
NRS M340	♂ ad.	215	23.3	246	27.2	181	23.5	51.1	15.4	—	—
NRS 2846	♀ ad.	196	19.2	222	21.8	169	18.7	46	14.3	33	12.6
<i>fennicus</i>											
NRS 4684	ad.	249	25.2	287	28.9	209	27.7	181	23.5	51.1	15.4
NRS 4685	♂ ad.	255	19.1	300	34.7	264	24.0	—	—	—	—
NRS 4679	ad.	198	21.3	201	23.0	—	—	—	—	—	—
NRS 5-II	♂ ad.	—	—	—	—	201	23.2	56.2	15.7	42.2	14.8
NRS 1-VI	♂ ad.	—	—	—	—	214	28.7	59.1	16.8	44.3	16.1
<i>eogroenlandicus</i>											
ZMC 647	♂	—	—	—	—	174	23	—	—	—	—
ZMC 592		—	—	—	—	168	20.0	—	—	—	—
NRS 1919	♂	210	—	239	—	171	—	—	—	—	—
NRS 1389	♀	190	—	220	—	158	—	—	—	—	—
ZMC 982		—	—	226	—	—	—	—	—	—	—
ZMC Dødemans- bugd.		—	—	247	—	—	—	—	—	—	—
<i>groenlandicus</i>											
ZMC 886	♂	250	28	289	34	206	28.5	—	—	—	—
ZMC 1048	♂	243	28	276	36	200	29	—	—	—	—
ZMC 2736	♂	—	—	—	—	197	22.5	—	—	—	—
ZMC 2726	♂	—	—	—	—	196	26.5	—	—	—	—
ZMC 2727	♂	—	—	—	—	190	24.8	—	—	—	—
ZMC 1611	♂	239	25.8	271	32	186	27.5	—	—	—	—
ZMC 2737	♂	—	—	—	—	184	24.7	—	—	—	—
ZMC 2720	♀	—	—	—	—	190	20	—	—	—	—
ZMC 709	♀	—	—	255	—	190	—	—	—	—	—
ZMC 2719	♀	—	—	—	—	179	18.6	—	—	—	—
ZMC 2718	♀	—	—	—	—	173	19.0	—	—	—	—
ZMC Kagsiarsuk Igaliko		—	—	—	—	191	26.2	—	—	—	—

NRS = Naturhistoriska Riksmuseet Stockholm; ZMC = Zoologisk Museum Copenhagen; *platyrhynchus* specimens NRS 4690 and 4689 are juveniles, ca. 15 months old. Data on *eogroenlandicus* and *groenlandicus* from DEGERBØL (1957).

material may show that the body length is in accordance with the rest of differences observed" (p. 409). They give a mean body length of 164.5 cm ($n = 10$, $SD = 4.2$) for males and 154.2 cm ($n = 18$, $SD = 6.9$) for females. LØNØ (1959, 1968) gives body lengths of several animals with adult males ranging from 135 to 155 cm and females from 125 to 140 cm. So these are indeed smaller than the animals measured by KROG et al. (1976). It must, however, be noted that the animals of LØNØ are from Nordaustlandet and Edgeøya, while those of KROG et al. (1976) are from West Spitsbergen. LØNØ (1959) mentions, that several people say, that the reindeer from Nordaustlandet are smaller than those from other places, but that this is improbable considering the data he presents. OOSTERVELD (1973)

Table 2
Measurements of the hind leg
(See remarks with table 1)

		Femur		Tibia		Metatarsus		1st phal.		2nd phal.	
		L	BT	L	BT	L	BT	L	BT	L	BT
<i>platyrhynchus</i>											
NRS 4690	juv.	—	—	—	—	188	14.5	42.0	12.1	32.2	10.5
NRS 4689	juv.	—	—	—	—	185	14.5	41.8	12.4	31.1	10.3
NRS 8326	ad.	222	21.5	248	22.6	196	19.2	41	12.4	31	12.3
NRS 8318	ad.	200	16.8	232	17.2	189	14.0	—	—	—	—
NRS 4700	ad.	—	—	—	—	191	17.5	42.3	12.6	30.6	10.7
<i>tarandus</i>											
NRS M340	ad.	268	22.8	297	25.8	255	19.9	54.6	14.3	—	—
NRS 2846	ad.	235	20.3	261	21.5	231	18.4	50	14.0	37	12.1
<i>fennicus</i>											
NRS 4684	ad.	312	27.6	354	29.8	285	24.6	64.4	17.0	44.5	15.5
NRS 4685	ad.	311	33.4	378	32.4	291	23.5	—	—	—	—
NRS 4679	ad.	243	21.4	276	21.5	233	16.5	—	—	—	—
NRS 5-II	ad.	—	—	—	—	269	20.3	59.9	16.5	44.8	14.0
NRS 1-VI	ad.	—	—	—	—	294	25.3	—	—	—	—
NRS 4-I	ad.	—	—	—	—	280	23.5	—	—	—	—
NRS 8-V	ad.	—	—	—	—	275	19.1	—	—	—	—
<i>eogroenlandicus</i>											
ZMC 647		—	—	—	—	246	21.5	—	—	—	—
ZMC 592		—	—	—	—	235	18.4	—	—	—	—
NRS 1919		—	—	285	—	237	19.4	—	—	—	—
NRS 1839		—	—	265	—	220	16	—	—	—	—
ZMC 982		—	—	—	—	240	20.5	—	—	—	—
ZMC Kap Dan		—	—	—	—	192	16	—	—	—	—
Angmagssalik											
ZMC Messervig		—	—	298	—	—	—	—	—	—	—
<i>groenlandicus</i>											
ZMC 886		—	—	346	30	288	24	—	—	—	—
ZMC 1048		—	—	334	—	277	26	—	—	—	—
ZMC 2736		—	—	—	—	274	19.5	—	—	—	—
ZMC 2726		—	—	—	—	278	23	—	—	—	—
ZMC 2727		—	—	—	—	268	21	—	—	—	—
ZMC 1611		—	—	328	28.5	—	—	—	—	—	—
ZMC 2737		—	—	—	—	263	22	—	—	—	—
ZMC 2720		—	—	—	—	266	18	—	—	—	—
ZMC 709		—	—	312	—	265	18	—	—	—	—
ZMC 2719		—	—	—	—	252	16.8	—	—	—	—
ZMC 2718		—	—	—	—	240	17.5	—	—	—	—

states that "The reindeer-population of West Spitsbergen makes generally a somewhat more robust impression than the population of Edgeøya" (p. 18). The data available now, are too few to decide on whether such local differences exist, but they do not disprove a difference between the West Spitsbergen population and the Edgeøya and Nordaustlandet populations.

The legs of the Svalbard reindeer are relatively short. This fact has been noticed by many investigators, but measurements are scarce. ANDERSÉN (1862) compared the bones of the Svalbard reindeer with the Greenland, Lapland and fossil Skåne reindeer. He states, that humerus, radius and metacarpus are shortest in the Lapland reindeer. The tibia is shortest in the Svalbard reindeer and longest in the Greenland reindeer, while the metatarsus is

Table 3

Length of limb bones as a percentage of the total length of the three long bones
of front resp. hind leg

(For abbreviations see table 1)

	Humerus	Radius	Metacarp	Femur	Tibia	Metatars
<i>platyrhynchus</i>						
NRS 8326	34.40	39.89	25.71	33.33	37.24	29.43
NRS 8318	—	—	—	32.15	37.37	30.48
<i>tarandus</i>						
NRS M340	33.49	38.32	28.19	32.68	36.22	31.10
NRS 2846	33.39	37.82	28.79	32.32	35.90	31.77
<i>fennicus</i>						
NRS 4684	33.42	38.52	28.05	32.81	37.22	29.97
NRS 4685	31.14	36.63	32.23	31.73	38.57	29.69
<i>eogroenlandicus</i>						
NRS 1919	33.87	38.55	27.85	—	—	—
NRS 1839	33.45	38.37	27.82	—	—	—
<i>groenlandicus</i>						
ZMC 886	33.56	38.79	27.65	—	—	—
ZMC 1048	32.88	37.35	27.06	—	—	—
ZMC 1611	34.34	38.94	26.72	—	—	—

Table 4

Indexes of limb bones, calculated by dividing their total lengths (L)

	ra/hu	mc/hu	mc/ra	ph1 an hu	ph2 an hu	ti/fe	mt/fe	mt/ti	ph1 po fe	ph2 po fe
<i>platyrhynchus</i>										
NRS 8326	1.16	0.75	0.64	0.22	0.16	1.12	0.88	0.79	0.18	0.14
NRS 8318	—	0.79	—	—	—	1.16	0.95	0.82	—	—
<i>tarandus</i>										
NRS M340	1.14	0.84	0.74	0.24	—	1.11	0.95	0.86	0.20	—
NRS 2846	1.13	0.86	0.76	0.23	0.17	1.11	0.98	0.89	0.21	0.16
<i>fennicus</i>										
NRS 4684	1.15	0.84	0.73	0.24	0.17	1.13	0.91	0.81	0.21	0.14
NRS 4685	1.18	1.04	0.88	—	—	1.22	0.94	0.77	—	—
NRS 4679	1.02	—	—	—	—	1.14	0.96	0.84	—	—
<i>eogroenlandicus</i>										
NRS 1919	—	—	0.72	—	—	—	—	0.83	—	—
NRS 1839	—	—	0.72	—	—	—	—	0.83	—	—
<i>groenlandicus</i>										
ZMC 886	1.16	0.82	0.71	—	—	—	—	0.83	—	—
ZMC 1048	1.14	0.82	0.71	—	—	—	—	0.83	—	—
ZMC 1611	1.13	0.78	0.69	—	—	—	—	—	—	—
ZMC 709	—	—	0.75	—	—	—	—	0.85	—	—

hu = humerus; ra = radius; mc = metacarpus; fe = femur; ti = tibia; mt = metatarsus;
ph = phalange

longest in the Svalbard reindeer according to ANDERSÉN (1862). KROG et al. (1976) show, that, that the "metatarsal length" as a percentage of the total length is significantly shorter than in the domestic animals they studied. (They did not measure the metatarsal bone but took the measurement on the intact body, from the heel to the base of the toe.)

From the results presented in this paper, it is clear, that all limb bones are considerably shorter than in other subspecies. Considering the relative proportions of the limb bones, it appears, that the metacarpus is relatively more shortened than the other limb bones. The metatarsus, on the contrary, is relatively not shorter than in *fennicus*. It is, however, shorter in absolute terms.

The Svalbard reindeer forms an interesting parallel with other insular ruminants, hippopotamuses and elephants. A large number of fossil island forms is known, which show dwarfism and shortening of the limb bones, especially of the metapodia and the phalanges. They are known from the Pleistocene of many Mediterranean islands, but also from the Japanese archipelago, the Philippines and the Indonesian archipelago (SONDAAR 1977; DERMITZAKIS and SONDAAR 1979). Examples are *Myotragus balearicus* Bate, 1909, a bovid from the Balears, *Phanourios minor* (Desmarest, 1822), a dwarf hippopotamus from Cyprus, *Candiacervus cretensis* (Simonelli, 1907), a small deer from Crete (see KUSS 1965, 1973, 1975; DE VOS 1979) and *C. cerigensis* Kuss, 1975 from Karpathos and Kasos (KUSS 1967, 1969, 1973, 1975).

Table 5

Indexes of limb bones, calculated by dividing their total lengths (L)

	<u>humerus</u> femur	<u>radius</u> tibia	<u>metacarp</u> metatars
<i>platyrhynchus</i>			
NRS 8326	0.82	0.85	0.69
NRS 8318	0.83	—	0.69
NRS 4700	—	—	0.70
<i>tarandus</i>			
NRS M340	0.80	0.83	0.71
NRS 2846	0.83	0.85	0.73
<i>fennicus</i>			
NRS 4684	0.80	0.81	0.73
NRS 4685	0.82	0.79	0.90
NRS 4679	0.81	0.73	—
NRS 5-II	—	—	0.75
NRS 1-VI	—	—	0.71
<i>eogroenlandicus</i>			
ZMC 647	—	—	0.71
ZMC 592	—	—	0.72
NRS 1919	—	0.84	0.72
NRS 1839	—	0.83	0.72
<i>groenlandicus</i>			
ZMC 886	—	0.84	0.72
ZMC 1048	—	0.83	0.72
ZMC 2736	—	—	0.72
ZMC 2726	—	—	0.61
ZMC 2727	—	—	0.71
ZMC 1611	—	0.83	—
ZMC 2737	—	—	0.70
ZMC 2720	—	—	0.71
ZMC 709	—	—	0.72
ZMC 2719	—	—	0.71
ZMC 2718	—	—	0.80

DE VOS (1979) made a study of the limb bones of the pleistocene deer from Crete. He found a great variation in size and probably more than one species must be distinguished. In the smaller forms he found that the metacarpus was relatively more shortened than the metatarsus and the other bones, just as is the case in the Svalbard reindeer. My own (unpublished) measurements on the Karpathos deer show, that this is also the case in this animal.

Evolution of the Svalbard reindeer

To understand the selectional pressures which caused shortening of the legs and size diminishing, it is necessary to study the functional consequences of these changes. SONDAAR (1977) pointed out, that shortening of the leg reduces locomotion speed. Mainland ruminants need a high speed to escape from predators. The faunas, to which the dwarfish and short legged forms belong, are so-called unbalanced faunas (SONDAAR 1977; DERMITZAKIS and SONDAAR 1979). These faunas lack large carnivores. From the Pleistocene of Crete, for example, no other carnivore than an endemic otter, *Isolalutra cretensis* Symeonides and Sondaar, 1975 is known (SYMEONIDES and SONDAAR 1975; WILLEMSEN 1980).

For the island ruminants from those unbalanced faunas there was no need to be able to move at high speed, since there were no predators to escape from. The same is true for the Svalbard reindeer (LØNØ 1959; NORDERHAUG 1970). The only large carnivore is the ice bear, but they do not feed on reindeer.

On the other hand, short distal parts of the legs might be advantageous in fouraging in the mountainous environment of islands (SONDAAR 1977). It is known, that the Svalbard reindeer often climbs while it is fouraging, at least in some areas (HJELJORD 1975).

We might now try to reconstruct the evolution of the Svalbard reindeer. Where it comes from is not known, but the first reindeer in the Svalbard archipelago probably came from Novaya Semlya (LØNØ 1959; WOLLEBAEK 1926). The reindeer on Novaya Semlya are not extremely small (though, according to HEPTNER et al. [1961] they are of a small type) and do not have short legs. HEPTNER et al. (1961) consider these reindeer to form a separate subspecies, *R. t. pearsoni* Lydekker, 1922. BANFIELD (1961) shows, that there are no reasons to place it in a separate subspecies. He includes it in the subspecies *R. t. tarandus*.

No predators being present on Svalbard, the population could increase rapidly. Overpopulation could have caused food shortage, high mortality and even population crashes from time to time. It is known, that there is a high mortality among Svalbard reindeer nowadays (DE BIE 1977; DE BIE and VAN WIEREN 1980). Under conditions of food shortage selection would favour small sized animals, which need less nutrition. So they have a better chance to survive and are able to produce more offspring than larger conspecifics. The harsh climate may have reinforced this effect. Severe winters cause mass starvation, as happened in 1962–63 (LØNØ 1968; HEINTZ 1964). In the endemic Cretan deer mass starvation also occurred, as is indicated by certain fossils (SONDAAR 1977).

At the same time, selection may have favoured shortening of the legs as an adaptation to locomotion in mountainous areas. Obviously, this is an advantage in heavy competition for limited resources.

KROG et al. (1976) state, that reindeer and caribou get smaller and their legs get shorter further to the north. I do not think that the high latitude, i.e. the arctic climate, is the main cause for the size and the short legs of the Svalbard reindeer. These changes represent a pattern, seen in ruminants on both arctic and subtropical and tropical islands. The harsh climate may, however, as pointed out above, have reinforced the effect.

Some other reindeer show the same characteristics, but not as clearly as *platyrhynchus*. *R. t. eogroenlandicus*, the East Greenland reindeer, extinct since the turn of the century, was also a small form with rather small metapodia. This animal lived on an "ecological island", effectively isolated by the ice from other parts of Greenland where reindeer occur. No

predators were present, the polar wolf is not found in this part of Greenland (DEGERBØL 1957). On West Greenland, where the polar wolf is present, lives another reindeer, *R. t. groenlandicus*, which is normally sized.

On Queen Charlotte Island, for the western coast of Canada, lived a caribou, *R. t. dawsoni* Seton, which became extinct probably shortly after 1935. It was small sized (BANFIELD 1963) but no data are available on bone measurements. Unfortunately, not much material remains of this animal. The only large carnivore on Queen Charlotte Island is the black bear, which is probably not very important as a predator on reindeer.

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Zusammenfassung

Einige osteologische Maße und Bemerkungen über die Evolution des Svalbard-Rens (Rangifer tarandus platyrhynchus)

Einige Maße des Gliedmaßenskeletts vom Svalbard-Ren (*Rangifer tarandus platyrhynchus*) werden mitgeteilt und mit entsprechenden Daten von anderen Unterarten des Rens verglichen. Das Svalbard-Ren erweist sich als eine ziemlich kleine und relativ kurzbeinige Form. Mit diesen Merkmalen bildet es eine interessante Parallele zu vielen pleistozänen Inselformen aus der Gruppe der Ruminantia. Einige Bemerkungen über die mögliche Evolution des Svalbard-Rens werden gemacht. Wichtige Ursachen der Veränderungen scheinen Abwesenheit von Feinden und eingeschränktes Nahrungsangebot zu sein.

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Author's address: Drs. G. F. WILLEMSSEN, Engelenburgstr. 72, NL-6825 KR Arnhem, The Netherlands

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Circadian oscillations of locomotor activity in *Crociodura suaveolens* (Soricidae, Insectivora, Mammalia)

By RENATE SIEGMUND and L. SIGMUND

Department of Animal Behaviour Sciences, Humboldt University, Berlin, GDR, and Department of Systematic Zoology, Charles University, Praha, Czechoslovakia¹

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Although the daily activity pattern in Insectivora has already received much attention (e.g. VOGEL et al. 1981 and other references there), the existence of free-running rhythms has not yet been proved.

We observed and recorded the behaviour of 18 individuals of *C. suaveolens* captured in the Prague Zoological Garden and reared in the Department of Systematic Zoology in Prague from April to August 1982. The animals were kept in glass terraria sized 50 × 30 × 30 cm with a hiding place (box of 10 × 10 × 10 cm), at first at an artificial light-dark cycle (LD cycle 12 : 12 – white light, L: 0700–1900) and at natural light. Later they were exposed only to the artificial LD cycle of 12 : 12 (80 : 0 lux). Long-term variations of

¹ In honour to the 70th birthday of Professor Dr. J. ASCHOFF.

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