Relative growth of the Metapodals in a Juvenile island deer:
Candiacervus (Mammalia, Cervidae) from the Pleistocene of Crete*

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ABSTRACT: One of the diagnostic features of the Late Pleistocene deer of Crete, *Candiacervus*, is its apparent shortened metapodals, just as it is for other endemic island artiodactyls, e.g. *Myotragus* (Balearics, Spain) and *Cervus astylodon* (Ryukyu Islands, (Japan). The question remained whether this shortening is already present at birth or arises during postnatal ontogeny due to a difference in relative growth speed of the different limb elements. In the latter case food quantity and/or quality may have played a crucial role in the development of the diagnostic feature, whereas in the former case a genetic basis seems more likely.

From this study it appears that the shortening of the metacarpals is already present at birth. This shortening increases further during postnatal ontogeny due to a relative slower growth speed.

In addition to relative length and proportional growth, there is also the question of changes in massivity. In general a short metapodal correlates with a higher massivity. The metapodals of *Candiacervus ropalophorus* are far more massive than those of the compared mainland species. This study reveals that this is the case already at birth, and increases further during following ontogeny.

The *Candiacervus* material at our disposal is unique, as it consists of a large number of individuals from one layer in one cave, and which all belong to one population or herd, varying in age from newborn till very old.
Key-words: *Pleistocene, Crete, Candiacervus, Metapodals.*

ΠΕΡΙΛΗΨΗ: Ένα από τα χαρακτηριστικά στοιχεία του *ελαφιού Candiacervus* του Ανωτέρου Πλειστοκαίνου της Κρήτης, είναι τα φαινομενικά κοντά μεταπόδια, όμοια με αυτά άλλων ενδημικών νησιωτικών αρτιοδακτύλων, όπως *του Myotragus* (από τις Βαλεαρίδες τις Ισπανίας) και του *Cervus astylodon* (από τα νησιά Ryukyu της Ιαπωνίας). Το ερώτημα είναι εάν τα κοντά πόδια προϋπήρχαν από τη γένεση ή προέκυψαν κατά τη διάρκεια της μεταγενετικής οντογένεσης εξαιτίας της διαφοράς στο ρυθμό ανάπτυξης των διαφόρων μελών. Στην τελευταία περίπτωση η ποσότητα και/ή η ποιότητα του φαγητού ίσως έπαιξαν καθοριστικό ρόλο στην ανάπτυξη του διαγνωστικού μέλους, ενώ στην πρώτη περίπτωση η γενετική βάση φαίνεται να είναι πιο πιθανή. Στην παρούσα εργασία φαίνεται ότι η βράχυνση των μετακαρπικών εμφανίζεται ήδη από τη γέννηση. Η βράχυνση αυξάνεται κατά τη διάρκεια της μεταγενετικής οντογένεσης εξαιτίας μιας σχετικά πιο αργής ταχύτητας ανάπτυξης.

Εκτός από το σχετικό μήκος και αναλογίες, υπάρχει ακόμα και το θέμα της ευρωστότητας. Τα μεταπόδια *του Candiacervus ropalophorus* είναι πολύ πιο εύρωστα σε σύγκριση με αυτά των ειδών της ηπειρωτικής χέρσου. Όπως αποδεικνύει αυτή η μελέτη, η κατάσταση αυτή ισχύει από τη γέννηση και αυξάνει συνεχώς κατά τη διάρκεια της επικείμενης οντογένεσης.
Λέξεις-κλειδιά: *Πλειστόκαινο, Κρήτη, Candiacervus, Μεταπόδια.*

INTRODUCTION

Many larger mammals of the Mediterranean islands of the Pleistocene share the same characteristic relative shortening of the metapodals compared to their mainland ancestors (SONDAAR, 1977). This has been attested for the Cretan deer *Candiacervus* (KUSS, 1973; DE VOS, 1979; DE VOS & DERMITZAKIS, 1986; VAN DER GEER *et al.*, in press) (Fig.1), the Cretan dwarf hippo *Hippopotamus creutzburgi* (BOEKSCHOTEN & SONDAAR, 1966), the Cypriotic dwarf hippo *Phanourios minutus* (SONDAAR & BOEKSCHOTEN, 1967),

the Balearic mouse-goat *Myotragus balearicus* (ANDREWS, 1915; SPOOR, 1988). The same pattern is not restricted to the Mediterranean, see for example *Cervus astylodon* from the Ryukyu Islands of Japan (MATSUMOTO & OTSUKA, 2000), and also not to the Pleistocene, see for example the Late Miocene *Hoplitomeryx* from the Gargano, Italy (LEINDERS, 1984; VAN DER GEER, 2005). Exceptions are rare, and are as a rule elements of more or less balanced fauna. Example is the Sardinian elk *Megaloceros cazioti* (MALATESTA

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* Σχετική ανάπτυξη των μεταποδίων σε ένα νεαρό νησιωτικό ελάφι: *Candiavervus* (Mammalia, Cervidae) του Πλειστοκαίνου από τη νήσο Κρήτη.
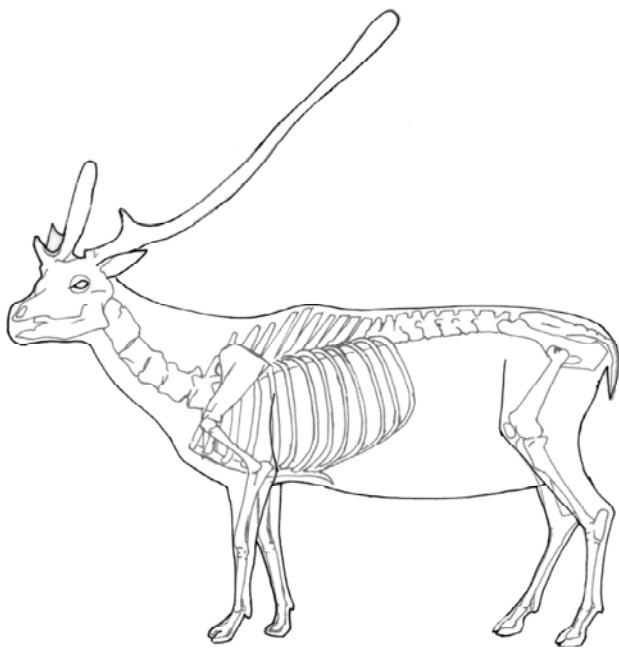
Fig. 1. Reconstruction of the Cretan deer *Candiacervus* size II from Liko Cave, based upon a mounted skeleton made for the Museum of Paleontology, National and Kapodistrian University of Athens (VAN DER GEER *et al*. 2005). From the mount it becomes clear that the limbs of *Candiacervus* are indeed short, especially the metapodals, and that the body is relatively heavy and massive.

Fig. 2. Metatarsals of the eight morphotypes of *Candiacervus* (following the taxonomy of DE VOS, 1979) compared to those of Pleistocene mainland deer. The smaller types deviate extreme from the mainland metatarsals, whereas the largest two sizes are more or less comparable to the mainland metatarsals.

& CALOI, 1974), which is found together with the canid *Cynotherium sardous* and archaic *Homo sapiens* (KLEIN HOFMEIJER, 1996). Other exceptions are the larger varieties of the island species; some times, an intraspecific adaptive radiation takes place in island endemics, resulting in a range of five to eight morphotypes, from small to large (DE VOS & DERMITZAKIS, 1986; DE VOS, 2000; DE VOS & VAN DER GEER, 2002). It is mainly the small and medium sizes which show the characteristic shortening, whereas the large morphotypes are more alike the mainland forms (Fig. 2).

Though this phenomen has been described various times for various species, there are no or little quantative data about the degree of this shortening. This has two main causes. One, only little biometrical research has been done on island mammals in general. Second, most fossil material comes from several individuals and as the variation is known to be larger in island species, any quantitative comparison fails.

The most comprehensive biometrical study has been done by DE VOS (1979) for the Cretan deer *Candiacervus*. In total *Candiacervus* is represented on the island by eight morphotypes as a result of adaptive radiation, distributed over six size classes and three antler morphotyes, from small to large classified as *C. ropalophorus*, *C.* spp. II (a, b and c), *C. cretensis*, *C. rethymnensis, C.* sp. V, and *C.* sp. VI (classification following DE VOS, 1979; DE VOS, 1984; DE VOS, 2000). Other taxonomies (e.g. CAPASSO BARBATO, 1989; CALOI & PALOMBO, 1996) recognize five species, but
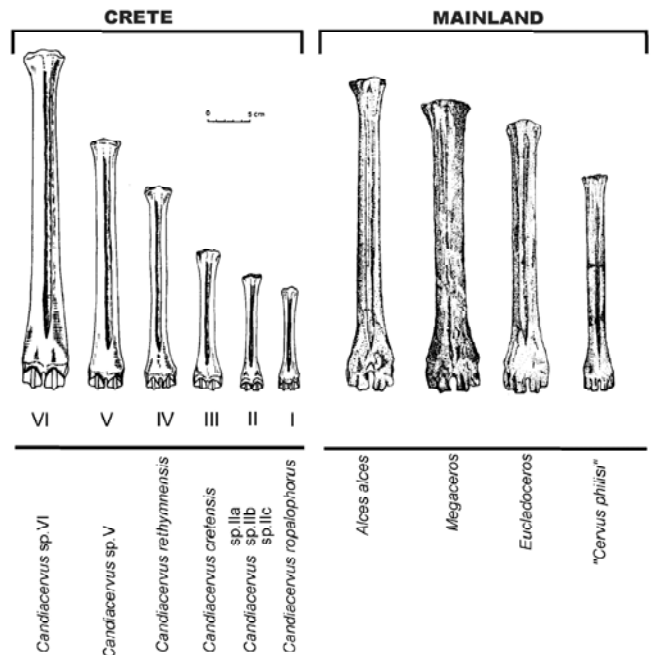
these opinions are not followed here; ontogenetic features may eventually contribute in solving this problem.

Ontogenetic studies on islanders are even more rare, with only BOVER & ALCOVER (1999 a,b) on *Myotragus* being an exception. Their description is not only the only one of a neonate skeleton for an island mammal, but in fact for any extinct artiodactyl.

In this paper we will try to check the presence of the metapodial shortening at birth and what happens during further ontogeny. This can be done only if a certain amount of juvenile as well as of adult material is available belonging to one herd or group. In addition, the effect of ontogeny on shortening will be the highest in the smallest variety. Therefore we focus only on size 1 (the smallest), described as *Candiacervus ropalophorus*. One locality catches the eye: Gerani 4. Here, the bones show a remarkable uniformity in size and the antlers are remarkably uniform in morphology, from which DE VOS (1979) concludes that here only one form of the Cretan deer can be present: size 1 (the smallest). This makes Gerani 4 the ideal site for an ontogenetic study.

It happens that this material consists of a large amount of individuals of varying age, from newly born to very old. It is very likely that we deal here with a natural herd, which died here, due to a natural disaster of an unknown type. This means that there are individuals of more than one life stage in the collection, from unborn and newly born upto aged animals. As such, the material provides us with the unique

opportunity of obtaining quantitative data about the relative growth and shortening of the various limb elements.

Aim of this study is to check whether indeed a shortening takes place of the metapodals. And if this shortening is already present at birth, or gradually occurs during growth into the adult stage, by relative differences in growth speed of the various limb elements in relation to each other.

MATERIALS AND METHOD

All material of *Candiacervus ropalophorus* c o m es from the locality Gerani 4 (Fig. 3). This locality is situated on the north-western coast of Crete, and consists of a cave along the coast, filled with fossiliferous sediment (KUSS, 1970; DE VOS, 1979). KUSS (1970) provided a radiocarbon dating of ± 43.600 BP for the calcareous layer that covers the fossils. This means that the deer of Gerani 4 lived during the Late Pleistocene.

The fossil material consists of a large number of skulls, antlers and postcranial elements in such ratios that it is likely to assume the presence of (almost) only complete individuals. For this study only the long bones of the limbs were used: humerus, radius, metacarpus, femur, tibia and metatarsus. Materials were classified ranging from newly born till of full-grown, with a large number of representatives per group. In the long bones five age groups could be distinguished (BISKOP, 1978), of which in this study the newborns and the full growns were used. Humerus: 49 newborn, 24 other juveniles, 56 full grown. Radius: 45 newborn, 28 other juveniles, 62 full grown. Metacarpal: 3 7 newborn, 38 other juveniles, 48 full grown. Femur: 47 newborn, 16 other juveniles, 33 full grown. Tibia: 27 newborn, 22 other juveniles, 62 full grown. Metatarsal: 36 newborn, 29 other juveniles, 54 full grown.

The material originates from one population only, as indicated by the presence of only one type of antler is present, whereas *Candiacervus* as a whole shows a wide variation in antler form (DE VOS, 1979). The material appears

Fig. 3. The cave Gerani 4 along the northwestern coast of Crete.

to comprise several age groups, which can be separated very precisely and do not overlap. These groups vary from newborns to adults.

The clearly distinguishable age groups fit to the presence of a complete herd, which most likely all died in a relative short time.

For recent comparison material, we used red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) from the following institutes: Anatomie Comparé, Paris, France; Biological Archeological Institute, University of Groningen, the Netherlands; Faculty of Earth Sciences, University of Utrecht, the Netherlands; Naturalis, National Natural History Museum, Leiden, the Netherlands; Natuurmuseum Rotterdam, the Netherlands (Rotterdam). Specimens marked with asterix (our mark) are the newborns.

The material of red deer belonged to ten individuals [nos. 1887-339, 1910-209, 1912-301*, 1938-45, 1944-293*, 2x n.n. (Paris); no. 192 (Groningen); 1x n.n. (mounted skeleton)*, no. 2169* (Leiden)].

The material of fallow deer belonged to nine individuals [nos. 1873-327, 1883-452, 1882-182, 1884-547, 1938-76, 1943-44, 1943-104*, 1974-217* (Paris); n.n. (Groningen); cat a, cat b, cat c, cat d (Leiden)].

The material of roe deer belonged to twenty individuals [nos. 26, 814, 842, 917, 957, 1001, 1045 (Groningen); nos. 39, 296, 297, 299* (Utrecht); nos. 50, 114, 119 (Rotterdam); nos. 1854-101, 1919-38, 1939-54, 1946-41, 2x n.n. (Paris); nos. 1041, 19654, cat. b (Leiden)]; in addition, we had six adult metatarsals to our disposal: nos. 34209, 34246, 34250, 34256, 34261, 34266 (Leiden).

The long bones are classified according to the developmental stage, as evidenced by the degree of fusion of the proximal and distal epiphyses to the diaphysis. As long b ones in deer are considered the humerus, radius, metacarpus, femur, tibia and metatarsus. Strictly speaking also the ulna and fibula belong to the long bones, but for practical reasons are not taken into consideration, as they are often lacking or heavily damaged, especially so in the youngest age classes. Classification is done according to the development of the bones from newly born till mature. As standard for full-grown or mature we chose the stage where both proximal and distal epiphyses are fully fused to the d i a p h ysis, with no trace of growth lines.

The following criteria are used to classify an element as newborn, based upon the comparison material of which age was known and on data from the literature (HEINTZ, 1970; POHLMEYER, 1985). Humerus: both epiphyses are unfused and the proximal articulation area is hardly developed. Radius: both epiphyses unfused. Metacarpal: the proximal epiphysis is already fused at birth, but on the proximal articulation the separation ridge between the internal and external facet is not yet developed (see HEINTZ, 1970). Femur: both epiphyses unfused, the proximal side of diaphysis hardly developed, especially the surface of the head-to-be, and the depth of fovea capitis hardly developed. Tibia: both epiphyses unfused, tibial crest hardly developed,

and distal end also hardly developed. Metatarsal: proximal epiphysis already fused at birth, proximal articulation however hardly developed; facet of cuneiform minor and the navico-cuboid posterior hardly developed (see also Heintz, 1970).

Measurements are in mm. Measurements of *Candiacervus* are partly taken from Biskop (1978). The measurements taken in this study necessarily deviate from the standard measurement. Reason is that such measurements are defined for adult specimens, in which the epiphyses are present. In the majority of this collection the epiphyses are missing. To compare newborn with full-grown, only diaphyseal length was taken. This is valid, as it is almost exclusively the length growth of the diaphyse which accounts for the total length growth of a bone. As it is not precise to measure the diaphyseal length from an adult bone where the growth lines are fully fused and invisible, we measured the epiphysal length at the development stage at which the corresponding growth line is, yet still (hardly) visible. This length is deducted from overal length of the just full-grown individuals in case of the comparison collection, where age is known, and of the full-grown average in the case of *Candiacervus*. Complete closure takes place at different ages for the proximal and distal epiphyses.

Measurements of maximal shaft length are taken as follows (Fig. 4). Humerus: on posterior side, the distance between the distal surface of the head and the lateral epicondylus at the distal side. Radius: on posterior side, the smallest distance between the widest part of the proximally present groove at the height of the articulation with os ulnare and the distal end of the diaphysis. Metacarpal: on anterior side, the smallest distance between the articulation with os unciforme and the distal end of the diaphyse. Femur: on anterior side, the smallest distance between the neck and the distal end of the diaphysis. Tibia: on posterior side, the smallest distance between the depression between both condylar facets and the distal end of the diaphyse.

Metatarsal: on anterior side, the smallest distance between the proximal articulation area with navicocuboid and the distal end of the diaphysis. All widths (DT) are measured at the narrowest part of diaphysis (Fig. 4).

RELATIVE SIZES IN FRONT AND HINDLIMB

From Table 1 it appears that the ratio between the three long bones in each limb changes during ontogeny in *Candiacervus ropalophorus*, *Cervus elaphus*, *Dama* and *Capreolus*. In addition, ratio's are not the same for all deer.

The humerus is relatively longer in *Candiacervus* and in *Capreolus* than in *Cervus* and *Dama* at birth; this remains much the same at full-grown age; in *Candiacervus* even the percentage stays exactly the same. In *Candiacervus* the humerus remains proportionally the same during ontogeny, even more pronounced than in *Cervus* and *Dama*.

The radius and metacarpal are equally long at birth, in contrast to the other species where the metacarpal is always longer. During ontogeny, the radius becomes proportionally much longer and the metacarpal stays behind in growth. In the other three species the difference between radius and metacarpal decreases, and at full-grown age the radius is longer than the metacarpal, but not much. The metacarpus is clearly shorter in *Candiacervus* at birth, compared to the other species; in these, *Capreolus* has the shortest. At full-grown age this is even more pronounced.

In the hind limb the situation is a bit different. The femur is at birth equally long in all species, this changes hardly, with only *Candiacervus* and *Dama* having a slightly longer femur when full grown. In *Candiacervus* the femur increases in relative length during ontogeny, similar to *Dama*, and more than in *Cervus* and *Capreolus*. At birth, the four species have almost the same relative femur length, whereas at full-grown age *Candiacervus* has proportionally the longest femur.
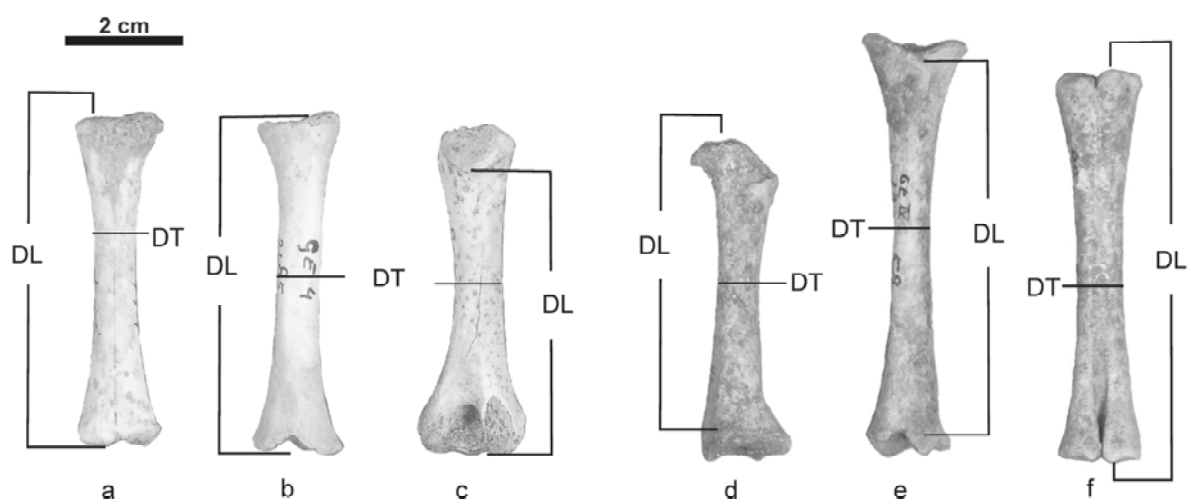

Fig. 4. Measurements of shaft length (DL) and shaft width (DT) of juvenile deer bones as used in this study.

TABLE 1

Shaft length as percentage of the total limb length. Shaft length is defined as maximal distance between proximal and distal epiphyseal line (growth line). Total limb length is defined as the combined length of the three long bones, and thus neglects the length of the carpus/tarsus and of the feet.

	Candiacervus ropalophorus		*Cervus elaphus*		*Dama dama*		*Capreolus capreolus*	
	At birth	Adult	At birth	Adult	At birth	Adult	At birth	Adult
Femur	29	32	28	29	28	31	28	29
Tibia	38	38	36	36	36	38	38	39
Metatarsus	33	30	36	35	36	31	34	32
Humerus	28	28	25	26	25	26	28	27
Radius	36	41	35	38	33	38	34	38
Metacarpus	36	31	40	36	42	36	38	35

The tibia is only slightly longer in *Candiacervus* and *Capreolus* in the newborns; when full-grown only *Cervus elaphus* has a relatively shorter tibia, while the other three are almost equal. The relative length of the tibia remains the same during ontogeny, as in *Cervus*; in *Dama* and *Capreolus* the tibia gradually increases in relative length.

The newborn metatarsus is clearly shorter in *Candia-cervus*, compared to *Cervus* and *Dama*, but hardly so compared to *Capreolus*. In the full-grown individuals, it is *Cervus* in which the metatarsus is relatively long, whereas it is only slightly shorter in *Candiacervus* than in *Dama* and *Capreolus*.

From these data we can extract the following order in relative lengths of the different limb elements, relative to the total limb length, for the newborns:

- *Candiacervus ropalophorus*: tibia-metatarsal-femur, metacarpal=radius-humerus
- *Capreolus capreolus*: tibia-metatarsal-femur, metacarpal-radius-humerus
- *Dama dama*: tibia=metatarsal-femur, metacarpal-radius-humerus
- *Cervus elaphus*: tibia=metatarsal-femur, metacarpal-radius-humerus
  And the same for the full-grown individuals:
- *Candiacervus ropalophorus*: tibia-femur-metatarsal, radius-metacarpal-humerus
- *Capreolus capreolus*: tibia-metatarsal-femur, radius-metacarpal-humerus
- *Dama dama*: tibia-metatarsal=femur, radius-metacarpal-humerus
- *Cervus elaphus*: tibia-metatarsal-femur, radius-metacarpal-humerus

Differences in relative length can also be approached in a different way. Indexes of each possible pair give another view on proportions (Table 2). It seems that proportions hardly change during ontogeny in *Capreolus* and in *Dama*, and much more so in *Cervus elaphus*. In most ratios *Candiacervus* does not differ essentially from the latter, except for the metapodals (the metatarsal grows longer than the metacarpal) and the proximal elements (the femur grows longer than the humerus). These ratios remain much the same in *Cervus*, but are (almost) exactly as in *Dama* and

TABLE 2

Change of massivity of the long limb bones during ontogeny. Massivity is calculated here as shaft width divided by shaft length. Shaft width is defined as minimal diameter of the diaphysis. Shaft length is defined as the maximal distance between proximal and distal epiphyseal line (growth line); for the adult bones, this is measured at an ontogenetic stage where the fusion lines are still visible.

	Candiacervus ropalophorus		*Cervus elaphus*		*Dama dama*		*Capreolus capreolus*	
	At birth	Adult	At birth	Adult	At birth	Adult	At birth	Adult
femur	7,3	7,78	8,9	9,56	8,52	9,09	10,21	10,37
tibia	10,62	9,73	10,89	10,81	11,09	10,79	13,79	13,77
metatarsus	9,79	8,59	12,39	11,58	11,84	11,38	14,07	13,56
humerus	5,79	5,77	6,90	7,15	6,31	6,13	8,66	8,64
radius	8,68	8,02	9,11	8,53	8,49	8,30	9,89	10,26
metacarpus	7,16	6,67	11,09	10,57	10,76	9,95	11,73	11,80

Capreolus. Ratio's in which the metacarpal or metatarsal is the first elements, show the relative shortening of the metapodals, as these ratio's are clearly lower than in the other deer. The ratio between the two metapodals is lower than in *Cervus* and *Dama*, but very similar to *Capreolus*, and proves the relatively longer hindlimb in these genera. During ontogeny this becomes more pronounced in both, but much more so in *Candiacervus*. Thus, *Candiacervus* indeed has shorter metapodals already at birth, and the metacarpal is shorter than the metatarsal, much more than the other three deer. The slightly larger species *Candiacervus* sp. II from Liko cave has in adult stage exactly the same relatively long metatarsal compared to the metacarpal, as indicated by an index of 0,79 (VAN DER GEER *et al*., 2005). Quite probably therefore also here the shortening of the metapodals and the low mc/mt ratio are already present at birth.

CHANGE IN MASSIVITY

From Table 3 it is evident that already at birth *Candiacervus* has the most massive bones, compared to *Cervus*, *Dama* and *Capreolus*; only *Dama* has a more massive radius. Of the latter three species, it is the smallest species, *Capreolus*, which has also the most slender bones. This makes the limb bones of *Candiacervus*, which is on its turn still smaller than *Capreolus*, even more exceptionally massive.

During further ontogeny, the long bones become even more massive, except for the femur (in all species). Obviously here length increases more than width. Hardly any change occurs in the humerus in *Candiacervus*, as in *Capreolus*; this is also valid for the tibia in *Cervus* and in *Capreolus*.

The following order in massivity for the newborns can be seen, according to increasing massivity:

- *Candiacervus ropalophorus*: tibia-metatarsal-femur, radius-metacarpal-humerus
- *Cervus elaphus*: metatarsal-tibia-femur, metacarpal-radius-humerus
- *Dama dama*: metatarsal-tibia-femur, metacarpal-radius-humerus

TABLE 3
Ratio's of all possible pairs of the long limb bones,
showing the relative length of each element.

	Candiacervus ropalophorus		Cervus elaphus		Dama dama		Capreolus capreolus	
	At birth	Adult	At birth	Adult	At birth	Adult	At birth	Adult
Humerus/radius	0,76	0,69	0,73	0,69	0,77	0,77	0,81	0,81
metacarpal/radius	0,98	0,75	1,15	0,94	1,29	1,29	1,11	1,11
metacarpal/humerus	1,28	1,08	1,58	1,36	1,68	1,68	1,36	1,36
femur/tibia	0,78	0,82	0,80	0,80	0,76	0,76	0,74	0,74
metatarsal/tibia	0,88	0,79	0,99	0,86	0,99	0,84	0,91	0,91
metatarsal/femur	1,13	0,96	1,23	1,07	1,30	1,03	1,23	1,09
metacarpal/metatarsal	0,87	0,80	0,91	0,90	0,91	0,89	0,86	0,84
radius/tibia	0,78	0,83	0,79	0,83	0,70	0,77	0,70	0,73
Humerus/femur	0,77	0,71	0,72	0,71	0,71	0,65	0,77	0,71

- *Capreolus capreolus*: metatarsal-tibia-femur, metacarpal-radius-humerus

This is exactly the same in the full-growns, except for *Capreolus*, in which species the metatarsal becomes more massive than the tibia.

It is evident that both metacarpal and metatarsal are already more massive at birth in *Candiacervus*, compared to *Cervus*, *Dama* and *Capreolus*, where these bones are the most slender of the long limb bones. During further ontogeny, this remains much the same.

CONCLUSIONS

The shortening of the metapodals as observed in adult *Candiacervus ropalophorus* is an obvious result of a different genetics and a different ontogeny. The relative shortening is already present at birth and this becomes more prominent for the metatarsal during postnatal ontogeny (Fig. 5). The end result are absolute and relative short metapodals. This is especially true for the metacarpal . The metacarpal is at all stages shorter than the metatarsal, as in all studied deer, but this is more pronounced in the full-grown *Candiacervus*, much more than in the other deer.

There are also differences in massivity. *C. ropalophorus* has, in contrast to the mainland species, a metatarsal that is more massive than the tibia. Also in the front limb the metacarpal of *C. ropalophorus* is more massive than the radius, this is already present at birth; in the other deer species the radius is always more massive. Thus, the shorter and more massive metapodals in island deer are already present at birth, and this becomes more evident during further ontogenesis.
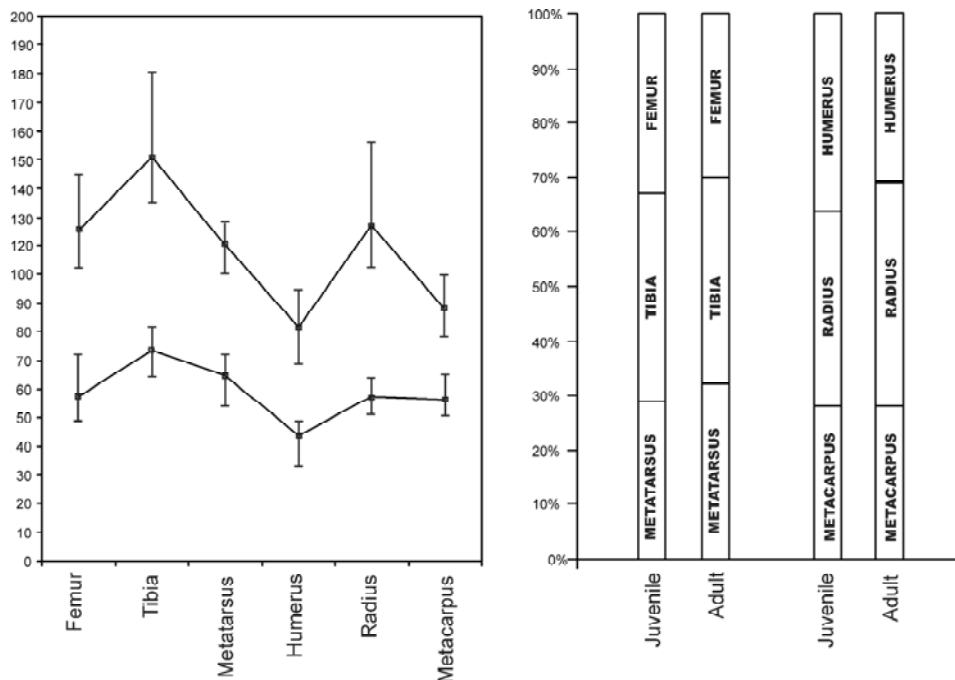
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Fig. 5. Diagrams showing the relative proportions of the three long limb bones in juvenile (lower graph) and adult (upper graph) *Candiacervus ropalophorus*. Left as a scatter diagram, giving also range; right as a block diagram for easy comparison. From the latter diagram, it becomes clear that proportions do not change much during ontogeny; the metapodals are already short at birth.

shortening of the limbs, which remained for Paul the proof of adaptation to a mountaineous island environment without terrestrial predators. Paul never got the time to check whether this shortening is indeed already present at birth (genotypic) or only arises during ontogeny (fenotypic), while this knowledge is crucial for further explanation of endemic, acquired (apomorphic) features.

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