



Morphology of articular surfaces can
solve a phylogenetic issue:
one instead of two ancestors for
Candiacervus (Mammalia: Cervoidea)

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Naturalis
Biodiversity
Center



Mediterranean Islands

Elephants, mammoths, deer, gorals,
hippos, hyaenas, hamsters, shrews,
pikas, hedgehogs, otters, dogs,
monkeys,



During the Plio-
Pleistocene, insular
faunas with dwarf
elephants, dwarf hippos,
dwarf deer and giant
rodents

What do we see in these fossil insular faunas?

Under absence of terrestrial, mammalian predators, the islands gradually harbour

a mini-megafauna

and

a mega-minifauna.



Drawing by Jemima Wedderburn
(in Andrews, 1870, on the fossil fauna of Malta)

Crete, no
exception





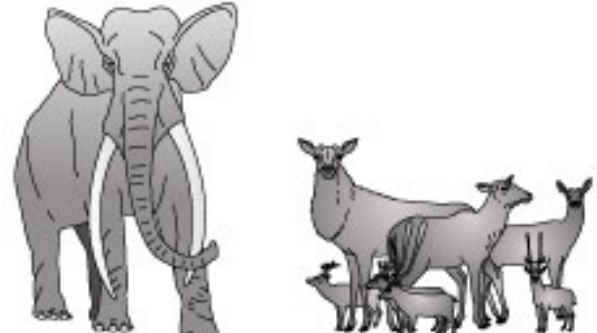





A mini-continent

Rugged topography with
high plateaus



Two Pleistocene insular periods, with two totally different faunas

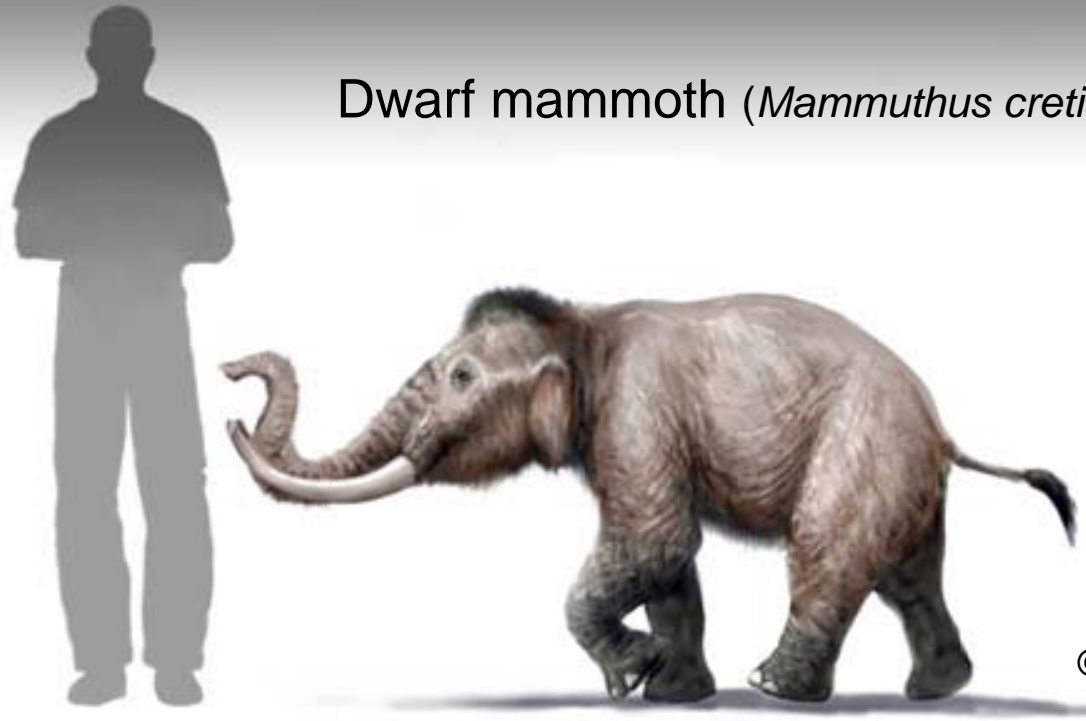
Zones	Sub-zones	Range-zones	Deer species Localities	Deer species	Localities	Illustrations	Period
				<i>Candiacervus</i> sp. VI <i>Candiacervus</i> sp. V <i>Candiacervus</i> cf. <i>orbiferentis</i> <i>Candiacervus</i> <i>eremus</i> <i>Candiacervus</i> sp. III <i>Candiacervus</i> <i>spaldani</i> <i>Candiacervus</i> sp. <i>indet.</i>			Holocene
<i>Mus</i>	<i>Mus minotaurus</i>	<i>Elephas creutzburgi</i>	Gerani 2, 3 Gerani 5 Gerani 6 Gerani 2, 3 Gerani 4 Gerani 2, 4 Base Cave Liko				Pleistocene
		<i>Elephas antiquus</i>	Macro Mount 6c Zoorids Redymnon Sissano Kalo-Chorafi Simonelli Cave Charsourbos 1				
			Charsourbos 2 Milatos 2 and 4 Milatos 3 upper Sarcos Cave inside Sarcos outside				
		<i>Mus latou</i>	Milatos 3 lower				
<i>Kritimys</i>	<i>Kritimys catnisi</i>	<i>Hippopotamus creutzburgi parvis</i>	Sarcos Cave outside Kato Zakros			Pleistocene	
		<i>Hippopotamus creutzburgi creutzburgi</i>	Katharo				
			Charsourbos A Sarcos Milatos 1 Rafi 2				
	<i>Kritimys kiridus</i>	<i>Elephas creticus</i>	Cape Melaka 1 Cape Melaka 5				
	<i>Kaff. kiridus</i>		Sinis 1				

Dramatic faunal turnover at middle Middle Pleistocene

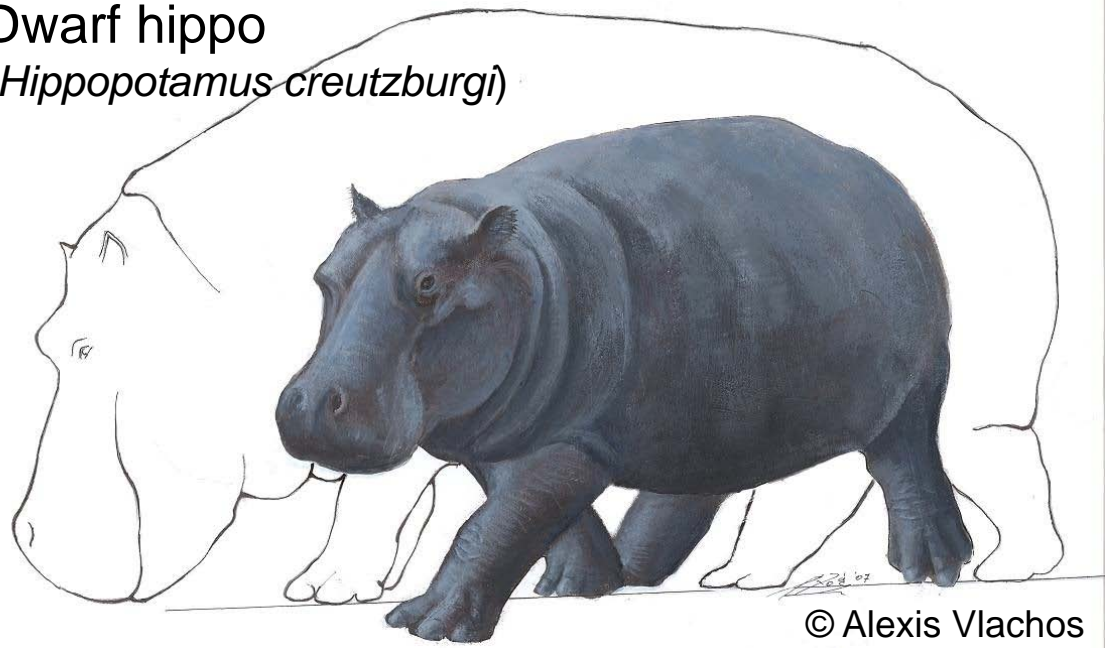
Kritimys zone:

Early – early
Middle
Pleistocene

Dwarf mammoth (*Mammuthus creticus*)



Dwarf hippo
(*Hippopotamus creutzburgi*)

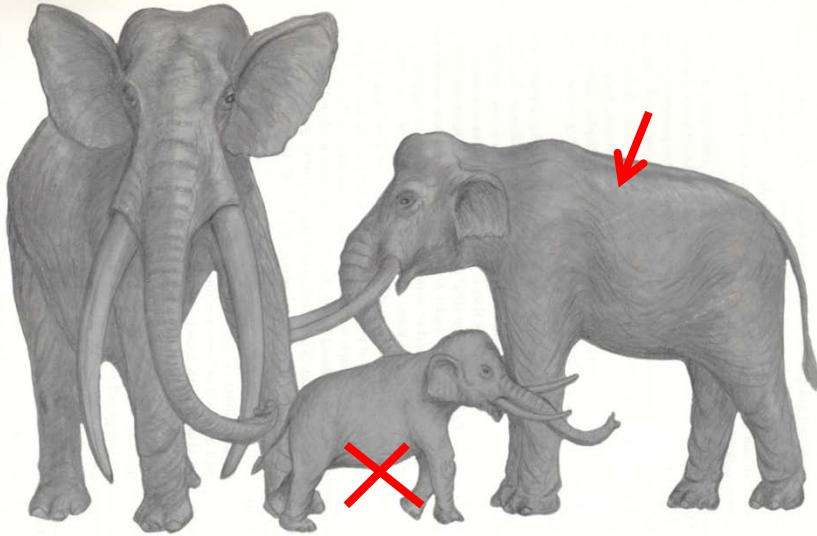


- + giant rat
(*Kritimys kiridus*)
- + shrew
(*Crocidura zimmermanni*)

© Alexis Vlachos

Mus zone:

late Middle – Late Pleistocene



Dwarf elephants (*Elephas creutzburgi*)

+ large mice *Mus minotaurus*,
flightless owls, shrews



otter (*Lutrogale cretensis*)



Dwarf, middle and giant deer
(*Candiacervus*)

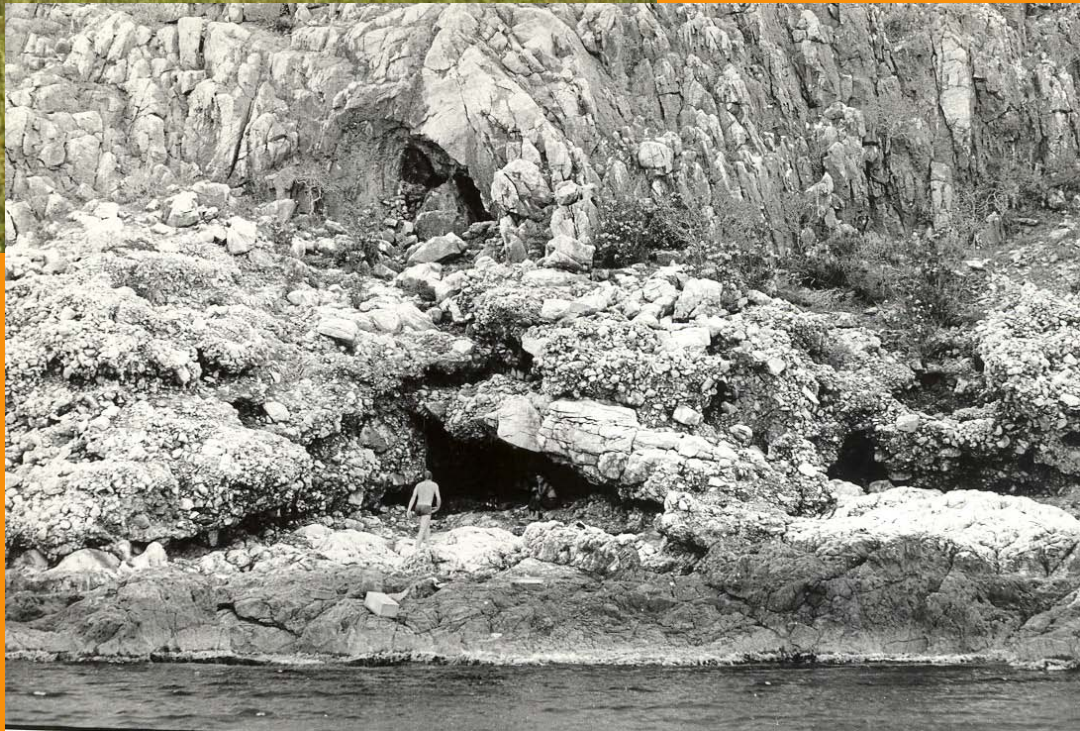


Coastal cave deposits with vast amounts of deer fossils





Mainly Liko Cave



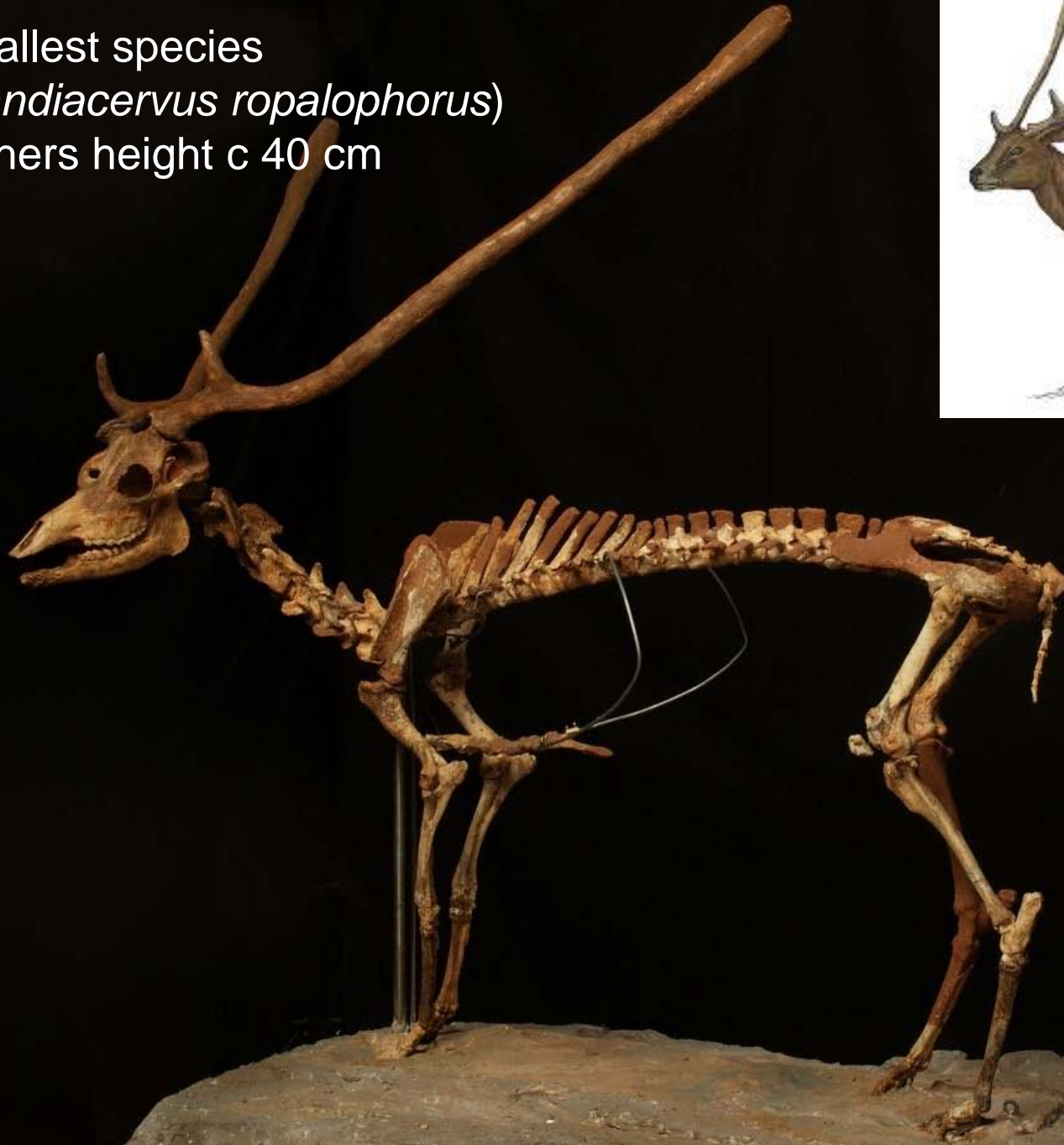


GEZICHT OP DE VERKITTE WAND, VOOR LIKO-OTTER. DE LOCALITEIT LIKO-OTTER LIGT ACHTER DEZE WAND.
 HET GEDROEGTE WAAK DUIDELIJK ROT IS TE ZIEN HEET LIKO, DABR WAAR DE LAMP STAAT LIKO-DIEP.

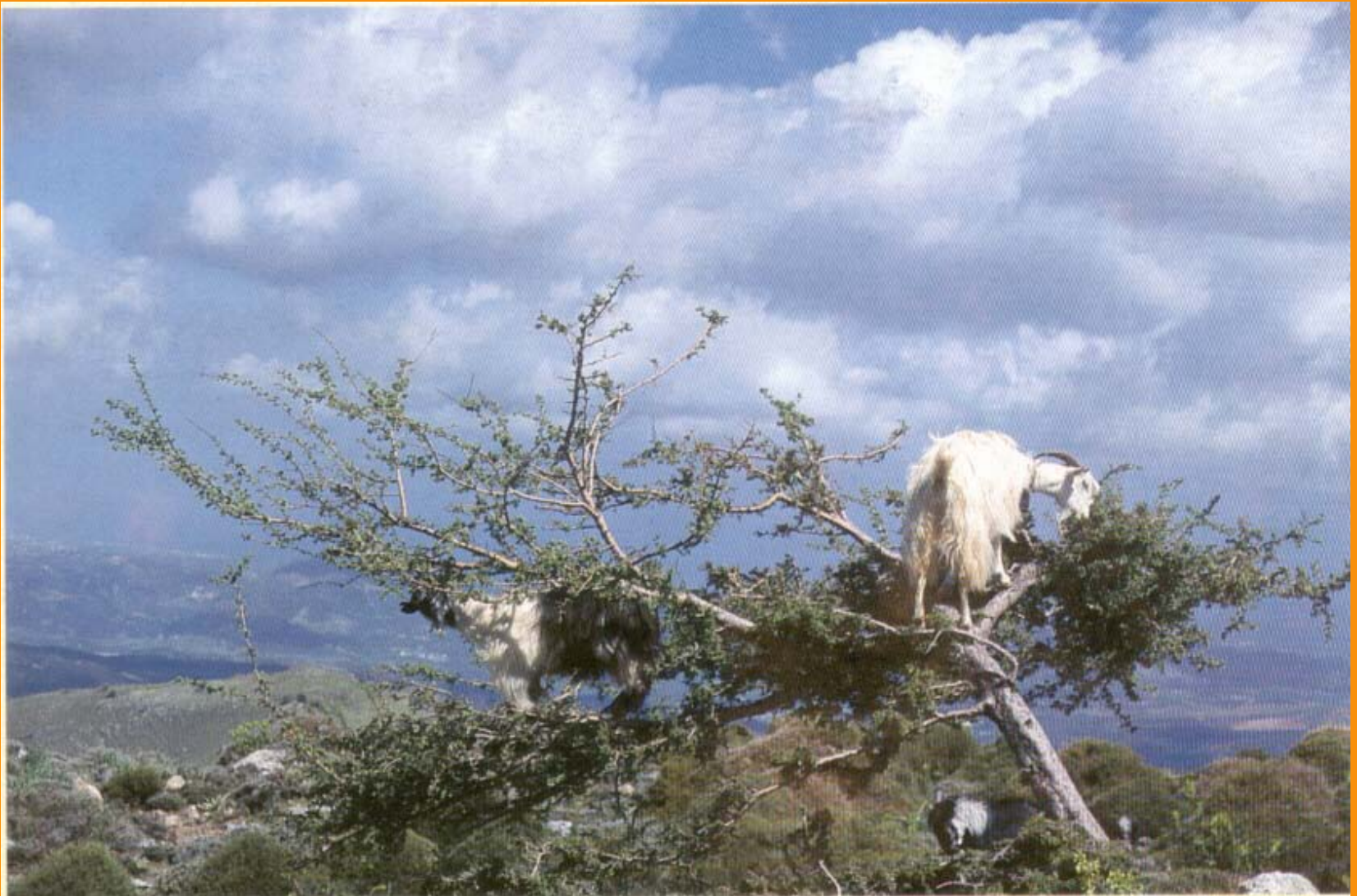


So much that we could reconstruct and assemble a skeleton

Smallest species
(*Candiacervus ropalophorus*)
Withers height c 40 cm



Short, massive limbs and hypsodont teeth: more a goat than a deer!



Domestic goats in trees along the road to Katharo, Crete

If a goat can do it,
then I can do it



Candiacervus – van der Geer





Largest species,
Candiacervus major

Withers height c 165 cm



Size variation

5cm

Withers height c 40 cm to 165 cm

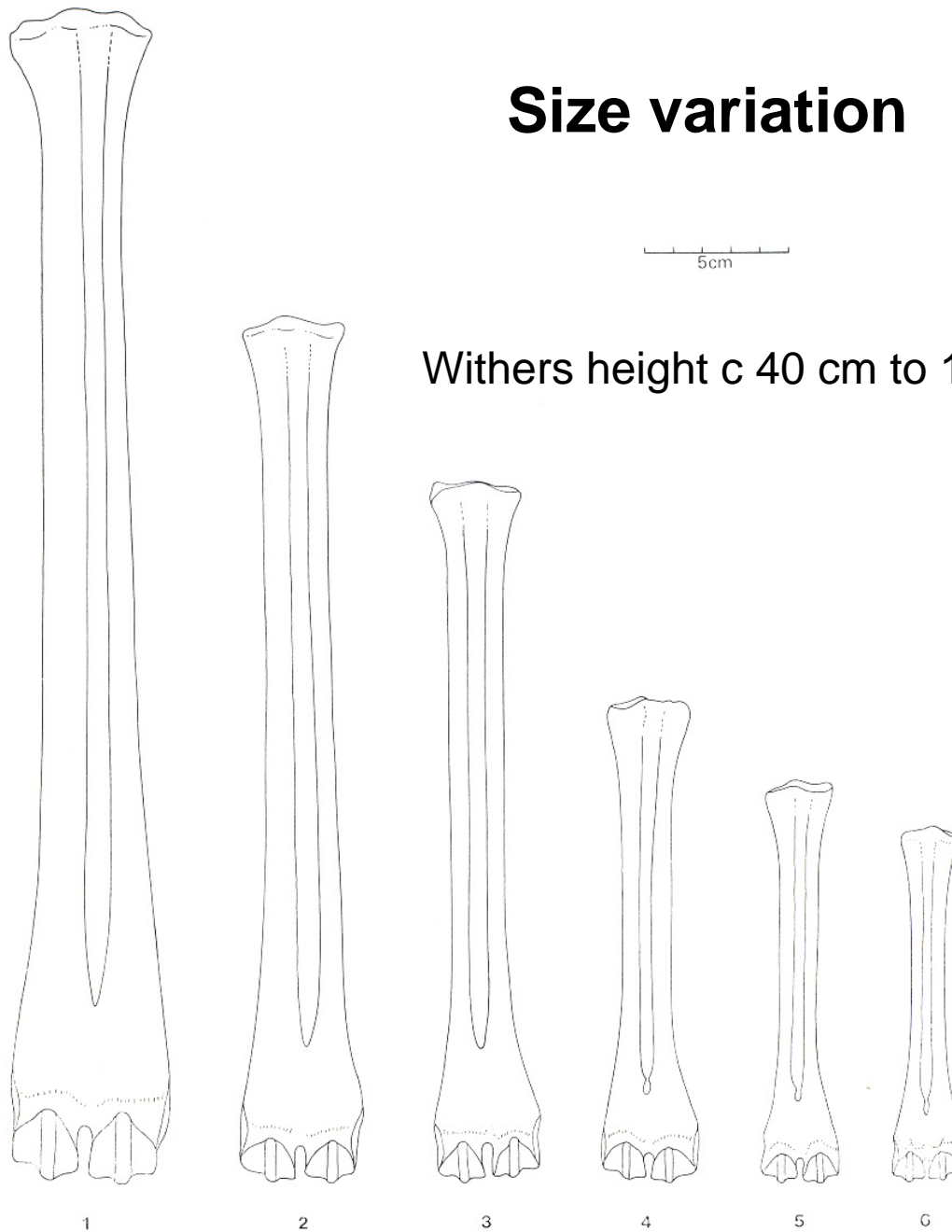
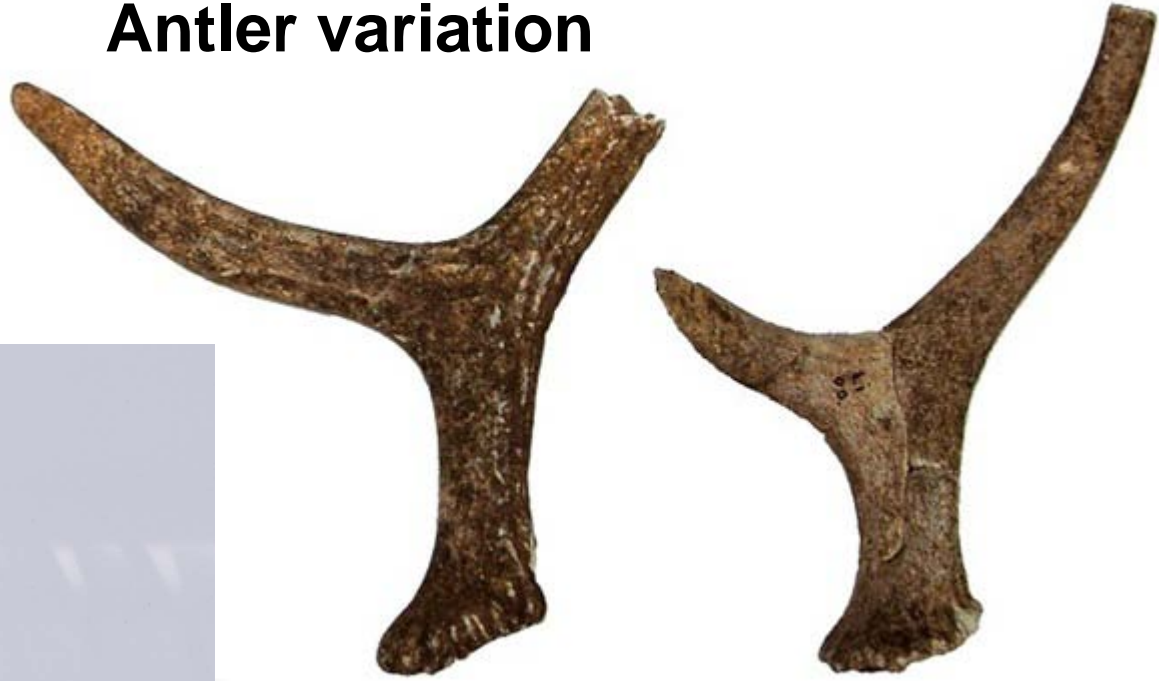


Fig. 8. The length of the metatarsals of the six groups compared to each other.

Antler variation



Taxonomical History

type species 1907-1975

1907 *Anoglochis cretensis*, new species for Crete, by SIMONELLI

1929 *Cervus (Eucladoceros) creticus* by VAUFREY analogue to Corsican *Cervus (Eucladoceros) cazioti* of Déperet 1897; species name *lapsus kalami*

1955 *Megaceros (Anoglochis) cretensis*, incl. Corsican species, in Comaschi Caria

1960 *Cervus cretensis* by SIGOGNEAU

1967 *Nesoleipoceros cretensis*, new genus for island “megacerines” by RADULESCO & SAMSON (type species *cazioti* of Corsica)

1967 *Megaceros cretensis*, transfer back to giant elk by SONDAAR & BOEKSCHOTEN

1968 *Praemegaceros cretensis*, genus name update by KURTÈN

1975 *Candiacervus cretensis*, new genus for Crete by KUSS (type species *cretensis*), link with Corsica-Sardinia dismissed

Taxonomical History other species (1967-1992)

1967 two more species (Bate Cave), " *Cervo taglia media*" and " *Cervo taglia grande*" in KOTSAKIS ET AL.

1975 a red deer-sized species is recognised as *C. rethymnensis* by KUSS; he also included Karpathos material: *cerigensis*, *pygadiensis*

1979 eight morphotypes (six size classes, three antler morphotypes), from small to large: *Candiacervus* sp. I, *C. spp.* II (a, b and c), *C. cretensis*, *C. rethymnensis*, *C. sp.* V, and *C. sp.* VI in DE VOS.

1984 smallest species is named *Candiacervus ropalophorus* by DE VOS.

1986 "Cervo taglia grande" of KOTSAKIS ET AL (=sp. VI of DE VOS) is named *Cervus major* by CAPASSO BARBATO & PETRONIO.

1989 size I and II (a, b and c) of DE VOS are lumped together into *Megaceros ropalophorus* by CAPASSO BARBATO.

1992 "Cervo taglia media" of KOTSAKIS ET AL. (=sp. V of DE VOS) is named *Cervus dorothenensis* by CAPASSO BARBATO.

Phylogenetic history

Single species, related to *Eucladoceros* (e.g. SIMONELLI 1907) or to *Praemegaceros* / *Megaloceros* (e.g. SONDAAR & BOEKSCHOTEN 1967)

Monophyletic (anagenetic) lineage (KUSS 1975), unrelated to megacerines

Monophyletic (cladogenetic) genus (DE VOS 2000), unknown relationship

Biphyletic group, small-sized species related to *Megaloceros* (= *Praemegaceros*) *verticornis* and large-sized species either to *Cervus peloponnesiacus* or to *Cervus philisi* (= *Metacervoceros rhenanus*) (e.g. CAPASSO BARBATO 1989)

Biphyletic group, small-sized species related to *Megaceroides* (= *Praemegaceros*) and large-sized species to ?*Pseudodama* (e.g. CALOI & PALOMBO, 1996)

A Radiating Bush or Multiple Invasions?

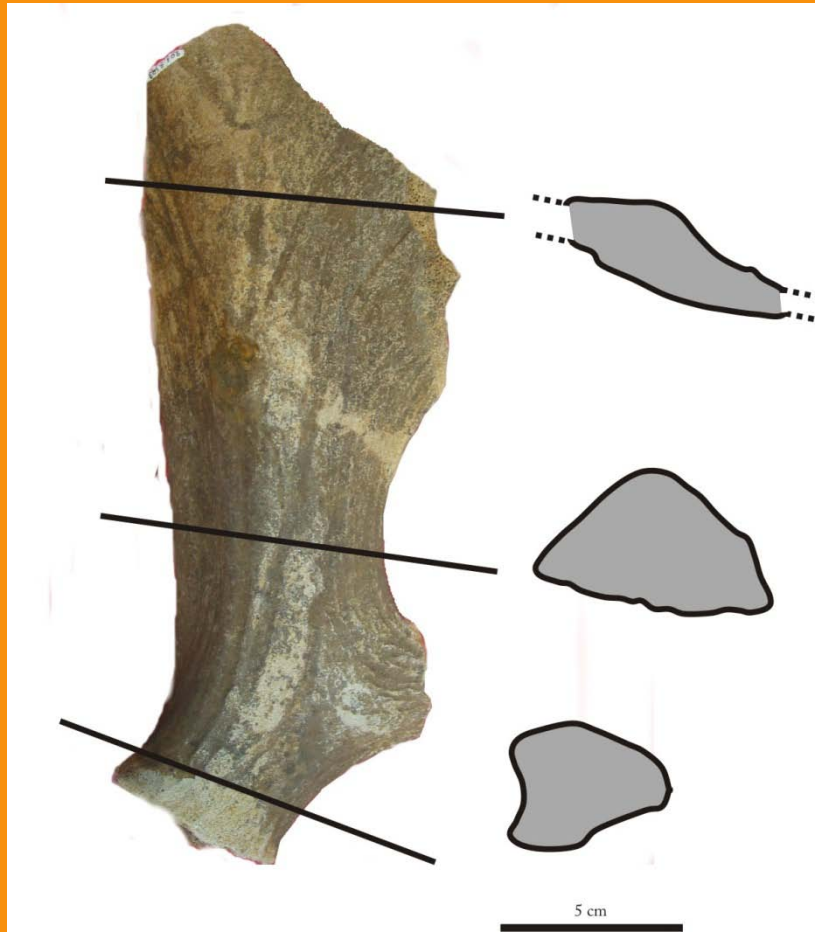
The Cretan deer is a typical example of taxonomical problems involving endemic insular mammals, due to the much larger variety than on the mainland, and the strong endemism, which obscures taxonomy. De Vos (1979, 1984) and de Vos and Dermitzakis (1986) include the eight morphotypes into one single genus (*Candiacervus*). Other scholars, starting with Capasso Barbato and Petronio (1986), do not follow this scheme, and include the three larger species either in a *Cervus*-like genus (*Leptocervus*) or a fallow deer-like genus (*Pseudodama*) and the two smaller species, regarded as one species only, in the genus *Megaloceros*, thus implying two different ancestors. Caloi and Palombo (1996) made a new division, recognizing three different groups. They assigned sizes 1 and 2 of De Vos both to *Megaceroides* (*Candiacervus*) '*ropalophorus*'. *Candiacervus cretensis* was renamed *Megaceroides* (*Candiacervus*) *cretensis*, the species *rethymnensis* was

Sizes	Names used by de Vos in 1979	Names used by Caloi and Palombo in 1996
I	<i>Candiacervus ropalophorus</i>	<i>Megaceroides</i> (<i>Candiacervus</i>) <i>ropalophorus</i>
II	<i>Candiacervus</i> sp. IIa, sp. IIb, sp. IIc	<i>Megaceroides</i> (<i>Candiacervus</i>) <i>ropalophorus</i>
III	<i>Candiacervus cretensis</i>	<i>Megaceroides</i> (<i>Candiacervus</i>) <i>cretensis</i>
IV	<i>Candiacervus rethymnensis</i>	? <i>Pseudodama rethymnensis</i>
V	<i>Candiacervus</i> sp. V	? <i>Pseudodama</i> (<i>Leptocervus</i>) <i>dorothisensis</i>
VI	<i>Candiacervus</i> sp. VI	? <i>Pseudodama</i> (<i>Leptocervus</i>) <i>major</i>



Katharo, “Middle Pleistocene” ?

Dermitzakis *et al.* 2007, Van der Geer *et al.* 2010 report new findings (antler fragment, postcranial) of a middle-sized deer from Katharo:
oldest evidence of *Candiacervus* on Crete -> close to ancestor = problem solved!



Katharo, “Middle Pleistocene” ?

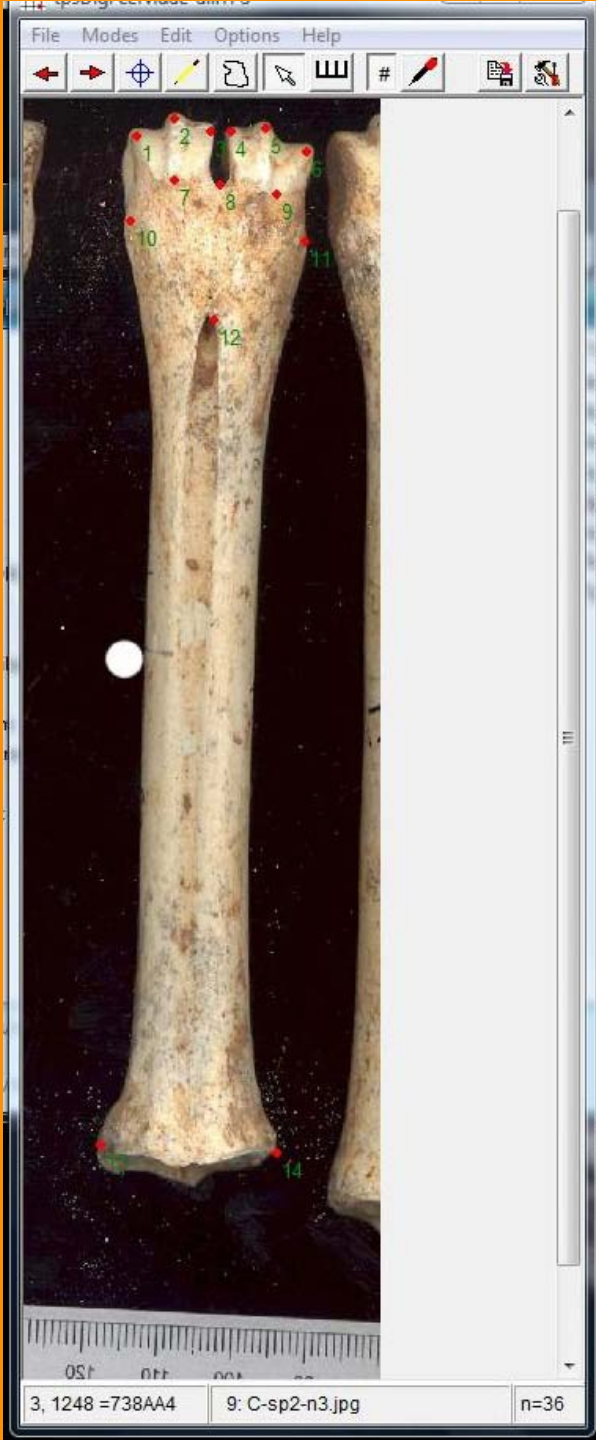


New geological research: two layers, with the latest / Late Pleistocene layer with deer above the Middle Pleistocene layer with hippo

No precise data yet, but clearly, the only info on *Candiacervus* available from the caves; Katharo can not resolve the mono/polyphyletic problem



Lee Arnold measuring background radiation of sample area



New approach: Morphometrics

Landmarks (14) on metatarsus

Indicators of body mass

Indicators of freedom of movement

Etc.

Data acquisition TPS, analysis MorphoJ

Why? Because at visual inspection of distal MT, articulation area does not scale proportionally; expansion stays behind in large *Candiacervus*

Candiacervus

C.ropalophorus

C. cretensis

C.rethymnensis

C.dorothisensis

C.major



Dama

Megaloceros



Results

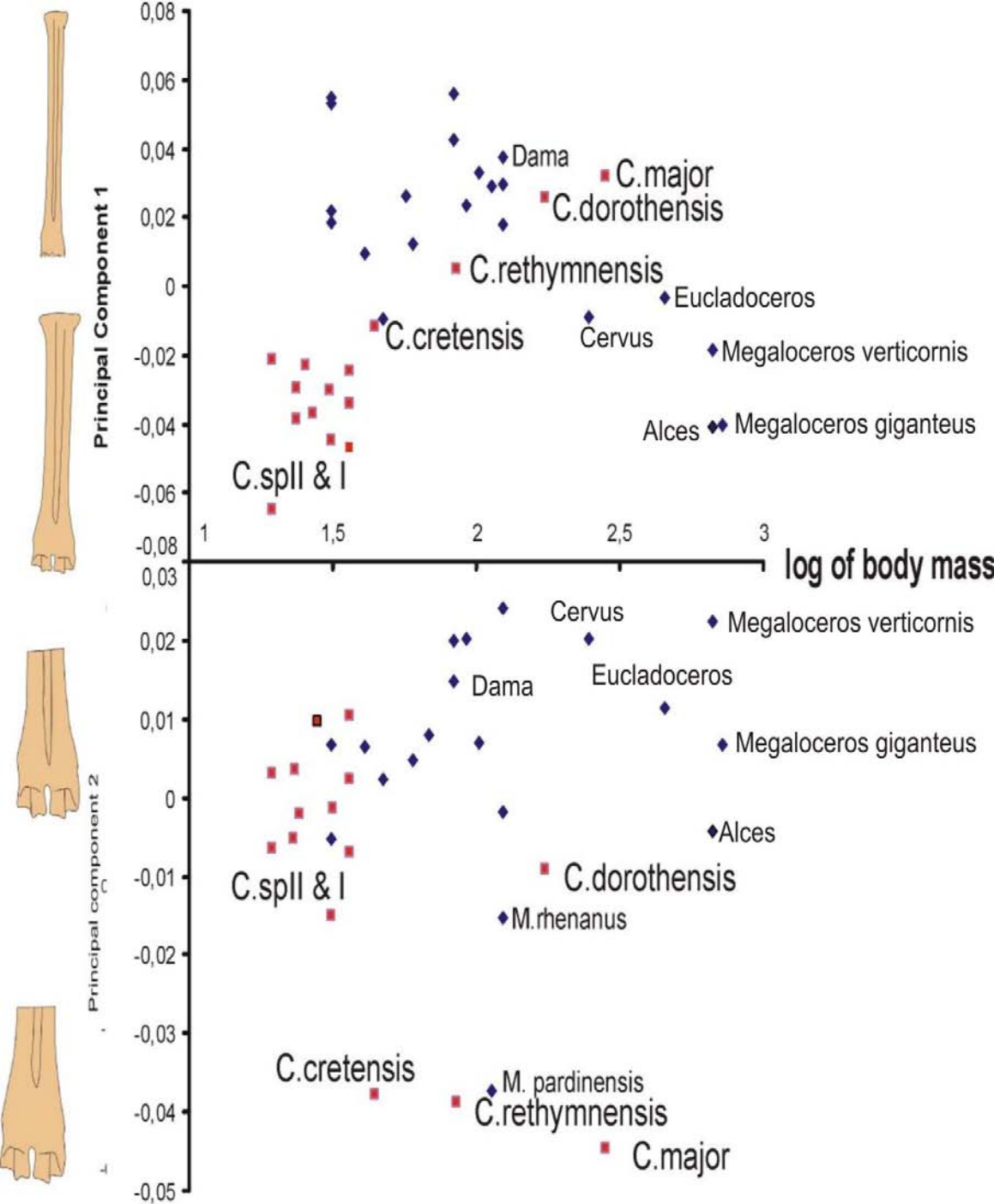
PC1 “robusticity”, c. 80% of variation

PC2 “post-gully length”, c. 15% of variation

Large morphological variation -> many species / ecomorphs

PC1: *Candiacervus* as robust as *Megaloceros* (size 1, 2, 3) and as slender as *Dama* (size 5, 6); straight line

PC2: *Candiacervus* higher distal gully end for BM than most other deer except for *Metacervoceros*; (size 5 outlier?)



Results

C.ropalophorus



Mainland Axis



C.cretensis



Mainland Dama



C.major

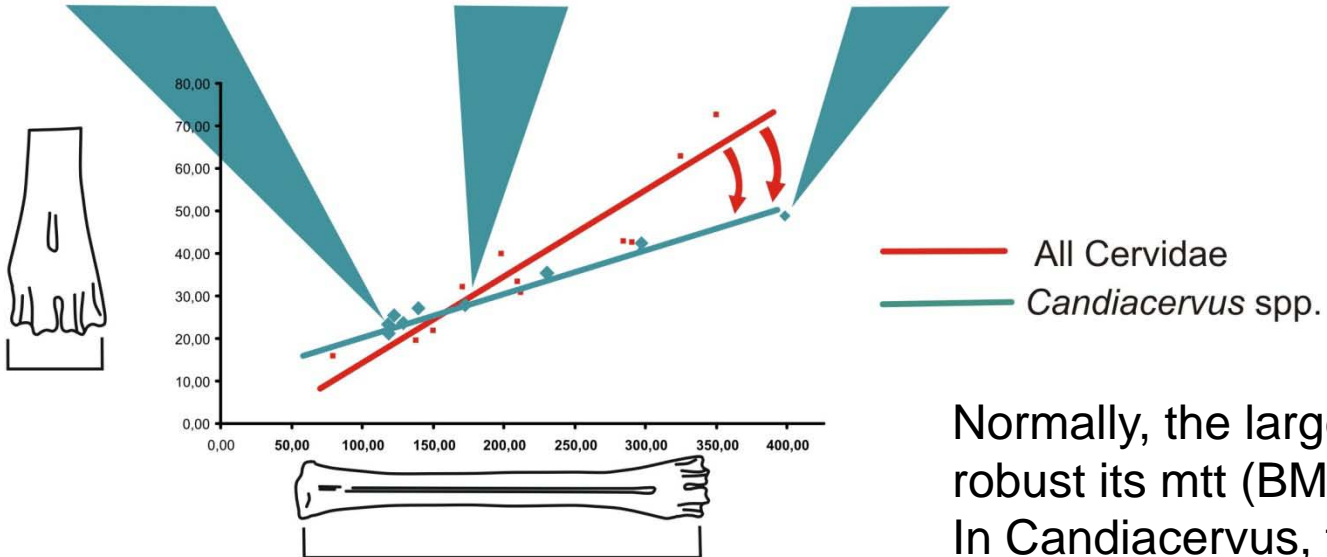


Mainland Megaloceros



Small *Candiacervus* species:
too robust for their size,

large *Candiacervus* species:
too slender for their size



Normally, the larger the deer, the more robust its mtt (BM increases proportionally)
In *Candiacervus*, the larger the deer, the more slender its mtt (-> BM does not increase proportionally)

**Not scaled-down
and scaled-up
versions of a
“middle” size**



ISOLARIO



Island biodiversity and cultural evolution



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Thank you for
your attention



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Capra aegagrus