Cour. Forsch.-Inst. Senckenberg | 256 | 131–137 | 5 Figs | Frankfurt a. M., 15. 11. 2006

New data on the Pleistocene Cretan deer *Candiacervus* sp. II (Cervinae, Mammalia)

With 5 figs

Alexandra van der Geer, John de Vos, Georg Lyras & Michael Dermitzakis

Abstract

A skeleton of the endemic Pleistocene Cretan deer *Candiacervus* sp. II (Liko, Crete, Greece) was mounted using bones of different individuals. This composite skeleton contributes to the study of the taxonomy of insular ungulates as it reveals some additional features which had not been detected in the isolated elements. *Candiacervus* sp. II differs from all known recent and extinct mainland deer, mainly in its proportions. Although its considerably shortened distal limbs had been already noted in the past, *Candiacervus* sp. II now appears at the same time to have had more or less the same vertebral column length as its large-sized continental counterparts, and a moderately upwards curved lumbar section, two features more remindful of the insular dwarf bovid *Myotragus* than of the small-sized mainland *Axis axis*. Combined with an increased massiveness of all the bones and with pronounced muscle scars, this change in body proportions indicates that *Candiacervus* sp. II evolved towards the niche of goat-like bovids in rocky environments. Other additional diagnostic features are the horizontally directed transversal processus of the vertebras, the fusion of the lateral metacarpal to the main metacarpal, a tail length of ten vertebras, a more pronounced difference of the anterior and posterior hooves, and the presence, both in the manus and pes, of lateral toes complete to the third phalanx.

Key words: Pleistocene, endemic, Cervinae, neso-evolution, composite skeleton, adaptation

Introduction

One of the most intriguing examples of insular evolution is that of the Pleistocene deer of Crete, *Candiacervus* Kuss, 1975. It is represented by eight morphotypes (see below for details on taxonomy), of which the smallest have the typical short limbs combined with a higher degree of bone fusions (de Vos 1979), seen in other island ruminants as well (Leinders & Sondaar 1974, Sondaar 1977, Moyá-Solá 1979, Bover 2004).

During the Late Pleistocene the climate gradually became warmer, the sea level rose and the island shrank. This resulted in a drastic decrease in number and species richness of the Cretan deer. The latest attested occurrence is in Simonelli cave I, which is AAR dated 21.500 ± 20% (Belluomini & Delitala 1983, combined with all available datings in Reese et al. 1996); here only one morphotype of *Candiacervus* occurs. Liko Cave, where six morphotypes are found next to each other, has AAR dates for deer ranging between 105.000 ± 20% and 87.000 ± 20% (Reese et al. 1996). At present *Candiacervus* is known to us only by isolated skeletal elements, except for a few articulated bones, and dental remains; no coprolites, no footprints, no natural endocast were ever found. This makes the reconstruction of its ecomorphotype quite complicate.

To know more about the ecology and taxonomy of *Candiacervus*, we needed to remount its skeleton. Only a mounted skeleton can show the reciprocal relationships of individual bones, and thus give insights in the body proportions, the presence and completeness of lateral toes, the length of the tail, the morphology of the vertebral column, which is all information impossible to obtain from isolated bones alone.

The mounted skeleton (fig. 1) belongs to an adult male of *Candiacervus* sp. II, which is in display in the new exhibition of the Museum of Paleontology (University of Athens, Greece), placed on the model of a small island, next to the reconstructions of the dwarf elephant of Tilos island (*Elephas* sp.) and of the dwarf hippopotamus of Crete (*Hippopotamus creutzburgi*). The skeleton is placed on a rocky, stepped surface, at a higher level than its mainland counterparts to show the different habitat of the Cretan deer.

Authors' addresses: Dr. Alexandra van der Geer, George Lyras & Michael Dermitzakis, Museum of Paleontology, Department of Geology, Section of Historical Geology and Palaeontology, National and Kapodistrian University of Athens, Panepistimiopolis 157 84, Athens, Greece, <geeraae@geol.uoa.gr>, <glyras@geol.uoa.gr>; John de Vos, National Museum of Natural History Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands, <vos@naturalis.nnm.nl>

Fig. 1 : The mounted skeleton of *Candiacervus* sp. II seen from the left.

Remarks on Taxonomy

Fossil deer material from Crete was originally described as *Anoglochis cretensis* by SIMONELLI (1907). Later authors placed his species in other genera and subgenera, namely *Cervus* (*Eucladoceros*) *creticus* (VAUFREY 1929), *Cervus cretensis* (SIGOGNEAU 1960), *Nesoleipoceros cretensis* (RADULESCO & SAMSON 1967), *Megaceros cretensis* (SONDAAR & BOEKSCHOTEN 1967), and *Praemegaceros cretensis* (KURTÈN 1968). KUSS (1975) named the genus *Candiacervus* for this species as well as for the fossil deer from the nearby island Karpathos.

The Cretan deer is represented by eight morphotypes, distributed over six size classes and with three different antler morphotypes. DE VOS (1979, 1984, 2000) classified the six size classes, in order of increasing size, as *C. ropalophorus*, *C.* spp. II (a, b and c), *C. cretensis*, *C. rethymnensis, C.* sp. V, and *C.* sp. VI . Other taxonomies recognize five species, as size I and II are lumped together into *Megaceros ropalophorus* by CAPASSO BARBATO (1989) or *Megaceroides “ropalophorus*” by CALOI & PALOMBO (1996). Species V is referred to as *Cervus dorothensis* by CAPASSO BARBATO (1989) or as ?*Pseudodama dorothensis* by CALOI & PALOMBO (1996). Species VI is referred to as *Cervus major* by CAPASSO BARBATO & PETRONIO (1986) or as ?*Pseudodama major* by CALOI & PALOMBO (1996). The eight or six taxonomic units belong to the monophyletic genus *Candiacervus* (DE VOS 2000), or alternatively, to the two genera *Megaloceros* and *Cervus* in the view of CAPASSO BARBATO (1989) or *Megaceroides* and ?*Pseudodama* in the view of CALOI & PALOMBO (1996).

Another problem, which is related to that of its taxonomy, is assigning an ancestor to the Cretan deer. Of course, there are different opinions, and several continental genera have been proposed: *Cervus peloponnesiacus* and *Cervus philisi* (CAPASSO BARBATO & PETRONIO 1986) or ?*Pseudodama* (CALOI & PALOMBO 1996) for the larger species, *Megaloceros* (CAPASSO BARBATO 1989, 1992) or *Megaceroides* (CALOI & PALOMBO 1996) for the smaller species. DE VOS (2000) maintains that the data available are still insufficient to establish the phylogenetic relationships of the Cretan deer.

Materials and Method

For the reconstruction we chose *Candiacervus* sp. II (for reasoning, see VAN DER GEER et al. 2005). This species is characterised by having shortened legs (the typical end result of ruminant neso-evolution). It is also the morphotype with largest geographical and chronological distribution of all *Candiacervus* representatives. Estimated withers height is about 50 cm (DE VOS 2000). The largest amount of species II bones comes from Liko cave (or Likotinara, north-western Crete), where 95,3% of the bones belong to this species (DE VOS 1979). We tried to select, as far as possible, all the bones we needed from single layer (Liko B), to limit the geological time range of the specimens. The majority of the bones was found disarticulated; the few articulated elements were used to check the proper combination of morphology, size and posture. This was especially useful for the extremities and the vertebral column (a T12-L6 series). We mounted a cast of the type skull (ampg(v) 1734 = Li-B 717; fig. 2a–c) of sp. II, both to avoid damaging the original but also because we had to drill the specimen to assemble it to the skeleton. The antlers are casts of the type specimen of antler type 1 [Ge4–2870, left antler, Cave Gerani 4, described and figured by DE VOS (1984); the right side is a mirrored cast]. Although this antler comes from a different cave (Gerani 4), it fits our reconstruction of the appendages which is based upon many fragmentary antlers of type 1 found in Liko. Actually, there are two antler types of sp. II, but the specimens are too fragmentary and too incomplete for a reliable reconstruction of them. The mandibles are casts of the hemimandibles of two different individuals.

The postcranials of sp. II show a certain amount of individual variation. Hence, we selected elements of average size and average proportions. The average proportions of the limb bones of an articulated skeleton were obtained by calculating the average values of a suitably large collection of disarticulated elements. This method has been tested on 30 disarticulated skeletons and 1 articulated one of *Cervus philisi* (HEINTZ 1970). The mean value is obviously unsuitable for this purpose, because smaller elements are far more abundant than larger ones due to the nature of the fossils as well as to excavation biases. The mean is therefore shifted towards a smaller-sized individual rather than towards an average-sized one which we would have obtained if all bones had the same chance to be retrieved and to be collected complete.

The most appropriate specimens were complete left and right bones of similar size and robustness, which showed the best anatomical fit with the elements articulated proximally and distally to them (as a reference we used complete skeletons of *Muntiacus muntjak*, which show similar degrees of bone robustness, and of *Axis axis*, which are comparable in size). Missing parts (vertebral processes, ribs, pelvic wings, shaft fragments, sacrum fragments) were reconstructed in epoxy putty, using other *Candiacervus* elements from Liko as a model or by interpolating the most parsimonious connection between two existing parts. The only composed skeletal elements are the pelvis and the sacrum, which are rebuilt using several incomplete specimens.

The final skeleton (for details about the mounting technique, see VAN DER GEER et al. 2005) steps with its front feet on a low elevation on a reconstruction of an island, and with its head lifted and bent 90 degrees to the left. The correct positions of the individual joints were obtained by comparing the articular surfaces of *Candiacervus* with those in articulated skeletons of extant deer. To give a

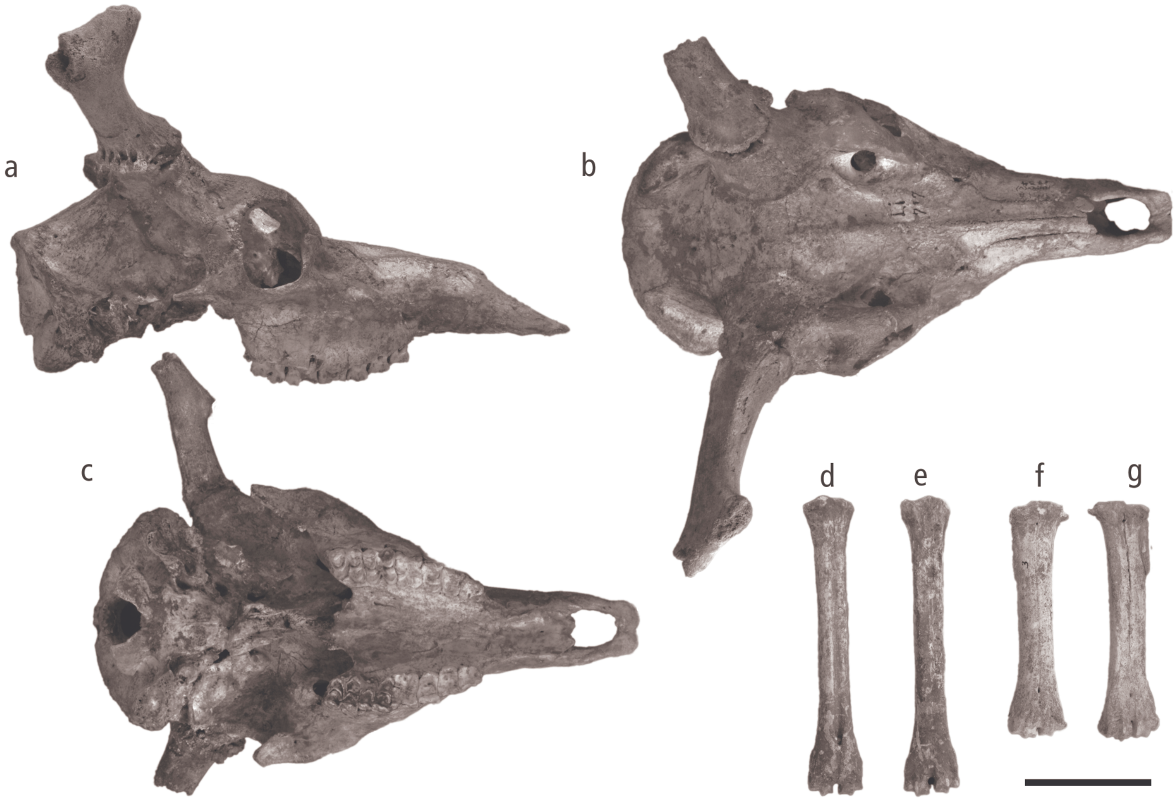

Fig. 2: The type skull of *Candiacervus* sp. II [collection number ampg(v) 1734 = Li-B 717] and the metapodals. a) skull in lateral view; b) same, in dorsal view; c) same, in ventral view; d) metatarsal, dorsal view; e) same, ventral view; f) metacarpal, dorsal view; g) same, ventral view, showing fused lateral metapodial. Scale bar 5 cm.

natural curvature to the vertebral column we inserted V-shaped cartilage disks, similar to those present in the extant deer skeletons that we used as a reference.

All the elements of *Candiacervus* used in the reconstruction are those unearthed by the 1973 to 1975 excavations carried out by a Dutch team, constituted by Hans Brinkerink, John de Vos, David Mayhew under the supervision of the late Dr. Paul Sondaar (at that time University of Utrecht, The Netherlands), at cave Liko (Likotinaras), in the Rethymnon area in the north-western part of the island. The material comes from the uppermost 75 cm of the cave deposits, which are attributed to the Upper Pleistocene. The material was brought to the Netherlands, cleaned, repaired, numbered (codes Li-B, Li-C, Li-OD), catalogued and measured. During the spring 2002, the material was returned to Greece (National and Kapodistrian University of Athens, Department of Geology, Section Historical Geology and Palaeontology), where it was partly renumbered [code AMPG (V)]. For measurements of the selected specimens, see van der Geer et al. (2005).

The reconstruction would have surely benefited from comparing with complete skeletons of fossil as well as of living island deer, which are extremely rare, or completely lacking. *Cervus astylodon* (Ryukyu Islands, Japan, Pleistocene) and *Hoplitomeryx matthei* (Gargano, Italy, Late Miocene/Early Pliocene) are represented by a mere assembly of disarticulated material. Other insular deer are insufficiently known (e.g. dwarf deer from Karpathos). Living island deer are rare too: *C. alfredi* and *C. mariannus* of the Philippines and four subspecies of *Odocoileus virginianus*, USA. They are also endangered species, and the study of their skeletons is therefore out of the question. The only skeleton we could measure is that of *C. mariannus* (National Museum of the Philippines, Manila), which is also the only existing skeleton in the world of this species.

Comparison with complete skeletons of other deer is a good alternative. The skeletons we used are all stored at Naturalis (Leiden, The Netherlands). They belong to the following extant deer: *Axis axis* (no. 1020, zoo, female; cat. a, wild, male; n.n., female), *Axis kuhlii* (n.n., wild, male), *Axis porcinus* (no. 4101, zoo, male; n.n., wild, female), *Capreolus capreolus* (no. 19654, male; no. 1041, zoo, male; cat. b, wild, male), *Cervus elaphus* (no. 2172, wild, male; no. 2169, female; no. 389, wild, male), *Cervus nippon* (no. 25991, wild, male, type specimen), *Dama dama* (cat. c., wild, male; cat. b, wild, female; cat d, wild, male; cat a, wild, male), *Muntiacus muntiac* (cat. d, wild, male), *Rusa unicolor* (cat. a, wild, male; cat. b, wild, female). One skeleton (compiled) of an extinct deer was studied: *Megaloceros giganteus* (in display at Naturalis). Alive fallow deer (*Dama dama*) were observed in a private zoo (Leidse Hout, Leiden, The Netherlands).

Results

Skulls, antlers, and limb bones of Cretan deer have already been described, measured and figured by numerous authors (Simonelli 1907, Kuss 1975, de Vos 1979, Malatesta 1980, Capasso Barbato & Petronio 1986, Dermitzakis & de Vos 1987). We therefore do not need to describe them here again in detail. The outstanding characters of this deer though, which we feel the need to remark, are its unusual sturdiness and the powerful muscular scars on practically all its elements. The original diagnosis of Kuss (1975), which was based upon the species *cretensis*, can be summarized as follows: *Candiacervus* is a plesiometacarpal Cervinae of varying size, from large to dwarf, whose ethmoidal and lacrimal fossae were weakly developed or even completely absent, which had hypsodont molars, a relatively long and robust axis, an antler with brow tine at least 5 cm from the burr, and which seems to have lost its lateral toes. In his diagnosis Kuss (1975) considered also the specimens now classified as *ropalophorus*, spp. II, and *rethymnensis*. In contrast, the larger-sized Cretan deer species were not included, because they were not known to Kuss.

Because we used the method proposed and tested by Heintz (1970), we now have a compiled skeleton which is very close to a natural articulated skeleton. A detailed analysis of the skeleton reveals new diagnostic features of *Candiacervus* sp. II. Some were disclosed during the reconstruction itself, because they emerge only from the combination of the different bone elements. Other characteristics were exposed by statistical processing, because for the first time we had a large amount of elements all gathered together and unpacked, which gave us a more complete overview of the deer. Diagnostic are the body proportions, several aspects of the vertebral column, the tail length, the degrees of fusions, and different aspects of the phalanges.

With the compiled skeleton on hand we understand the mutual combination of metacarpals (fig. 2f and g) and metatarsals (fig. 2d-e). The resultant mc/mt index = 3D 0,79, indicates that the metacarpal is relatively short in *Candiacervus* sp. II compared to *Cervus elaphus* (0,89), while it is similar to that of *Hoplitomeryx* size 1 (calculated from data presented by van der Geer 2005b).

If we compare the length of the limbs with that of the thoraco-lumbar region, we see that the reconstructed *Candiacervus* sp. II approaches the living Cretan mountain goat *Capra aegagrus* and even more the Pleistocene *Myotragus balearicus* from Mallorca (fig. 3). The lumbar and rear thoracic vertebral column (fig. 4a-b), however, is only slightly curved upward (fig. 4a), more or less as it is in a giant deer as *Megaloceros giganteus* than in a small deer as *Dama dama*. The approximately horizontal transversal processes of the vertebras (fig. 5a-c), recall those of heavier bodied medium-sized artiodactyls as *Myotragus* and *Ovis*. In general, the morphology of the vertebral column suggests a heavy, massive trunk.

The number of vertebras is typical of all cervids: 7 cervical, 13 thoracic and 6 lumbar vertebras (fig. 4). The caudal vertebras are ten, one for each morphotype represented in the large collection of caudal vertebras (fig. 5d-e),

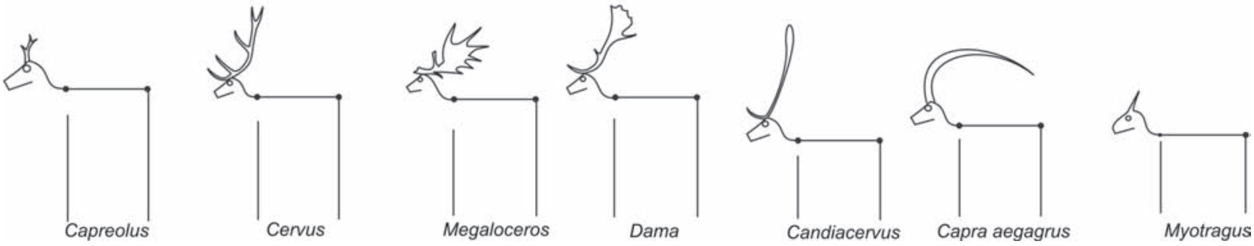

Fig. 3: Body proportions of some artiodactyls, in which thoraco-lumbar length has been equated to 100, and lengths of front leg (sum of lengths of humerus, radius, metacarpal) and hind leg (sum of lengths of femur, tibia, metatarsal) are indicated in proportion (adapted from Hildebrandt 1952). Data of living deer and *Megaloceros* from Geist (1998), data of *C. aegagrus* from personal data, data of *M. balearicus* from Spoor (1988). The limbs are not drawn attached to the vertebral column, but standing on the horizontal, as in Hildebrandt (1952). The thoraco-lumbar length is the total length of the complete series of thoraco-lumbar vertebras strung on a wire to facilitate handling, again as in Hildebrandt (1952).

Fig. 4: The thoraco-lumbar column of *Candiacervus* sp. II. seen from lateral (a) and from dorsal (b). The column shows a mild upward bent, as seen in the heavier deer like *Rusa unicolor* and *Cervus elaphus*. Scale bar: 10 cm.

which is a fairly low number of for a deer: *Muntiacus*, for example, has 15 caudal vertebras. The size drop from one caudal vertebra to the next could only be estimated, as no articulated specimens are present in the collection.

Radius and ulna are generally fused together, as also is the fifth metacarpal, while the second one is never fused to the third metacarpal (fig. 2g). In a minority of cases (10%, de Vos 1979), the cubonavicular is partially fused to the metatarsal. In mainland artiodactyls, such fusions are pathological, while in island artiodactyls it is a common phenomenon (Leinders & Sondaar 1974, van der Geer 2005a).

The difference between the anterior (fig. 5f-h) and the posterior hooves (fig. 5i-k) is fairly evident in such a large collection – although we were helped by some articulated extremities – but the phalanges largely overlap. Posterior ph III (fig. 5k) is lower, and somewhat shorter, more massive, more pointed, and straighter anteriorly than the anterior hooves (fig. 5h), while the latter have a more convex anterior surface. *Candiacervus* sp. II must have been equipped with lateral phalanges, as there are quite a lot of lateral third phalanges present in the collection. This contradicts the original diagnosis delivered by Kuss (1975).

Discussion and Conclusion

Articulated skeletons, and ad hoc remounted ones as well, can certainly provide us much more information on the morphology of a complete animal than any collection of individual bones. Features that are not otherwise obvious can be revealed when the bones are properly articulated and combined. The features disclosed by our remounted skeleton of *Candiacervus* are the difference in length of the metatarsal respect to the metacarpal, the changed body proportions represented by the shortened limbs compared to body length, the lesser bent lumbar region than in similar-sized mainland deer, the more horizontally orientated transversal vertebral processes, the difference in morphology of the anterior and posterior hooves, the solid fusion of radius and ulna, the loose fusion, if present, of the metatarsal and cubonavicular, the presence of lateral toes, in both the manus and the pes, which still preserve all their phalanges. Shortened limbs in relation to thoraco-lumbar length also characterize the Cretan wild goat, *Capra aegagrus*, and the Pleistocene Mallorcan mouse-goat *Myotragus balearicus*. The former lives, as *Candiacervus*, on the mountains of

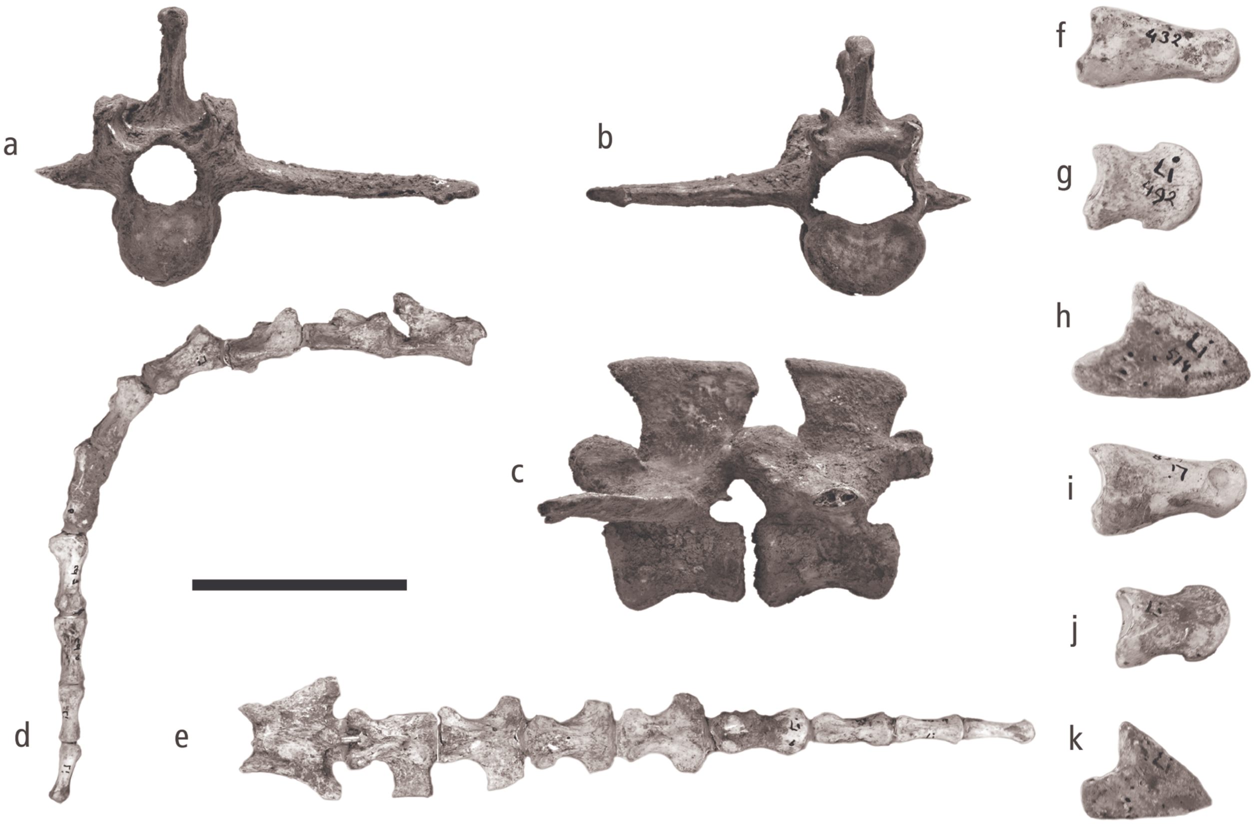

Fig. 5: The tail, three lumbar vertebras, and the phalanges of the composite mount of *Candiacervus* sp. II. The tail is bent in the characteristic way of living deer, and consists of ten vertebra, gradually decreasing in size. The transversal processes of the lumbar vertebrae are more or less orientated horizontally in *Candiacervus* size II; this is more typical for bovids like *Ovis aries*. The posterior third phalanges appear to be lower, shorter, more massive, more pointed, and with a more straight anterior surface than the anterior hooves, yielding a triangular shape. In the anterior hooves, the anterior surface is more convex and the tip is not pointed. The other phalanges clearly show the differences between anterior and posterior as described for deer (Heintz 1970).
a) lumbar vertebra, cranial view; b) same, caudal view; c) an associated pair of lumbar vertebras; d) tail, lateral view; e) same, dorsal view; f) phalanx I anterior; g) phalanx II anterior; h) phalanx III anterior; i) phalanx I posterior; j) phalanx II posterior; k) phalanx III posterior. Scale bar: 5 cm.

Crete and feeds on not easily digestible plants. The latter lived under similar conditions, and maybe its diet was even poorer and with limited variation, as its coprolites prove that it consumed lots of the otherwise toxic box, *Buxus balearica* (Alcover et al. 1999). Food is therefore the limiting factor for survival on restricted areas such as islands; this likely applied to *Candiacervus* as well. We can thus assume that *Candiacervus* evolved in the direction of island goats, and had to consume plants with a lower nutritional value and higher fiber contents, as indicated by its higher crowned molars and massive trunk, parallel to what is observed in *Myotragus*. The morphological aspects of the vertebral column are a consequence of a heavier and more massive mounted on short, sturdy limbs. The marked difference between the anterior and posterior hooves, added to the various skeletal fusions, are also the result of this unusual body structure, as well as modifications for living in a rocky environment. Advanced fusions give more stability (Leinders & Sondaar 1974), especially to an animal with a heavier trunk. This was certainly an advantage in the mountains of Crete.

The various features and particular proportions developed by *Candiacervus* show that this deer had to adapt to a completely different ecological environment than the large continental cervids of the Pleistocene, one of which must have been its ancestor. As a rule, deer are opportunistic luxury feeders, and are found in habitats with forage of high-quality and fairly low fiber contents, whereas bovids adapted even to much poorer environments with tough-fibered forage (Geist 1998). On the island, the deer had to eat what was available. Although living as well as known extinct deer never adaptated perfectly to a mountaineous environment with low quality forage, in other words, never turned into a “goat”, *Candiacervus* seems to have gone a good way in that direction.

Acknowledgements

First of all, honour and gratitude are due to the late Paul Sondaar, who was the promotor behind all the Liko Cave excavations, and who never became tired of stressing the importance of the study of the evolution of island endemics, especially *Candiacervus*. From a more practical point of view, we’d like to thank Cor Strang for assisting us during all the stages of preparation and mounting and Chris Smeenk (both Nationaal Natuuhistorisch Museum, Leiden, The Netherlands) for enabling us to study the skeletons of the living deer. We also thank Aart Walen (Creatures Features, Doornenburg, The Netherlands) for the fruitful discussions we had with him on technical and anatomical subjects and Hans Brinkerink (Vista Natura, Baarn, The Netherlands) for making the cast of the skull and antlers. Finally, we thank Jan van der Made (Museo Nacional de Ciencias Naturalis, Madrid) and Laura Abbazzi (Universita degli Studi, Firenze) for their critical and valuable remarks on the manuscript and plates.

References

Alcover, J. A., Perez-Obiol, R., Errikarta-Imanol, Y., & Bover, P. (1999): The diet of *Myotragus balearicus* Bate 1909 (Artiodactyla: Caprinae), an extinct bovid from the Balearic Islands: evidence from coprolites. — Biological Journal of the Linnean Society, **66**: 57–74; London.

Belluomini, G., & Delitala, L. (1983): Datazione di resti ossei e denti del Pleistocene superiore e dell'Olocene dell'area mediterranea con il metodo della racemizzazione degli aminoacidi. — Geografia Fisica e Dinamica Quarternaria, **6**: 21–30; Roma.

Bover Arbós, P. (2004): Noves aportacions al coneixement del gènere *Myotragus* Bate 1909 (Artiodactyla, Caprinae) de les Illes Balears. — PhD Thesis: 1–469; Palma de Mallorca (IMEDEA).

Caloi, L., & Palombo, M. R. (1996): Functional aspects and ecological implications in hippopotamus and cervids of Crete. — In: Reese, D. S. (Ed.): Pleistocene and Holocene Fauna of Crete and its First Settlers. — Monographs in World Archaeology, **28**: 125–151; Madison, Wisconsin (Prehistory Press).

Capasso Barbato, L. (1989): Cervidi endemici del pleistocene di Creta, Vol. I and II. — PhD Thesis: 1–214; Modena-Bologna.

Capasso Barbato, L. (1992): Observations on the biostratigraphy of Cretan Pleistocene vertebrates. — Il Quaternario, **5** (1): 67–76; Roma.

Capasso Barbato, L., & Petronio, C. (1986): *Cervus major* n. sp. of Bate Cave (Rethymnon, Crete). — Atti della Accademia Nazionale dei Lincei, Memorie, classe di Scienze fisiche, matematiche e naturali, Serie VIII, **18** (2, 2): 59–100; Roma.

Dermitzakis, M. D., & de Vos, J. (1987): Faunal succession and the evolution of Mammals in Crete during the Pleistocene. — Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **173** (3): 377–408; Stuttgart.

Geer, A. A. E. van der (2005a): Island ruminants and parallel evolution of functional structures. — In: Cregut, E. (Ed.): Les ongulés holarctiques du Pliocène et du Pléistocène. Actes Colloque international Avignon, 19-22 septembre. — Quarternaire, hors-série **2**: 231–240; Paris.

Geer, A. A. E. van der (2005b): The postcranial of the deer *Hoplitomeryx* (Pliocene; Italy): another example of adaptive radiation on Eastern Mediterranean islands. — In: Alcover, J. A., & Bover, P. (Eds.): Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach", September 16-19 2003 Mallorca. — Monografies de la Societat d'Història Natural de les Balears, **12**: 325–336; Palma de Mallorca.

Geer, A. A. E. van der, Vos, J. de, Lyras, G., & Dermitzakis, M. (2005): The mounting of a skeleton of the fossil species Candiacervus sp. II from Liko Cave, Crete, Greece. — In: Alcover, J. A., & Bover, P. (Eds.): Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach", September 16-19 2003 Mallorca. — Monografies de la Societat d'Història Natural de les Balears, **12**: 337–346; Palma de Mallorca.

Geist, V. (1998): Deer of the world: their evolution, behaviour, and ecology. — 1–421; Mechanicsburg (Stackpole Books).

Heintz, E. (1970): Les Cervidés villafranchiens de France et d'Espagne. — Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série, Série C, **XXII**, fascicule unique (2 volumes): 1–303; Paris.

Hildebrandt, M. (1952): An analysis of body proportions in the Canidae. — American Journal of Anatomy, **90** (2): 217–256; Philadelphia.

Kurtèn, B. (1968): Pleistocene Mammals of Europe. — viii + 1–317; London (Weidenfeld and Nicholson).

Kuss, S. E. (1975): Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpatos und Rhodos (Griechenland). — Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau, **65** (1–2): 25–79; Freiburg i. Br.

Leinders, J. J. M., & Sondaar, P. Y. (1974): On functional fusions in footbones of Ungulates. — Zeitschrift für Säugetierkunde, **39** (2): 109–115; Hamburg, Berlin.

Malatesta, A. (1980): Dwarf deer and other late Pleistocene fauna of the "Simonelli" Cave in Crete. — Quaderni Accademia Nazionale dei Lincei, **209:** 1–97; Roma.

Moyà-Solà, S. (1979): Morfología functional del tarso en el género *Myotragus* Bate, 1909 (Artiodactyla, Rupicaprini). — Acta Geologica Hispanica, **3** (3): 87–91; Madrid.

Radulesco, C., & Samson, P. (1967): Sur un niveau à Cerf mégacérin du Pleistocène moyen de la dépression de Brasov (Roumanie). — Geologica Romana, **9**: 317–344; Roma.

Reese, D. S., Belluomini, G., & Ikeya, M. (1996): Absolute Dates for the Pleistocene Fauna of Crete. — In: Reese, D. S. (Ed.): Pleistocene and Holocene fauna of Crete and its first settlers. — Monographs in World Archaeology, **28**: 47–52; Madison, Wisconsin (Prehistory Press).

Sigogneau, D. (1960): Étude d'un cervidé du Pléistocène de Corse. — Annales de Paléontologie, **46**: 4–77; Paris.

Simonelli, V. (1907): Mammiferi quaternari dell'isola di Candia, I. — Memorie, Accademia delle Scienze dell' Instituto di Bologna, Classe di Scienze Fisiche, Serie VI, **4**: 251–267; Bologna.

Sondaar, P. Y. (1977): Insularity and its effect on mammal evolution. – In: Hecht, M. K., Goody, P. C., & Hecht, B. M. (Eds.): Major Patterns in Vertebrate Evolution. — 671–707; New York (Plenum Publications Corporation).

Sondaar, P. Y., & Boekschoten, G. Y. (1967): Quaternary mammals in the south Aegean island arc with notes on other mammals from the coastal regions of the Mediterranean, I/II. — Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **7**: 556-576; Amsterdam.

Spoor, C. F. (1988): The body proportions of *Myotragus balearicus* Bate 1909. — Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **91**: 295–305; Amsterdam.

Vaufrey, R. (1929): Les élephants nains des îles méditerranéennes et la question des ìsthmes Pléistocènes. — Archives de l'Institut de Paléontogie Humaine, **6**: 1–220; Paris.

Vos, J. de (1979): The endemic Pleistocene deer of Crete. — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **82** (1): 59–90; Amsterdam.

Vos, J. de (1984): The endemic Pleistocene deer of Crete. — Verhandelingen Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, eerste reeks, **31**: 1–100; Amsterdam.

Vos, J. de (2000): Pleistocene deer fauna in Crete: Its adaptive radiation and extinction. — In: Otsuka, H., Ota, H., & Hotta, M. (Eds.): International Symposium The Ryukyu Islands — The Arena of Adaptive Radiation and Extinction of Island Fauna. — Tropics, **10** (1): 125–134; Kagoshima (Japan Society of Tropical Ecology).

Manuscript submitted 2005–10–04
Revised manuscript accepted 2006–08–14