32

The mounting of a skeleton of the fossil species *Candiacervus* sp. II from Liko Cave, Crete, Greece

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

Resum

S'ha muntat un esquelet del cérvol pleistocènic endèmic de Creta per a la nova exhibició del Museu de Geologia de la Universitat d'Atenes. Aquest cérvol difereix de tots els cérvols continentals vivents i extingits, principalment en les seves proporcions. Les mesures i comparacions confirmen aquesta observació, però això no és prou com per a que el públic general se n'adoni del seu impacte. Per contra, un esquelet muntat deixa clar que aquest cérvol tenia uns membres considerablement escurçats, especialment els metàpodes, mentre que la llargària del cos, o la llargària de la columna vertebral, eren més aviat normals. La impressió global és més propera a la d'un bòvid nan insular, com ara *Myotragus,* que a la d'un cérvol petit, tal com *Axis axis.*

El primer problema a resoldre fou la selecció de material. Ja que mai s'ha trobat un esquelet articulat complet, se n'ha de fer un de compost. Amb aquest motiu, només es varen seleccionar ossos de la classe de talla II (de Vos, 1979 ; Dermitzakis & de Vos, 1987) provinents d'un nivell d'una cova (cova de Liko, estrat B). D'aquesta manera es garanteix un interval geològic estret. Tot seguit, es varen mesurar tots els espècimens disponibles, i es va calcular el promig per a tots els elements. D'acord amb això, es va triar l'exemplar de cada element que més s'apropava a la mitjana calculada. Les peces dretes i esquerres havien de ser de la mateixa mida i robustesa, i els elements contigus havien de casar anatòmicament. Només en alguns casos s'ha hagut de recórrer a triar algun element que faltava a partir d'un nivell diferent, però mai a partir d'una cova diferent i mai a partir d'una classe de talla diferent. S'ha prioritzat la mida, la robustesa i l'ajustament anatòmic, i després que els ossos fossin complets i el color. Hi havia alguns peus articulats disponibles, encara que de mida i robustesa diferents, que s'han emprat per determinar les proporcions correctes i la posició correcta entre les falanges individuals, i els ossos carpians i tarsians. La mateixa cosa fou vàlida per a la columna vertebral. Per a l'establiment de la postura es van fer servir cérvols vivents com a comparació; per a l'extrapolació dels teixits tous (discos intervertebrals, cartílags de les articulacions) també es va recórrer al model dels cérvols vivents.

De cara a amagar els bastiments de suport, es va inserir dins els ossos una armadura metàl·lica interna fent forats i fitxant-la amb goma de poliuretà. S'ha fabricat l'esquelet complet en parts modulars bones d'ajuntar pel seu transport fàcil a la mostra. Parts absents petites (principalment processos vertebrals, parts costals i les ales pèlviques) s'han reconstruït amb apoxy, en base a altres elements disponibles de *Candiacervus* de la cova de Liko o per interpolació del millor ajustament entre dues parts absents. Les traces de la matriu original han estat estretes, per a una impressió millor del material fòssil. Per completar l'esquelet s'ha fet una rèplica del crani de l'espècimen tipus de la classe de talla II de de Vos (1979) i una rèplica de l'espècimen tipus del banyam tipus I de de Vos (1984).

Paraules clau: Pleistocè, endemisme, cérvol, reconstrucció, esquelet muntat.

Summary

For the new exhibition in the Museum of Palaeontology and Geology of the University of Athens a skeleton of the endemic Pleistocene Cretan deer was mounted. This deer differs from all known recent and extinct mainland deer, mainly in its proportions. Measurements and comparisons confirm this observation, but are not enough to make the public realize its impact. A mounted skeleton on the contrary makes it at once clear that this deer had considerably shortened limbs, especially the metapodals, whereas the body length and the vertebral column length are rather normal. The overall impression is closer to that of an insular dwarf bovid like *Myotragus* than to that of a small deer such as the spotted deer (*Axis axis*).

The first problem to be tackled was the selection of the material. Since a complete articulated skeleton has never been found, a composite had to be made. For this purpose, only bones of size class II (de Vos, 1979; Dermitzakis & de Vos, 1987) coming from one layer of one cave (Liko Cave, layer B) were selected. In this way a narrow geological range was assured. Subsequently, the available specimens were measured, and of all elements the average size was calculated. Accordingly, of each element the specimen that came the most close to the calculated average was selected. Left and right had to be of exactly the same size and robustness, and adjoining elements had to fit anatomically. Only in some cases a missing element had to be chosen from a different layer (layers C and D), but never from a different cave, and never from a different size class. Priority was first given to size, robustness and anatomical fitting, and next to completeness and colour. Several articulated feet were available, although of the wrong size or robustness, which were used in determining the right proportions and right stance between individual phalanges, tarsal and carpal bones. The same was valid for the vertebral column. For postural aspects, living deer were used as comparison; for extrapolation of soft tissue (intervertebral disks, articulation cartilage) also living deer stood model.

In order to keep the supporting fabrication as hidden as possible, an internal metal armature was inserted in the bones through drilled holes and fixed with polyurethane glue. The complete skeleton is fabricated in ready-to-assemble modular parts for easy transportation and reassembly on the spot. Minor missing parts (mainly vertebral processes, costal parts and the pelvic wings) have been reconstructed in epoxy putty, based on other *Candiacervus* elements from Liko or by interpolating the best fit between two existing parts. For a better impression of the fossil material, traces of the original matrix were left on the bones. A cast of the skull of the type specimen of size II of de Vos (1979) and a cast of the type specimen of antler type 1 of de Vos (1984) were made to complete the skeleton.

Keywords: Pleistocene, endemic, deer, reconstructing, mounted skeleton.

INTRODUCTION

Recently, the Museum of Palaeontology and Geology of the University of Athens reorganized its exhibition completely, in accordance to the latest insights in palaeontology and climatology. The pattern of the new exhibition follows the patterns of global climatological changes throughout time. These climatological changes had a great impact on the palaeoenvironment and were the cause of extinctions and evolutionary changes in many mammalian species. One of the clearest examples is the extinction of the endemic island deer of Crete, *Candiacervus*. Once this deer roamed the island, and was represented by eight morphotypes as a result of adaptive radiation, distributed over six size classes and three antler morphotypes, 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, 1984, 2000). Other taxonomies (e.g. Capasso Barbato, 1989; Caloi & Palombo, 1996) recognize five species, but these opinions are not followed here, furthermore, taxonomic problems are irrelevant for the reconstruction at the moment. At the end of the Pleistocene the climate gradually became warmer; at the same time the island became smaller by a sea level rise. This resulted in a drastic decrease in number and species richness of the Cretan deer. At present it is known to us only by its fossilized bones.

Bones alone, however, have no high educational value in a modern exhibition, so a reconstruction of the complete animal appeared necessary. How else to show the public that this endemic creature really looked so completely different from the deer we know, even if we include an island deer like *Cervus marianus* from Philippines? A mere assemblage of bones is not enough to stress the essential different nature of the Cretan deer; this can be done only with the help of a complete skeleton. Unfortunately such a skeleton was never found, so the only way is to reconstruct a skeleton out of individual elements, assemble them in a feasible, life-like articulation, and reconstruct a possible mode of locomotion and other postural aspects. We choose to assemble a skeleton out of size II elements, all adult and male. In the exhibition the skeleton is placed on the model of a small island. In order to stress the different habitat of the Cretan deer from the mainland species, we let it stand on the higher level of a rocky cliff. The skeleton is mounted with its head turned towards the spectator, so that both antlers are shown in their full length and a certain contact with the visitor is created.

METHOD

Selecting elements

First of all, we want to show a species that shows the characteristic endemic feature of the shortened legs. Only size classes I, II and III as defined by de Vos (1979) (= *C. ropalophorus,* the three spp. II, and *C. cretensis*) come therefore into consideration. Of these three taxonomical units, we choose not to build the largest or the smallest size, as in such a way a rather exceptional individual is built. Therefore sizes I and III were skipped and we proceeded with spp. II, of which there are three types, but all with the same size (estimated withers height about 50 cm; de Vos, 2000).

Secondly, the appropriate elements had to be selected. Within spp. II there is a certain amount of individual variation, amongst which an average type should be selected, but at the same time the proportions between the elements should be correct. It appears that the proportions between limb bones of an articulated skeleton can be reliably approached by merely taking the average values of a large enough collection of disarticulated elements; this method has been tested for *Cervus philisi* with 30 disarticulated skeletons and 1 articulated skeleton (Heintz, 1970). For all practical reasons, this means that if we take the average bone from a large collection of disarticulated elements, we approach the correct articulated skeleton close enough to be reliable.

Another choice that has to be made is that of gender. In the case of deer, a male individual is the obvious choice as the antler informs us not only about the deer's taxonomic position, which is good for the visiting scientist, but also it is the most attractive feature for the general public, which happens to be our most important target group.

The excavation at Liko cave (north-western Crete) yielded a large amount of (adult) deer bones (Fig. 1), of which size II is by far the most common: 95,3% (de Vos, 1979). The fossils were from numerous disarticulated individuals, with the exception of a few articulated parts. Fortunately, the number of bones was large enough to apply the abovementioned method. For each bone we calculated the mean value and this made it possible to select within each bone category the specimen with the average measurements. We choose almost entirely from one layer (Liko B), with only a few additional specimens from other layers (Liko C, Liko OD), to assure a narrow geological time range for the selection. After the selection of the average, more or less complete adult specimens, the best fitting specimens were selected from this selection. Most important discriminative

Fig. 1. Cave Liko (northwestern Crete) contained a large amount of *Candiacervus* bones, mainly of size II. With the exception of only a few articulated parts, the fossils came from disarticulated individuals.

Fig. 1. *La cova Liko (nord-oest de Creta) contenia una gran quantitat d'ossos de* Candiacervus, *principalment de la classe de mida II. Amb l'excepció d'unes poques parts articulades, els fòssils provenen d'individus desarticulats.*

factors were, in this order, equal size of left and right side, similarity in robustness of left and right side, completeness, anatomical fitting with proximal element, anatomical fitting with distal element. Anatomical fitting was checked for each combination with a skeleton of a muntjac (chosen for its robustness) and of a spotted deer (chosen for its comparable size). In case a right and a left element were of equal size, equal robustness but one of the two was severely damaged, glued together and lacking major parts of the epiphyseal areas, this specimen was discarded, and quite often also the other specimen as no exact mirrored copy could be found, and we had to start with a fresh combination. To our surprise, many elements fitted so well, not only anatomically but also in colour and fossilization, that most likely they originated from one individual.

Technique

The complete skeleton is fabricated in ready-to-assemble modular parts, which can be reassembled on the final spot. This allows not only easy and comprehensive transportation, but gives at the same time opportunities for minor changes in the future, mainly of course in the posture of the animal. Minor missing parts (mainly vertebral processes, costal parts and the pelvic wings) have been reconstructed in epoxy putty, based on other *Candiacervus* elements from Liko or by interpolating the best fit between two existing parts, again with the spotted deer and muntjac as reference. The reconstructed parts were shaped with a grinder and sand paper, and then painted with water colour to which coarse sand was added. The colour does not approximate too well the real fossil in order to make the reconstruction apparent. The addition of sand gave a sandstone-like texture to the reconstructed parts, which does not distract the eye from the rest of the mount. The reconstructed edges of the neural spines slightly diverge from the smooth curve that should connect their tips. This was done on purpose in order to make clear to the visitors that the mount was made of fossil elements composite out of many individuals. For a better impression of the fossil material, traces of the original matrix were left on the real bones. Because the selected skull is the type specimen of sp. II (see below), it was preferable to keep the original in the research collection. Furthermore, the process of attaching new, more complete antlers to that skull would have resulted in an alternation of the type specimen, which would confuse future researchers. For these reasons we substituted it with a cast. Because of all parts of the skele-
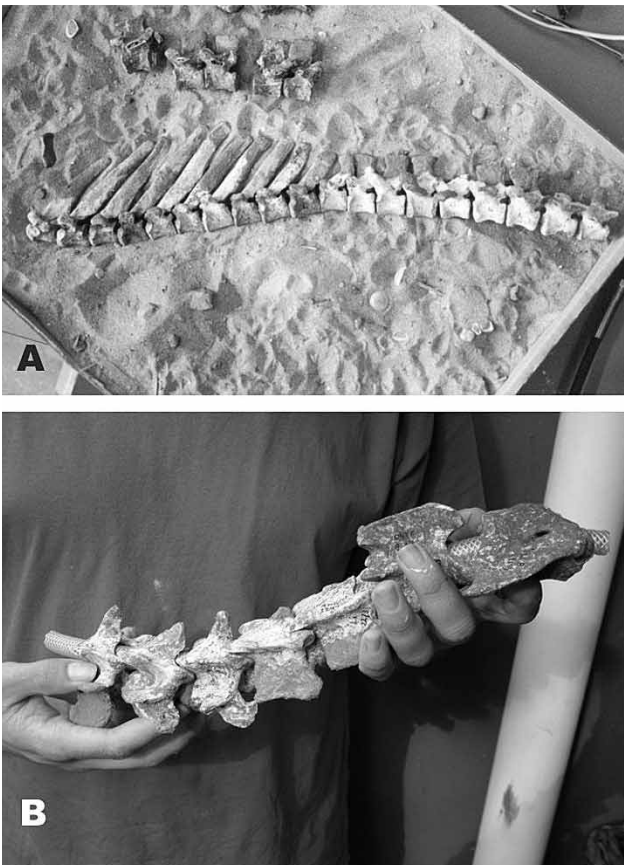

Fig. 2. **A.** Finding the correct position of the vertebrae of *Candiacervus* with the use of sand failed, because of the very fragile and thin aspect of the transversal processes. **B:** The best approach was that with the help of a flexible tube that was inserted in the vertebral canal (technique Aart Walen). **C:** The front limb bones are hanged as one unit to the skeleton into an armature that holds the scapula. **D:** The hindlimb is attached with a screw through the femoral head that is screwed into a metal plate at the interior side of the pelvis.
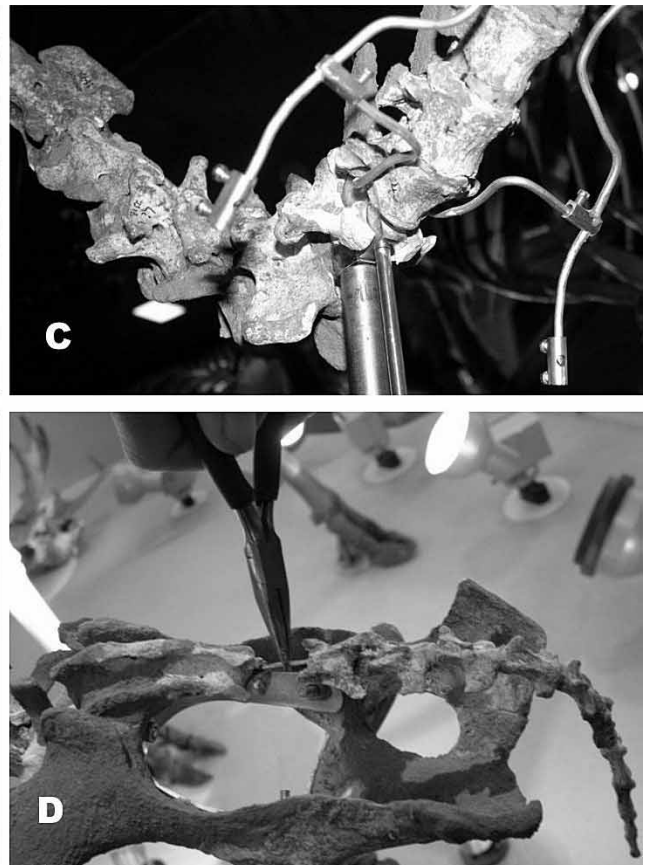
*Fig. 2. **A.** L'establiment de la posició correcta de les vèrtebres de* Candiacervus *amb l'ús d'arena va fallar, degut a l'aspecte molt fràgil i prim de les apòfisis transverses. **B.** La millor aproximació es va aconseguir amb l'ajut d'un tub flexible que s'inseria al canal vertebral (tècnica Aart Walen). **C.** Els ossos de les cames de davant es pengen com a una unitat a l'esquelet mitjançant un ànima metàl·lica que s'aferra a l'escàpula. **D.** El membre posterior s'uneix amb un pern a través del cap del fèmur que s'enrosca a una placa de metall situada al costat intern de la pelvis.*

ton the head is the most closely examined element by visitors (Madsen, 1973), the cast was realistically painted, contrary to additions to the postcranial elements (see above). Finally replica polyurethane antlers were made to complete the skeleton. We choose to cast the type specimen (Ge4-2870, left) of antler type 1 coming from Cave Gerani 4 and described and figured by de Vos (1984); the right side is a mirrored cast. Although this specimen comes from a different cave (Gerani 4), we think it fit for our reconstruction, based upon the many fragmentary antlers from Liko that correspond exactly to this holotype, not only in morphology but also in size. This means that antler type 1 not only occurred in the Liko population, but was also not rare. In addition, a complete antler was never found in Liko, and a reconstruction with fragments only would be a hazardous operation.

In order to keep the supporting fabrication as hidden as possible, an internal metal armature was inserted in the bones through drilled holes and fixed with polyurethane glue to the bone to prevent damage caused by friction between bone and metal. The hindlimb was attached in this way: a screw through the femoral head was screwed into a metal plate at the interior side of the pelvis at the position of the acetabulum (Fig. 2; Fig. 3). The internal iron rod exits the metatarsals and is placed immediately on the base. The phalanges are placed in front of the iron rod. They are attached together and to the metatarsals with the use of thin electric wires: their PVC cover was inserted in the two bones at the opposite sides of the articulation facets of the diaphysis and the two elements are hold together with the wires' copper core. This ensured a better stability, and prevented too much damage to these small elements. The method of building a fully free skeleton could not be applied in this case because the diameter of the bones of the anterior limbs is too small to drill them safely in order to pass a wide rod. However, the support at the front was necessary because of the huge torque of the heavy skull and backward orientated antlers. So in order to prevent the skeleton from falling forward, we had to install a heavy steel rod between the front feet and the first thoracic vertebra (Fig. 3). The front limb bones were attached to each other with wires and were hanged as one unit to the skeleton with the use of small nuts
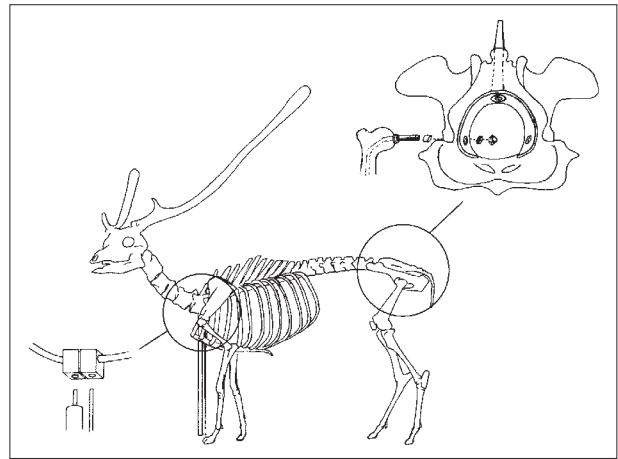

Fig. 3. Detail drawing of the supporting system at the front limb and the attachment system of the hindlimb. **Left**: A heavy steel rod turned out to be inevitable, due to the huge torque of the heavy skull with antlers. It was fixed to the wire through the vertebral canal. **Right:** The femoral head is screwed into a metal plate that is attached to the interior side of the pelvis.

Fig. 3. Dibuix de detall del sistema de suport del membre anterior i del sistema d'unió del membre posterior. Esquerra. Una pesada barra d'acer és inevitable, degut al pes de pesat crani amb el banyam. Fou fitxada al fil de ferro de l'interior del canal vertebral. Dreta. El cap del fèmur s'engranpona a una placa metàl·lica situada al costat intern de la pelvis.

and bolts (Fig. 2). The ribs are for the larger part sculpted due to strength considerations and the lack of complete bones, and are epoxied and glued to the frame.

The skeleton is articulated in a life-like, natural pose, which requires choices about the angles of articulation and the ranges of flexion, extension, abduction and adduction. To ensure this, the articular surfaces were studied in detail with living deer as reference, and the best fit or close-packed situation was chosen to assure the rest position of the articulation, with the exception of the front limb and the cervical vertebras. In the case of the phalanges, we checked the resulting position with alive *Dama dama* and x-rays from anatomy handbooks. The front limb is articulated in such a way that the animal steps on an elevation of about
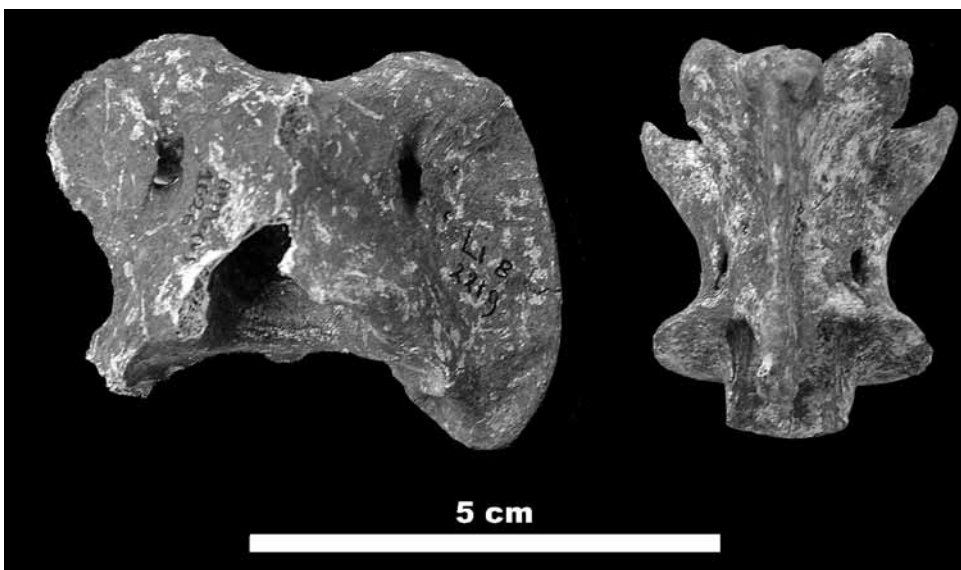

Fig. 4. The selected atlas (ampg (v) 1626) and axis (Li-B 2240), which both belong to males, based upon their more robust morphology with much more pronounced muscular attachment areas in comparison to equal sized female specimens.

Fig. 4. L'atles (ampg(v)1626) i l'axis (Li-B 2240) seleccionats, tots dos pertanyents a mascles, segons la seva morfologia més robusta, amb unes àrees d'inserció musculars més pronunciades, en comparació amb espècimens femenins de la mateixa mida.

Fig. 5. Above, left: The right calcaneum (Li-B 403) and right astragalus (Li-B 1468) in volar view. **Above, right**: The selection of fitting phalanges was eased by the presence of several associated feet in the collection, of which this is one example. **Below**: As a complete, medium-sized sacrum was not available, it had to be composed out of three damaged specimens.

*Fig. 5. A dalt, a l'esquerra. Calcani dret (Li-B 403) i astràgal dret (Li-B 1468) en norma volar. **A dalt, a la dreta.** La tria de falanges que articulessin va acabar gràcies a la presència de diversos peus associats a la col·lecció; aquest n'és un exemple. A sota. Com que no es disposava de cap sacre complet de mida mitjana es va haver de recrear un a partir de tres espècimens espanyats.*
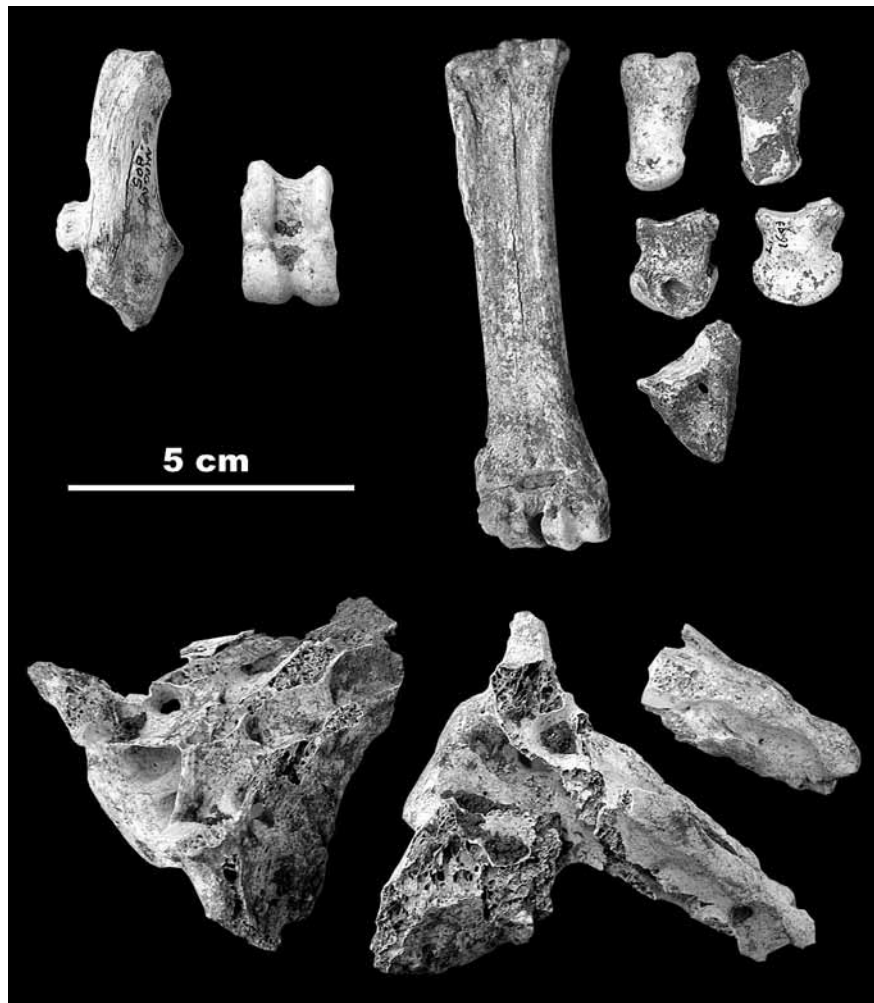
10 centimetre. The cervical column is adjusted to an upheld position of the head, which makes in addition a turn of 90 degrees in order to look to the spectator. The best fit for the other vertebras was in first instance approached with the help of a metal rod through the vertebral canal, but this appeared impossible due to the stiff nature of metal: each bending to conform the right curvature between two vertebras caused at the same time an error in another pair of vertebras. Also the method with the use of sand (Fig. 2) failed, as with every corrective movement the transversal processes ran the risk to break off. A far better approach was that with the help of a flexible tube that was inserted in the vertebral canal (Fig. 2), a technique suggested by Aart Walen (pers. comm. 2003). That tube can be considered as a simulation of the neural canal, and it helped us to find the exact anatomical position of the vertebrae. In addition, the vertebrae with the tube inside appeared to be a construction stable enough to allow us to pass the metal rod through the tube itself. After that, the whole construction was fixed with epoxy putty and glue. For the right shape of the vertebral column we further assumed a V-shaped cartilage disk to have been present in the living animal, similar to those seen in recent deer; for this we compared with *Axis axis, Rusa unicolor, Dama dama* and *Cervus elaphus)*. The caudal vertebras were attached to each other and to the sacrum with a system similar to the one that we used for the phalanges.

A final step was to cover all exposed metal or plastic parts of the mount (with the exception of the central metal rod between the anterior limbs). For that purpose we imitated the calcite deposits of Liko cave, by mixing epoxy putty, glue and clay collected from the cave itself.

Material

All used elements of *Candiacervus* are stored at the University of Athens (Greece), Department of Geology, Section Historical Geology and Palaeontology. The material originates from the 1973 to 1975 excavations at cave Liko (Likotinaras) in the Rethymnon area at the north-western part of the island, carried out by a Dutch team consisting of Hans Brinkerink, John de Vos, David Mayhew under supervision of the late Dr Paul Sondaar (at that time University of Utrecht, The Netherlands). The material collected from Liko comes from the uppermost 75 cm of the cave deposits, attributed to the Late Pleistocene. The material was transported to the Netherlands, cleaned, repaired, numbered (codes Li-B, Li-C, Li-OD), catalogued and measured. During spring 2002, the material was returned to Athens, where it is presently stored and in the process of being renumbered (code AMPG (V)). All materials chosen for the

composite skeleton originate practically speaking from one level, level B, with some additions from level C and level OD. All specimens belong to adult individuals.

The living deer used for comparison are all stored at Naturalis, Nationaal Natuurhistorisch Museum, Leiden (The Netherlands), and consist of *Axis axis*, *Cervus elaphus*, *Rusa unicolor*, *Dama dama*. Alive fallow deer (*Dama dama*) were observed in a private zoo (Leidse Hout, Leiden, The Netherlands).

CRANIAL SKELETON

The skull is actually the most important element of the skeleton as it embodies so much of an animal's "personality" (Antón, 2003). The most stringent requirements for the skull, apart from size, are that it belonged to a male, and that it is as complete as possible. This immediately implies that the possibilities are limited. The possibilities increase when we forget about the antlers and the jaws, and substitute them for separately found, unassociated specimens. The possibilities further increase when we include damaged, incomplete skulls into consideration that can easily be filled up with epoxy. The selected skull comes from Liko B (ampg(v) 1734 = Li-B 717).

For the antler, we could select from the three types as known and described for size II (Dermitzakis & de Vos, 1987: fig. 10a-c). None of the antlers, however, was complete; a complete left antler (Ge4-2870) was only known from Cave Gerani 4, described as type specimen for antler type 1. Fortunately this type also occurred in Liko, and indeed many fragmentary antlers were present in the collection which fitted in morphology and size exactly to this type specimen. This warrants the combination of this antler type with the type skull and our postcranial skeleton. The other two antler types are too fragmentary and too incomplete to be a reliable basis for a reconstruction.

The lower jaw constituted an additional problem: age. Not only the size and the robustness have to be similar for right and left, but also the degree of abrasion of the dental elements. The individual age of the right and left jaw should not differ too much.

AXIAL COLUMN

For the atlases, only the robust, presumably male specimens were considered. In the male atlas in living deer, the ventral arch is thicker at the median vertebral entry, in the dorsoventral direction, than the height diameter of the

Fig. 6. Some of the postcranial elements selected for the mounting. A, B: The frontlimbs (for numbers, see Table 1). C: The right hindlimb (for numbers, see Table 1). D: Left cannon bone (Li-B 898). E: The exceptionally complete left scapula Li-B 605. F: Left femur (Li-B 1325).

Fig. 6. Alguns dels elements postcranials seleccionats per al muntatge. A, B. Cames anteriors (per als números, veure Taula 1). C. Cama dreta posterior (per als números, veure Taula 1). D. Os canon esquerre (Li-B 898). E. Escàpula esquerra excepcionalment completa (Li-B 1325).

overlying spinal canal. The most appropriate atlas is specimen ampg(v) 1626 (male; original number Li-B 2219) (Fig. 4). For the axis, a similar approach was taken, with as additional criterion that it should fit the chosen atlas. In the male deer axis, the spinous process is higher than in the female, but in many *Candiacervus* specimens this process is unfortunately broken-off, so features of overall robustness and pronounced muscular scars constitute better criteria. The resulting specimen was Li-B 2240. These atlas and axis can be attributed to males without doubt, at the basis of their more robust morphology compared to equal sized female atlases and axes. The muscular attachment areas are much more pronounced on the first cervical vertebras of all living male deer, due to the heavier skull with appendages.

The procedure for the remaining cervical vertebras was much easier, as they had to fit the preceding vertebra as natural as possible. The only feature to discard some fitting specimens was the obvious lack of robustness, a high degree of damage, or the lack of the caudal articulation. In case a caudal articulation is missing, the procedure of fitting one by one is blocked. The resulting cervical column consists of C3 (Li-B 2273), C4 (Li-B 2289), C5 (Li-B 2313), C6 (Li-B 2343), and C7 (Li-B 2357).

For the thoracic vertebras the procedure was simply continued, resulting in a sequence T1 - T13, unfortunately all unnumbered, though all from Liko B. No already associated specimens of average size could be found in the collection, but of other sizes instead. These associated pairs were used to check the resulting morphology. The same is valid for the lumbar vertebras L1-L6, all unnumbered, all from Liko B. Here a larger associated series, consisting of T12 up to and including L6, was used as reference.

A complete, medium-sized sacrum (in the case of *Candiacervus* consisting of four sacral vertebras) was not available, but it appeared possible to compose one out of three damaged specimens (all unnumbered; Fig. 5) with the use of epoxy to fill up the gaps.
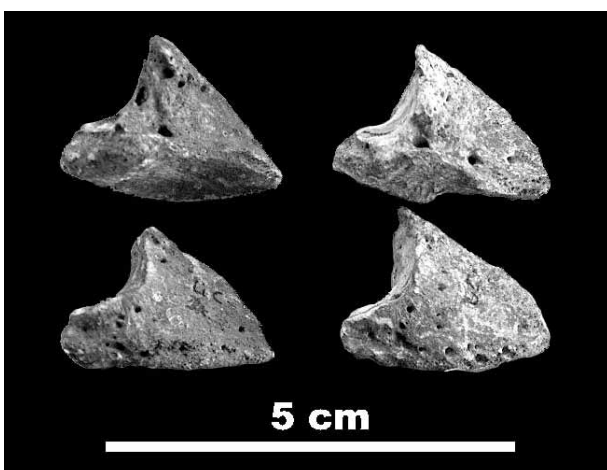

Fig. 7. Posterior third phalanges of *Candiacervus* appear to be lower, slightly shorter, slightly more massive, slightly more pointed, and with a more straight anterior surface than the anterior hooves. In the latter, the anterior surface is more convex.

Fig. 7. Les falanges terceres posteriors de Candiacervus *semblen ser més baixes, lleugerament més curtes, lleugerament més massisses, lleugerament més punxegudes i amb una superfície anterior més recta que les anteriors. A les darreres la superfície anterior és més convexa.*

The caudal vertebras finally appear to be ten in number, Cd1-Cd10, based upon the occurrence of only ten morphotypes among a large collection of caudal vertebras. For an estimation of the degree of size reduction from one tail vertebra to the next one, muntjac and spotted deer were used as reference. All caudal vertebras are unnumbered, and originate from Liko B; associated specimens were lacking.

SCAPULA AND PELVIS

To estimate the average sized scapula, the average measurements of the glenoid cavity are chosen, as almost all scapulae lack the body with the spina. The selected scapulae Li-B 588 (dex) and Li-B 605 (sin) are slightly, though insignifantly, larger, mainly due to the fact that we had to select a robust type, muscular enough to be associated with an individual that has to carry a heavy skull with a long antler of 60 cm. The left scapula Li-B 605 is exceptionally complete (Fig. 6), and is the only size II scapula from Liko B of which the total length can be estimated rather accurate. Missing parts are sculptured in epoxy, based upon the overall size and shape of *Axis axis*, as this deer corresponds best in size to *Candiacervus.*

Complete pelvic girdles are lacking all together. In order to provide a fitting specimen, we selected a pelvis with complete acetabulum (left and right), and a more or less complete ischial wing (left or right), to make contact with the sacrum. Missing parts are sculptured in epoxy. As average measurements those of the acetabulum are chosen, which are done on sight only, as no undamaged acceptable parts are available. The main criterion for average size was the best fit with the head of the chosen average-sized femur (see below). The differences in morphology between male and female *Ovis* and *Capra* were considered valid also for *Candiacervus*. The male pelvis is bigger and more sturdily, its ilium wing is larger and the width of the ventro-medial border of the acetabulum is about twice as large as in a corresponding large female pelvis (Boesneck *et al.*, 1964). As partial pelvis were chosen Li-B 623 (dex) and Li-B 630 (sin).

LONG BONES OF THE LIMB

For the measurements of the selected limb bones, the reader is referred to Table 1.

The choice of two humeri was complicated by the fact that in this large bone a large variation in morphology is found. The muscular scars should be more or less the same for the right and the left humerus, but this was not an easy task. Also the height of the greater tubercle in respect to the height of the humeral head differed significantly between the many specimens. Another problem was the amount of damage, as especially the humeral head is subject to erosion and damage, whereas the trochlea is much stronger. One of our criteria was that the head should be intact, as it is supposed to fit to the glenoid cavity of the scapula. As average measurement we give priority to maximal length,
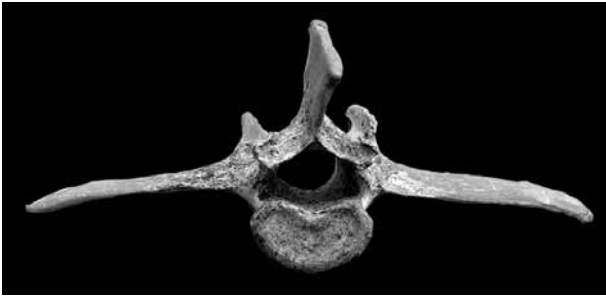
Fig. 8. The transversal processes of the lumbar vertebrae are more or less orientated horizontally in *Candiacervus* size II.

Fig. 8. Els procesos transversals de les vèrtebres lumbars estan orientats més o menys horitzontalment a Candiacervus *de la classe de mida II.*

as massivity is more dependent on gender than length. We were able to select humeri that are very close in the average length: Li-C 3 (dex) and Li-B 140 (sin).

The radius and ulna appear to be fused in the major part of the collection, which results in a 100% fitting of corresponding radius and ulna. For the establishment of an average-sized radius-ulna we took the radius as main reference, as the olecranon is broken off in many cases, which decreases the amount of judgeable specimens enormously. We were not able to find a fitting radius of the average size, whereas slightly smaller specimens appear to fit the selected humeri perfectly well. For the reason of fitting, we selected radius-ulna Li-B 269 (dex) and Li-B 265 (sin) (Fig. 6). In addition, our selected humeri have no distal DAP that deviates from the average.

The next step should consist of the selection of the carpal bones, but we decided to select the metacarpal bone first. The reason is that small deviations from the average measurements in the separate carpal bones are added, so that the fitting proximal metacarpal bone may deviate quite substantially from the average size. It's easier to fill in the carpal bones starting from an already selected distal humerus and proximal metacarpus. The selected metacarpal bones are Li-B 3 (dex) and Li-C 9 (sin), which are slightly but insignifantly smaller than the average, and proximally as well as distally slightly wider. Other specimens that were also close to the average in length were too gracile to be attributed to an adult male with a full-grown antler.

We continued our composition with the femur. Here, we encountered the same problems as with the femur. Most specimens were critically damaged, or lacking one or both epiphyses. Differences in robustness and place and shape of muscular scars are obvious to the spectator, and should therefore be taken as important criterion. The selected femurs are Li-Bc OD (dex) and Li-B 1325 (sin, including associated patella; Fig. 6). For the right femur we selected a right patella that is very similar to the associated left-sided specimen: Li-B 581. In all measurements the selected specimens deviate less than 0,5 mm from the average.

For the selection of the tibia the fitting with the distal femur is less helpful, due to the characteristics of the knee joint, in which there is no close-packing situation of the constructing elements. The only criterion is that the maximal width of the distal femur should be in accordance with the maximal width of the proximal tibia, as checked with the spotted deer and muntjac. The selected tibias, Li-B 212

(dex) and Li-C 197 (sin), are slightly smaller (2,5 mm), proximally slightly less wide (1,5 mm), but distally slightly wider (0,7 mm); overall they are close enough to the average size. The condyls of the selected femurs roll very well over the trochleas of the selected tibias, in the same way as those of a spotted deer. With the selected tibias at hand, the selection of the corresponding malleolar bone (remnant of distal fibula) is easy by fitting alone. Perfectly fitting are Li-B 1843 (dex) and Li-B 2206 (sin).

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
Mc dex	Li-B 3	108,2	17,9	24,7	16,5	26,4
Mt dex	Li-B 61	136,1	23,2	23,2	15,9	26,3
Mt sin	Li-B 898	138,3	22,2	22,6	16,5	26,2
humerus sin	Li-B 140	146,5	48,4	42,3	17,4	37,9
tibia dex	Li-B 212	186,5	36,8	44,6	22,7	28,2
radius dex	Li-B 269	135,4	17,7	33,6	21,5	28,8
radius sin	Li-B 265	137,8	18,0	34,2	21,4	28,2
ulna dex	Li-B 269	169,3	29,4	-	-	-
ulna sin	Li-B 265	173,5	29,4	-	-	-
femur sin	Li-B 1325	161,0	22,7	28,6	56,2	23,2
patella dex	Li-B 581	25,6	13,2	23,7	-	-

Table 1. *Candiacervus* size II, measurements (in mm) of the limb bones of the composite skeleton.

Taula 1. Candiacervus *classe de mida II, mesures (en mm) dels ossos de les cames de l'esquelet compost.*

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
scaphoid sin	Li-B 1820	-	19,1	8,8	-	-
scaphoid dex	Li-B 566	-	22,6	10,9	-	-
lunare sin	Li-B 574	-	21,6	11,6	-	-
lunare dex	Li-B 1831	-	20,8	11,8	-	-
ulnare sin	Li-B 2204	-	16,9	10,1	-	-
ulnare dex	Li-B 577	-	15,9	10,2	-	-
magnum sin	Li-B 559	-	16,4	15,1	-	-
magnum dex	Li-B 557	-	16,0	14,1	-	-
unciform sin	Li-B 2199	-	13,6	11,2	-	-
unciform dex	Li-B 563	-	14,4	11,1	-	-
cubo-nav. sin	Li-B 1789	-	25,0	26,6		
malleolare dex	Li-B 1843	14,0	8,5	10,9	-	-
malleolare sin	Li-B 2206	14,8	7,5	11,6	-	-
calcaneum dex	Li-B 403	63,0	25,8	19,1	-	-
calcaneum sin	Li-B 1397	63,5	26,3	19,4	-	-
astragalus dex	Li-B 1468	32,5	-	20,4	-	19,1
astragalus sin	Li-B 424	32,5	-	19,7	-	17,9

Table 2. *Candiacervus* size II, measurements (in mm) of the carpal and tarsal bones of the composite skeleton.

Taula 2. Candiacervus *classe de mida II, mesures (en mm) dels ossos carpians i tarsians de l'esquelet compost.*

More or less the same is valid for the tarsus as for the carpus, so that's why we proceed with the metatarsal cannon bone instead of with the tarsal bones. The selected cannon bones Li-B 61 (dex, including the cubonavicular bone), and Li-B 898 (sin; Fig. 6) are very close (less than 0,5 mm deviation) to the average sizes.

For the lateral metapodals (plesiometapodals) we selected five more or less equal-sized specimens (all unnumbered). As the corresponding size of a lateral metapodal is not known, nor whether there is size difference between front laterals and hind laterals, the selection is a mere guess. Of all bones, these bones are the most likely to be wrong. The variation in the lateral metapodals between the different living plesiocarpal/plesiotarsal deer is large, and we cannot reliably select one of the living deer to guide us.

THE CARPUS AND TARSUS

For measurements of the selected carpal and tarsal bones, see Table 2.

The selection of the carpal and tarsal bones is done almost entirely on fitting; this could be checked with available associated elements. For the left front limb, top row, the following carpals are selected: Li-B 1820 (scaphoid), Li-B 574 (lunare), Li-B 2204 (ulnare), and for the bottom row: Li-B 559 (magnum), Li-B 2199 (unciform), 2x unnumbered pisiform (both same side (sin?), one to be assigned to the other limb), and seven unnumbered sesamoids. For the right front limb, top row, the following carpals are selected: Li-B 566 (scaphoid), Li-B 1831 (lunare), Li-B 577 (ulnare), and for the bottom row: Li-B 557 (magnum), Li-B 563 (unciform), and seven unnumbered sesamoids. For the hindlimb, the following tarsals were selected: Li-B 1397 (calcaneum, sin), Li-B 403 (calcaneum, dex; Fig. 5), Li 1468 (astragalus, dex; Fig. 5), Li-B 424 (astragalus, sin) and four unnumbered sesamoids

The right cubonavicular was already associated with the metatarsal, so the selection of the left cubonavicular was more or less a question of finding the mirrored equivalent. The selected specimen, Li-B 1789 (sin), is not fused neither with the larger cuneiform nor with the lesser cuneiform. The right cubonavicular on metatarsus Li-B 61 is only very loosely fused to the metatarsal.

THE PHALANGES

For measurements of the selected phalanges, see Table 3.

The selection of fitting specimens was immensely eased by the presence of several associated feet in the collection, not only associated phalanges, but also in association with metapodals (Fig. 5). This made it possible to study the morphology of phalanges that for sure belong together. It appears for example that the posterior ph III are lower, slightly shorter, slightly more massive, slightly more pointed, and with a more straight anterior surface than the anterior hooves (Fig. 7). In the front hooves, the anterior

surface is more convex. The overlap is, however, large, and only in combination with the corresponding opposite hooves this feature becomes obvious. The morphology of the first and second phalanges on the other hand can be attributed to front and hind limb with much more certainty.

To make things even more convenient, within the average size II selection, an articulated left front and left hind foot were available. The left front foot consists of Ph I (Li-B 435 + 436), Ph II (Li-B 480 + 481), Ph III (Li-B 538 + 537), and unnumbered sesamoids. The left hind foot consists of Ph I (Li-B 432 + 433), Ph II (Li-B 478 + 479), Ph III (Li-B 539 + 540), and unnumbered sesamoids. For the right front and hind foot, similar counterparts were chosen. Because of the huge quantity of phalanges in the collection, we could afford a very critical attitude. The following specimens were chosen for the front foot: Ph I (Li-B 458 and Li-B 1572), Ph II (Li-B 483 and Li-B 492), and Ph III (Li-B 515 and Li-B 514). For the hind foot were chosen Ph I (2x unnumbered Li OD), Ph II (2x unnumbered Li OD), and Ph III (Li-B 520 and Li-B 528). As spare for the right front limb, we included one phalanx I and two phalanges II that belonged to one individual (unnumbered, Li-Ba). The reason to select these spares was the nature and degree of damage to the selected specimens.

There are quite a lot of lateral third phalanges, so we assume for the moment that also size II had those lateral phalanges. The size is of course a delicate matter, due to the fact that the measured average size will tend to be larger

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
ph I ant dex	Li-B 458	29,6	16,7	14,5	10,3	12,8
ph I ant dex	Li-B 1572	29,1	16,2	13,6	10,2	11,8
ph I ant sin	Li-B 435	28,6	14,1	12,9	11,5	11,9
ph I ant sin	Li-B 436	27,9	15,0	13,4	10,4	11,9
ph II ant dex	Li-B 483	22,6	17,4	12,4	15,9	11,3
ph II ant dex	Li-B 492	21,3	16,5	12,4	17,2	11,8
ph II ant sin	Li-B 480	21,2	15,7	12,4	17,4	11,8
ph II ant sin	Li-B 481	21,6	15,4	12,7	17,0	11,6
ph III ant dex	Li-B 514	31,7	21,0	15,3	-	-
ph III ant dex	Li-B 515	30,4	20,3	15,2	-	-
ph III ant sin	Li-B 537	31,0	19,3	12,2	-	-
ph III ant sin	Li-B 538	32,6	19,8	12,5	-	-
ph I post sin	Li-B 432	29,8	15,4	12,7	10,1	11,9
ph I post sin	Li-B 433	29,2	15,0	12,9	9,8	11,9
ph II post sin	Li-B 478	21,2	15,4	11,7	15,5	11,0
ph II post sin	Li-B 479	21,8	15,2	11,5	15,5	10,6
ph III post dex	Li-B 520	27,8	18,5	11,3	-	-
ph III post dex	Li-B 528	27,6	18,6	12,4	-	-
ph III post sin	Li-B 539	25,6	18,5	12,6	-	-
ph III post sin	Li-B 540	25,8	18,5	12,8	-	-

Table 3. *Candiacervus* size II, measurements (in mm) of the phalanges of the composite skeleton.

Taula 3. Candiacervus *classe de mida II, mesures (en mm) de les falanges de l'esquelet muntat.*
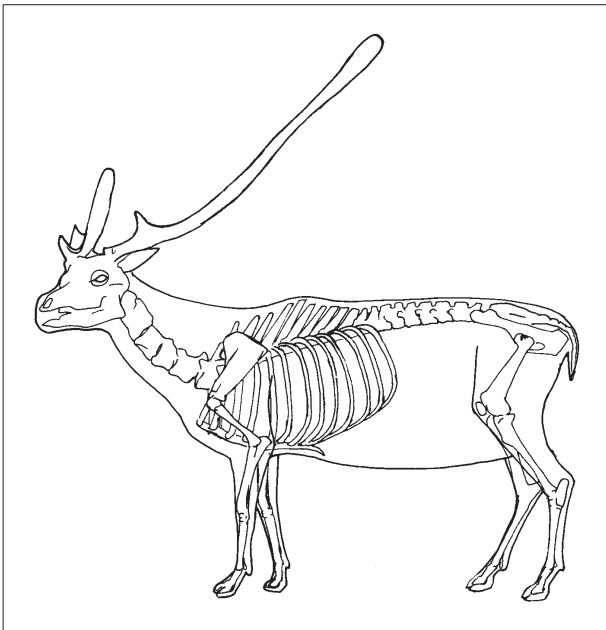
Fig. 9. *Candiacervus* size II from Liko Cave (Crete, Greece) appears to have had a heavy and massive trunk, a powerful neck and shoulder part, and stocky built and short but strong legs.

Fig. 9. Candiacervus *classe II de la cova de Liko (Creta, Gràcia) sembla haver tingut un tronc pesat i massís, un coll i unes espatlles poderosos, cames en forma de pilars, curtes, però fortes.*

than the real average size as the smallest specimens are more likely to have been lost. We select therefore four lateral third phalanges (all unnumbered) merely on common sense. The difference between adult, full-grown lateral phalanges and juvenile phalanges is easy to establish in this collection. All juvenile bones have a spongy and abrased appearance, are less firm, and have a lower weight.

DISCUSSION

The great additional value of a reconstructed skeleton above individual bones is that it informs us about the morphology of the complete animal. From the collection of metapodials it could already be inferred that the metatarsal is longer than the metacarpal, but now that we have a complete skeleton it is an undeniable fact. The average size of the metatarsal for size II is 137,2 mm, that for the metacarpal 108,2 mm, which results in a difference of 29 mm and a metacarpal/metatarsal index of 0,79, which is low compared to *Cervus elaphus* (0,89); this indicates that the metacarpal is relatively short in *Candiacervus* size II. Another striking feature of the complete animal is the curvature of the lumbar and lower thoracic region (Fig. 2). It appears that the back is only slightly curved (upward), more similar to a large deer like *Megaloceros verticornis* than to a small deer like *Axis axis*. The transversal processes are more or less orientated horizontally (Fig. 8) as in heavier bodied medium-sized artiodactyls like *Ovis*. In total, the animal has a heavy and massive trunk, a powerful neck and shoulder part, a stocky built and short but strong legs (Fig. 9).

An unexpected additional advantage of the composite skeleton is that we have now articulated bones, with the help of which functional morphologic interpretations can be made. Till now, such interpretations could only be done at the basis of individual bones, but not with articulations. The degree of flexion and other movements can now be checked with the joints themselves, not merely by extrapolating from articular surfaces.

The articulated, composite skeleton has illustrated once again the value of assembling a set of bones into a three dimensional animal. Features that are not otherwise obvious can be revealed when the bones are properly articulated and combined. The above mentioned difference in length between metatarsal and metacarpal, and the bending of the lumbar region are such cases. As a result, the animal gives a much different impression than expected.

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