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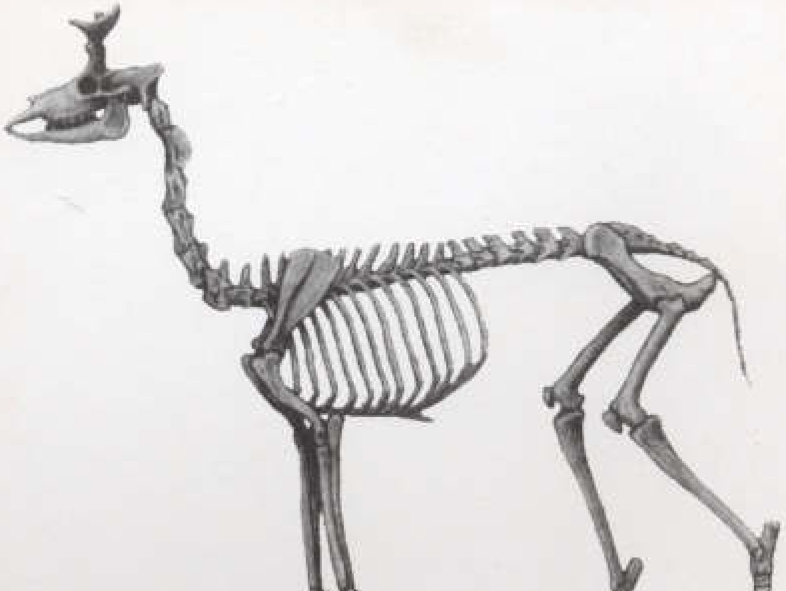

Orangemeryx hendeyi

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On the nature of the multibranched cranial appendages of the climacoceratid *Orangemeryx hendeyi*

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The climacoceratid *Orangemeryx hendeyi* has frontal apophyses which are branched and decorated with buttons and points. The nature of these appendages is examined megascopically and microscopically in order to determine their growth patterns and their affinities with other lineages of ruminants.

Version française abrégée

Le ruminant climacocératid *Orangemeryx hendeyi* présente des apophyses frontales complexes avec des tübercules à la partie proximale et des pointes distales. L'étude de la microstructure des apophyses révèle que ces dernières diffèrent de celles des frontaux des autres ruminants, incluant les daims (Cervidae), les antilopes (Bovidae) et les girafes (Giraffidae), et de certains goupes éteints, comme les Palaeomerycidae, les Lagomerycidae et les Merycodontidae.

L'étude microscopique montre que les apophyses frontales d'*Orangemeryx* étaient des structures permanentes, à la différence de celles des daims actuels chez qui elles sont remplacées de manière saisonnière. Elles sont formées d'os compact immature avec un centre plus poreux et un cortex plus dense montrant que le flux sanguin pouvait encore circuler au moment de la mort des spécimens étudiés. La ramification de l'extrémité distale n'est pas comme chez les daims, mais se forme par exostoses (A.B. Bubenik, 1990). Il peut y avoir eu une base génétique pour la formation des tübercules et des pointes, car ces derniers sont généralement situés au même endroit sur les appendices. Ainsi, l'extrémité distale présente 3 pointes et le corps de l'appendice des tübercules antérieur et postérieur situés près de sa base. Chez *Climacoceras*, le corps de l'appendice présente des pointes plutôt que des tübercules. Les appendices frontaux d'*Orangemeryx* ne sont pas déprimés par les marqués des vaisseaux sanguins (comme c'est le cas sur les ossicones de Giraffidés). Les appendices sont de type apophysaires et non épiphysaires comme chez les Bovoidea et les Giraffidae. Ces différences suggèrent que les Climacoceratidae ne sont pas le groupefrère des Giraffidés.

Introduction

Climatoceratids are stem giraffoid ruminants, most of them bearing multipointed or multibranched cranial appendages the nature of which has been actively debated. The climatoceratid appendage has been considered either as an ossicone or an antler-like, non-deciduous protuberance. Consequently its taxonomic status is not clear. One of the earliest known climacoceratids bearing cranial appendages is *Orangemeryx hendeyi* Morales, Soria & Pickford, 1999, described from the basal Middle Miocene deposits at Arrisdrift (Namibia). In this work, the nature of the appendages of *Orangemeryx* is investigated based on their morphology and microstructure.

The climacoceratid remains collected at Arrisdrift were originally attributed by Hendey (1978) to *Climacoceras* sp. The genus *Climacoceras* was first identified as a deer by MacInnes (1936), who described *C. africanus* based on fragments of antler-like appendages from Maboko Island, Kenya (ca 15.5 Ma) which bore short, irregularly placed knobs or processes. Pilgrim (1941a, b) did not agree with MacInnes because by its branched, non-deciduous appendages, *Climacoceras* seemed to be better placed with *Lagomeryx* and *Procervulus* in the Lagomerycidae, which he considered to be precocious giraffoids. However, the possibility that some lagomerycids with simple, non-deciduous appendages may have given rise to the periodically shed cervid antler, was also pointed out by Pilgrim (1941b). However, the protoantlers of Lagomerycidae and *Procervulus* could be aperiodically shed (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997). The cervoid affinities of Lagomerycidae and the status of Procervulinae among Cervidae, now seem to be firmly established (Azanza & Ginsburg, 1997). Hamilton (1978 a, b) interpreted *Climacoceras* as a giraffoid because of its possession of a bilobed lower canine, as preserved in a mandible identified as *C. gentryi*. Consequently, Hamilton (1978a) defined the family Climatoceratidae as giraffoids having large ossicones carrying many tines. However, the presence of a bilobed lower canine in *C. gentryi* is uncertain and the status of climatoceratids as stem giraffoid ruminants should be confirmed by other characters (Churcher, 1990).

Recently, Morales *et al*., (1999) defined the family Climacoceratidae by the incipient elongation of the neck and the limbs. This definition allows the inclusion in the family of the hornless ruminants *Sperrgebietomeryx* and *Propalaeoryx* in which the presence or absence of cranial appendages is unknown. Both *Sperrgebietomeryx* and *Propalaeoryx* are found in the early Miocene locality of Elisabethfeld (Namibia), and are the oldest known representatives of the family, while the earliest climacoceratids bearing cranial appendages are found in the basal Middle Miocene. Thus, cranial appendages were developed within the climatoceratids at the same time as, but independently from, other lineages of ruminants. It corroborates the hypothesis that the appearance of cranial appendages could have been a biological response to global scale environmental changes that occurred towards the end of the early Miocene (Janis, 1990, Morales *et al.*, 1993). This hypothesis is reinforced by the fact that the multibranched appendages of Climacoceratinae represent a unique feature among the Giraffoids.

Morphology of the frontal bone and appendages

The frontal bone of *Orangemeryx hendeyi* is very thick but not pneumatised (Morales *et al.*, 1999). The cranial appendages are supported by the supraorbital process of the frontal bone but its base is large and, in contrast to protoantlers, leaning on the braincase. There is no trace of any suture lines. As in protoantlers, we can distinguish a proximal (basal) part from a distal (branched) part. The size of the distal part relative to the proximal one is one third of the total length. Although they are vertically oriented in lateral view, the frontal appendages of *Orangemeryx* diverge outwards from the sagittal plane similar to the pedicles of lagomerycids, but without any curvature. In most primitive cervids the pedicles are parallel and upright. The proximal part has a rounded or laterally flattened cross-section but its base is more compressed transversely. In *O. hendeyi* the surface of the frontal appendages is smooth but occasionally very slight striations and shallow grooves are present. One difference from protoantlers is the presence of points or knobs near the base. A peculiar type of morphology occurs in which two buttons are present on the anterior border and another better developed one on the posterior border (Pl. 1, fig. 2). However, there is a clear variability in their position of development and in some individuals there is no development of these buttons.

The distal part of the frontal apophysis is multibranched. In the best preserved specimens (AD 594’94, AD 120’00, AD 743’97), there are three branches variously developed. In AD 912’97 only two branches are preserved, but by the morphology of their basal emplacement it could be similar to AD 120’00. In other specimens, it is less evident, such as in PQAD 131 which could be bifurcate. There are two morphotypes of the branched distal part. The branches depart from approximately the same zone in specimens AD 120’00, AD 594’94 and AD 743’97. In contrast, in AD 912’97 two of them branch off closer together and more distally. An additional knob, similar to those present near the base of the proximal part, is observed in AD 120’00 (Pl. 2, fig. 1). The area of branching has a flattened section, but without any palmation being developed. This morphology resembles greatly that of the lagomerycid *Ligeromeryx* and the merycodontine *Ramoceros* (Azanza & Ginsburg, 1997). The branch emplacements are situated approximately longitudinal to the compression plane of the proximal part. As in lagomerycids, the branches are long, subcircular in section, and terminally pointed, their apices not being polished (Pl. 2, figs. 2, 3 and 4). Some are slightly curved while others are almost straight. There is no evidence that this distal part could be spontaneously shed. No specimens of distal parts have been found in which the ventral surface is concave with bony spicules as occurs in protoantlers, indicating that the specimens could not have been shed (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997).

Microstructure

The microstructure of specimen AD 743’97 (Pl. 3, figs. 1) was studied in detail using transverse and longitudinal thin sections. This appendage comprises a long proximal part without the base, and a trifurcate distal part with the branches broken. Transverse sections were made at the middle of the proximal part, just below the branching area, and at the basal emplacements of two of the branches. A longitudinal section of the proximal part was made which cuts the branching area.

Macroscopically it could be seen that the appendage consists of a thick cortex of solid bone surrounding a more porous core (Pl. 3, figs, 2 and 3) but this central region is not spongy bone as in deer antlers or long bones. Natural sections in other specimens seem to indicate a thinner cortex and a core which is more finely porous, indicating that ontogenetic or individual variations can occur.

The appendage is constructed of rather immature compact bone (PI 4, figs. 1,2,3 and 4). Though the core is more porous than the cortex, spongy bone trabeculae typical of the cores of antlers or long bones are not developed (compare fig. 1 with figs. 8 and 10 of Pl. 4). This microstructure resembles that of the merycodontine appendage (A. B. Bubenik, 1990) and the lagomerycid protoantler (Azanza & Ginsburg, 1997), but the core and the cortex are not so clearly delimited as in these taxa.

In contrast to deer antlers, haversian osteons of secondary bone lamellae are observed mainly in the inner part of the cortex region (Pl. 4, fig. 1), but a dense haversian tissue with successive generations of haversian systems superimposed as in mature giraffe ossicones (Rothschild & Neuville 1910, Pl. 6), is not developed. It could be interpreted that the animal bore this appendage for more than one year and if so, it would confirm the suggestion of A. B. Bubenik (1990) that mineralization in *Climacoceras* appendages progressed centrifugally from the inner part of the cortex to the periphery. However, the lamellae of the osteons of the cortex are not oriented in any preferred direction in transverse or longitudinal sections of specimen AD 743’97 (Pl. 4, figs. 1 3, 4 and 5), and thus do not confirm appositional lamellae as suggested by A. B. Bubenik for *Climacoceras*.

A radiograph of this specimen (Pl. 5, fig. 1) shows that the appendage is not completely mineralized and blood flow was still possible throughout the entire appendage at the time of death. Radiographs of other specimens (Pl. 5, figs. 2 and 3), a fragment of the frontal bearing the basal part of the appendage (specimen AD 173’97) and a fragment with two branches (specimen AD 912’97), show more intense mineralization with no traces of vascularization. It could be that specimen AD 743’97 is relatively younger than the other specimens which could be constructed of more mature compact bone.

The longitudinal section of the distal part (Pl. 3, fig. 3 and Pl. 4, fig. 5) shows that the mechanism of ramification in *Orangemeryx* is not by beam splitting which is the usual mechanism of ramification in deer, but by the rarer mechanism of sprouting which proceeds through exostosis (A. B. Bubenik, 1990). The anterior branch is a sprout having the basal emplacement of compact cortex and distally a porous core separate from that of the proximal part which is prolonged in the postero-internal branch. As described above, the appendage of *Orangemeryx* shows numerous protuberances or knobs that also seem to be cortical structures (Pl. 3, fig. 2). Some of them could have a genetic basis as they have frequently been found in the same position but many others have not. As occurs in lagomerycids, it seems that sprouting could be an important process of ramification, if not the only one, which translates into enormous versatility in the construction of appendages.

Discussion

The cranial appendages of *Orangemeryx hendeyi* are similar to those of *Climacoceras*. The peculiar plate-like morphology of the appendages of *Prolibytherium* is difficult to relate to the appendages of these two genera. Macroscopically, the appendages of *Prolibytherium* are composed of a thin cortex of compact bone and a very porous core that seems to be constituted of spongy bone. The surface shows deep grooves reflecting an intense vacularization of the skin (Arambourg, 1961) which is not present in *Orangemeryx* or *Climacoceras africanus* (MacInnes, 1936). However, *Climacoceras gentryi* from Fort Ternan, Kenya (ca 13-12.5 Ma) shows fine ridging with grooves running along the beam (Hamilton, 1978a).

Orangemeryx and *Climacoceras* share a morphological pattern in which the distal part is ramified, probably all of them trifurcate. In *Climacoceras* ramifications also occur in the proximal part, whereas in *Orangemeryx* this part only exhibits knobs or buttons which develop mainly in the basal zone, which is well developed, and quite different from the cylindrical aspect of *Climacoceras* appendages.

Even though more data is required, it seems that the structures of the appendages of *Climacoceras Africanus* and *Orangemeryx hendeyi* are similar. The bone has a well developed compact cortex and a more porous nucleus, and the process of ramification is by sprouting and not splitting, according to the sections figured by MacInnes (1936, fig. 3a, b, c). Moreover, the appendages do not show grooving but only a fine striation of the bone surface (MacInnes, 1936).

As mentioned above, the nature of the climacoceratid appendages has been variously interpreted by different authors, either as ossicone-like or antler-like “horns”. Ossicones and antlers are entirely different types of appendages. The term ossicone refers to the “horn” of the extant giraffids, which are epiphyseal structures. Developmentally, the ossicone appears as a separate fibrocartilaginous structure originating in the subcutaneous connective tissue, which enlarges, ossifies and fuses to the skull late in life (Lankester, 1907; Solounias & Tang, 1990). In contrast, the term antler refers to the “horn” of extant cervids, its apophyseal growth having been experimentally verified (Goss, 1983, 1990). Deer antler originates as an upgrowth from the frontal periosteum, the overlying skin playing a passive role (Goss, 1990).

The nature and homology of cranial appendages should be based on comparisons of the details of the developmental processes and the inducing and contributing tissues, which is very speculative in fossil organisms. In the next sections the climacoceratid appendages are compared with those of other ruminants which developed either as epiphyseal or as apophyseal growths.

Comparison with epiphyseal “horns”

The appendages of epiphyseal nature are typically found in extant Bovoidea. Their epiphyseal growth has been experimentally demonstrated in the *os cornu* of bovids and clearly identified in the ossicone of giraffids. By extension the epiphyseal nature is assumed in extinct bovids, but a controversy exists about the epiphyseal or apophyseal growth of the “horns” of extinct giraffids (A. B. Bubenik, 1983, 1990; Geraads, 1986, 1991; Janis & Scott, 1987; Solounias, 1988; Solounias & Moellenken, 1991). Despite this controversy, these authors agree on the apophyseal nature of the branched appendage of *Climacoceras*. Among Cervoidea, the epiphyseal appendages are also assumed in two extinct groups. Leinders (1983) suggests homology with bovid horns for the appendages of Hoplitomerycidae, but there is no evidence of their mode of growth. In turn, the supraorbital appendages of Palaeomerycidae have been referred to as ossicones, but not their occipital protuberances. The nature of palaeomerycid appendages is poorly investigated but it seems clear that the supraorbital ones fuse to the skull late in ontogeny, since it can be found isolated (Ginsburg & Heintz, 1966) or not completely fused to the skull showing a suture line at its base (Duranthon *et al.*, 1995; Astibia & Morales, 1998).

The structure of bovid horns has few points in common with that of *Orangemeryx*. In particular bovid horns have an unbranched, non-deciduous bony horn core (*os cornu*) covered by a skin which early in ontogeny is keratinised and forms a perennial horn sheath. Its origin is epiphyseal as in ossicones but the horn core ankyloses to the cranial roof at much earlier stages of embryogenesis, in such a way that at no stage in its development can one observe it as a separate bone (Dove, 1935). Moreover, the ossification is intramembranous instead of being preformed as a cartilage with subsequent endochondral ossification (Janis & Scott, 1987). The climacoceratine appendage differs not only by the pattern of ramification and the lack of horny sheath, but also in its microstructure which reveals a greater development of the cortex whilst the porous core does not develop coarse trabeculae wrapped around cavities of different sizes and shapes (compare figs. 1 and 2 with fig. 11 of Pl. 4).

Comparison with giraffid ossicones deserves more attention since Climacoceratidae are probably related to Giraffidae though they are not its sister group (see corresponding chapter in this volume). Giraffid ossicones are straight, unbranched, non deciduous and skin-covered appendages. The apex in mature males becomes cornified after completion of basic ossification. In *Okapia* this skin is lost at about 3 years of age whereupon bare bone is exposed. The tips become polished, and there may be areas of necrosis where the bare bone and skin meet (Spinage, 1968b). In *Orangemeryx* there are no indications that the apices of the appendages could have been exposed.

According to Lankester (1907a) and Spinage (1968b), ossicones originate in the connective tissues of the integument rather than in the osteogenetic tissue of the cranial roof, from which it is separated by a dense membranous periosteum. At birth, no ossification is present and the cartilaginous template is separated from the parietal vault by periosteal connective tissue. Later in life the ossicones fuse to the frontals through a boss-like upgrowth, which is not easy to recognise in *Giraffa*

(Lankester, 1907b; Janis & Scott, 1987; Solounias & Tang, 1990). It is not known whether the development of this boss is induced by the overlying ossicone, or whether it develops independently under the influence of the periosteum. In *Okapia* young animals have tumescences in the roofing bones of the skull and the early ossicones are formed as conical caps that fit over the tumescent bulges (Lankester, 1902). But in *Giraffa*, the formation of a boss on the frontal bone occurs later during development, since in neonatal animals figured by Lankaster (1907b) there is no corresponding boss on the frontal beneath the ossicone (Janis & Scott, 1987). However, Solounias & Tang (1990) show that the median nasal appendage typically found in northern giraffes is composed only of a median frontonasal boss without having any associated ossicone, suggesting that some control may reside in the periosteum. If that is the case, then giraffid horns are complex composite structures, with both apophyseal and epiphyseal elements as proposed by Solounias & Tang (1990). Climatoceratid appendages differ from giraffid ossicones by the absence of indications that they could have developed entirely or partially as an independent bone.

A few days after birth (Spinage, 1968b), ossification begins at several independent centres near the periphery of the distal half of the cartilage (Owen, 1849) and at the apex of the ossicone (Churcher, 1990) and apparently without hormonal control. During this time, the ossicone elongates through extension at the base where the cartilaginous area extends the bone in a manner analogous to the cartilaginous epiphyseal disc of a long bone (Churcher, 1990). Once the ossification is completed, growth in ossicone length slows and ceases after fusion or proceeds very slowly. Subsequent mineralization proceeds both externally and internally, external mineralization slightly increases the length and more strongly increases the diameter, and internal mineralization yields extremely compact ossicones (Geraads, 1988). Thus, the bone is very compact and ivory-like, but softer in young individuals (Churcher, 1990), and without signs of resorption (Geraads, 1986). After fusion, frontoparietal sinuses extend into the proximal half of the ossicones in *Giraffa* (Spinage, 1968b; Dagg & Foster, 1976). Solounias & Tang (1990) pointed out that the cranial pneumatization extends upwards into the large frontoparietal bosses. The internal structure of the ossicone is solid bone but appears pneumatized because the large spaces within the entire structure are part of the boss. In climacoceratids, there is no pneumatization of the basal emplacement of the appendage and, as described above, the bone is not completely compact but a porous core can be recognized. A dense haversian tissue with successive generations of haversian systems superimposed as in mature ossicones, is not developed in the studied specimen of *Orangemeryx*.

The branched pattern is the main argument used by the authors to conclude that climacoceratid appendages could not be related to giraffid ossicones because the epiphyseal nature of giraffid ossicones with the zone of growth at the base may preclude the possibility of branching (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). These authors assume the apophyseal nature of the climacoceratid appendage assuming that it had a typical deer branching pattern. Nevertheless, the appendages of Climatoceratidae ramify mainly by sprouting and not by beam splitting which is the usual mechanism of ramification in deer (see below). Branching by sprouting is not necessarily related to apical growth. This mechanism of ramification indicates a highly active cortex and could be linked to appendage mineralization progressing centrifugally (A. B. Bubenik, 1990). It is not clear if an epiphyseal ossicone with the zone of growth at the base could preclude this branching mechanism or not. In fact, once the cartilage is ossified and therefore growth in length prevented, external mineralization proceeds, thereby increasing the diameter of the ossicone (Geraads, 1991).

In giraffes, additional laminar bone is laid down throughout the life of males and occasionally in females. The accumulation of this secondary bone is primarily the result of male combat behaviour. Females are able to form secondary bone but the lack of major cranial impact experienced by males explains the small amounts of it (Solounias & Tang, 1990). Although secondary bone forms continuous surfaces, this growth is irregularly distributed and extends over the calvaria, producing sizeable growths over the median boss, the nasals, one side of the lachrymal bone ("azygous horns"), the superior side of the orbit and the dorsal region of the nuchal crest (Spinage, 1968). Even when sectioned, the boundaries between this growth and the ossicone are not easily determined owing to substantial bone remodelling throughout. Superficial blood vessels of the ossicones become buried by the bone laminae laid down in males, resulting in deep grooves on the surface. In *Orangemeryx*, the inflation of the frontal and the buttons or knobs present in the appendages do not seem to be comparable to this secondary deposition of bone in *Giraffa*. The bone surface of the knobs is regular and there are no deep grooves to indicate that secondary bone growth has encased vessels and nerves.

In the fossil record there is a great diversity of appendages among giraffids which could throw doubt on the assumption that the ossicones of the extant forms are representative of the family as a whole. Appendages in Sivatheriinae show a more complex pattern. They differ from those of climacoceratids by the strong ornamentation of the surface including channels and bumps. The few sections available reveal a very compact cortex but with an ample and cancellous centre, as was demonstrated by Geraads (1985) for *Sivatherium*. *Palaeotragus* has much simpler ossicones with weaker ornamentation and no formation of bumps. Its internal structure is finely porous from the base upwards, with a much weaker development of the cortex, whilst the apex is constructed entirely of compact bone. The diversity of the structures in cranial appendages of giraffids needs more detailed research.

Comparison with apophyseal "horns"

Among mammals, the occurrence of apophyseal appendages seems to be more common than epiphyseal ones (Solounias, 1988a, 1988b). However apophyseal growth has been experimentally demonstrated only in deer antlers (Goss, 1983), which are branched and periodically deciduous structures. In extinct ruminants there are other kinds of branched appendages and aperiodically deciduous structures, that probably were also of apophyseal nature. These are the protoantlers of Lagomerycidae and primitive deer and the antler-like appendages of Merycodontinae.

All these appendages are composed of two parts: the stem (proximal) part or pedicle and the branched (distal) part. The distal part in extant deer is the antler itself. The cycle and growth of deer antlers are dependent on the rise and fall of different androgen secretions, among which testosterone plays a dominant role (G.A. Bubenik, 1990). After growth is completed, the deer antler mineralises profoundly, induced by a sudden rise of testosterone secretion. The blood supply to the surface is cut off and the tissues above the pedicle die, following which a compact bridge between antler and pedicle is built up (A. B. Bubenik, 1983, 1990). As soon as the testosterone levels approach the minimum this bridge is demineralized and a narrow zone of bone at the junction of the living bone of the pedicle and the dead bone of the antler is simultaneously destroyed by numerous osteoclasts (Goss, 1970). The points of attachment between the antler and the pedicle are so attenuated that the weight of the antler itself effects the detachment. The base of a cast antler shows numerous spicules of bone that are remnants of the osteoclastic erosion (Goss, 1970, 1983). The regenerated antler is marked by the burr or coronet, a bony rim at the base of the antler which seals the pedicle skin.

In primitive deer and lagomerycids, the distal part of the frontal appendage was capable of spontaneous autonomy in its entirety, since the ventral surface of some specimens is concave and shows these spicule remnants of osteoclastic erosion (Ginsburg, 1985; Azanza, 1993; Azanza & Ginsburg, 1997). However, radiographs and longitudinal sections of these specimens show that their rejection was produced without the protective bridge at the joint with the pedicle (A. B. Bubenik, 1990; Azanza & Ginsburg, 1997). Indeed, the mineralisation was not enough to cut off the blood supply from the pedicle and consequently the protoantler tissues were still alive when their rejection occurred. A similar casting process of tines or distal parts has been studied in the antlers of castrate deer (A. B. Bubenik *et al.*, 1990). Thus, shedding of the distal part could occur from time to time, despite no coronet-like structure being formed. For this reason, A. B. Bubenik (1990) named it the protoantler.

The antler-like appendage of merycodontines shows many resemblances to protoantlers but there is little evidence of casting. According to A. B. Bubenik (1990), a few pedicles (eg the right appendage of FAM. 32895 figured by Frick 1937, fig. 37) exist with a bare surface above the uppermost pseudocoronet, which are not homologous to the coronets of antlers. Curiously there is no evidence of cast specimens of distal parts.

As described above, these two parts are also recognized in the appendages of *Orangemeryx*, but they are not so clear in *Climacoceras* because the appendage ramifies from its base. There is no evidence that the distal part could be shed. Climacoceratid appendages would have been perennial structures.

The antler bone is composed of an outermost layer of compact bone containing haversian systems and a central region of spongy bone formed by fewer, coarser lamellae with wider marrow spaces. Secondary and tertiary haversian systems and interstitial lamellae are absent in deer antler, presumably because the life of the antler bone is limited and the antler is laid down anew annually over its entire width (Chapman 1975).

The protoantler is constructed of rather immature compact bone. Although the core in lagomerycids is more porous than the cortex, spongy bone trabeculae typical of the antler core is not developed (Azanza & Ginsburg, 1997) (Pl. 4, figs. 6-7). In the primitive deer *Dicrocerus elegans*, this microstructure is reversed with dense bone in the centre and more porous bone at the periphery, mineralization progressing from the core to the periphery and not centripetally as in antlers (A. B. Bubenik, 1990, fig. 15; Azanza, 1993). Peripheral layers can be observed in lagomerycids (Azanza & Ginsburg, 1997; Pl. 2, fig. 5) and in *Dicrocerus* (Pl. 4, Fig. 9). The antler-like appendage of merycodontines shows similar osseous microstructure: they are also constructed of immature compact bone, with the cortex being highly active allowing deposition of peripheral layers (A. B. Bubenik, 1990, text-fig. 16a).

The microstructure of the *Orangemeryx* appendage resembles that of the lagomerycid protoantlers because it is also constructed of rather immature compact bone with a cortex of bone more compact than the core which is porous. Nevertheless, the cortex is thicker and not well delimited from the core as in lagomerycid protoantlers (Pl. 4, Figs 1, 2). As described above, a more intense mineralization seems to be present in the inner part of the cortex region as indicated by the greater development of haversian osteons of secondary bone lamellae. It would confirm the suggestion of A. B. Bubenik (1990) that mineralization in climatoceratid appendages, as in protoantlers and antler-like appendages, progressed centrifugally from the inner part of the cortex to the periphery. However, we have not observed peripheral layers that would confirm the appositional lamellae suggested by A. B. Bubenik, whereas they occur in the merycodontine *Cosoryx* (A. B. Bubenik 1990, text-fig. 16a), the lagomerycid *Ligeromeryx* (Azanza & Ginsburg, 1987; Pl. 2, fig. 5) and also in the primitive cervid *Dicrocerus* (Pl. 4, fig. 9). This could indicate that growth of *Orangemeryx* appendages was continuous, and could not thus have been controlled hormonally. This interpretation should be taken with caution since it is based on only one specimen.

Deer antlers usually grow from the base upwards by virtue of proliferating fibroblasts in their apices. These cells later become cartilaginous and are eventually incorporated into the bone trabeculae and thereby strengthen the shaft (Goss 1970). As a result, splitting of the beam axis is the usual mechanism of ramification in deer. Antlers can also ramify through exostosis which forms sprouts. The sprouting is present in *Rangifer*, in the first antler of *Cervus elaphus*, in the second antler of north American *Alces* and the prong in the antlers of *Odocoileus* (A. B. Bubenik 1990).

Protoantlers can ramify through both mechanisms observed in deer antlers (A. B. Bubenik, 1990). In primitive deer the primary mechanism of ramification is splitting, but it is not rare for accessory branches or knobs to be produced through sprouting (Azanza, 1993). In lagomerycid protoantlers the frequency and versatility of the accessory branches and knobs is so great that a lineal ontogenetic sequence cannot be proposed. It seems that sprouting could be a very important process of ramification in this family (Azanza & Ginsburg, 1997).

The antler-like appendages of merycodontines are also multibranched protuberances but they differ from protoantlers by the total absence of sprouts. A simple ontogenetic sequence can be determined: small yearling appendages and adult specimens are morphologically similar, variability being confined to individual variation in size and certain proportions (Frick 1937; Voorhies 1969).

As noted above, the appendices of climacoceratines share with all these appendages the ramified morphology, but the mechanism is not a typical deer branching pattern contrary to what has been assumed (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). As observed previously for *Climacoceras* (MacInnes, 1936; A. B. Bubenik, 1990), the branches and knobs in *Orangemeryx* are cortical structures indicating that the appendages ramify by sprouting which translates into enormous versatility in their construction. According to A. B. Bubenik (1990), this mechanism of ramification indicates a highly active cortex which is consistent with a centrifugal mineralization of the appendage. Thus, major similarities exist to the protoantlers of Lagomerycidae which also ramified predominantly by sprouting, but nevertheless it should be noted that the ramification was not limited to the distal part.

Conclusions

The cranial appendages of *Orangemeryx hendeyi* are similar to those of other climacoceratines in microstructure and the ramification mechanism, suggesting that all of them correspond to a similar constructional pattern that is exclusive to this subfamily. The inclusion of *Prolibytherium* in this subfamily has been suggested by several authors, including Morales *et al.*, (2002) in this volume. The dental and postcranial characters would support this hypothesis, whereas differences in the structure of the appendices are apparent, suggesting that caution needs to be exercised. Further information and more detailed studies of *Prolibytherium* are necessary before a clarification of the phylogenetic relations of this peculiar ruminant can be made.

Despite the controversy about the epiphyseal or apophyseal growth of the “horns” of extinct giraffids, there has lately been an agreement about the apophyseal nature of the climacoceratid appendage. The main arguments are based on the bone microstructure and branching pattern. Taking into account the similarities to and differences from the appendages developed in other ruminant lineages, we conclude that the nature of the climacoceratine appendage is uncertain.

The epiphyseal growth can be easily identified if the appendage fuses to the skull late in ontogeny, since it can be found isolated or not completely fused to the skull via a boss, showing a suture line at its base. If that is not the case, appendages formed from a dermal ossification centre and frontal outgrowths will appear identical (Janis & Scott, 1987). A. B. Bubenik (1983) and Geraads (1986) state that the apophyseal nature can be recognised by the microstructure of the bone composed of a cortex of compact bone and a typical bone marrow, as occur in deer antler.

However, Janis & Scott (1987) questioned the reliability of these criteria since the only certainly identified apophyseal appendages are cervid antlers and it is difficult to say whether their unique histological appearance relates to their mode of development or to their deciduous nature. In fact, because the cycle and growth of deer antlers is regulated by sex hormones, individual variations occur in the microstructure that can affect the major or minor development of the cortex according to the different levels of hormones (G. A. Bubenik, 1990) or even reverse the microstructure with dense bone in the centre and more porous bone at the periphery (A. B. Bubenik *et al.*, 1990) in some castrated deer.

The microstructure of climacoceratid appendages resembles more that of lagomerycid protoantlers in which the core is more porous than the cortex but is not composed of spongy bone. However, the cortex is thicker and poorly delimited in the bone of *Orangemeryx* appendages. The mineralization of the appendage seems to progress centrifugally from the inner part of the cortex, but in *Orangemeryx* appendages there is no evidence of peripheral layers that would indicate successive periods of additive growth. Lagomerycid protoantlers are aperiodically deciduous but climacoceratine appendages were probably lifelong structures judging from the lack of cast specimens.

The branched pattern is the other argument used by authors to support the view that climacoceratid appendages are of an apophyseal nature assuming that their mechanism of ramification was beam splitting (Janis & Scott, 1987; Geraads 1986, 1991; Solounias 1988a, 1988b; Solounias & Moellenken, 1991). Once more the major resemblances are with lagomerycid protoantlers. Both appendages are multibranched structures in which sprouting seems to be the prevalent mechanism of ramification. In climacoceratid appendages this mechanism could be the only one and it is not limited to its distal part. Thus, the branched pattern in climacoceratids is not necessarily related to apical growth as assumed by previous authors, but to a highly active cortex which is consistent with centrifugal mineralization (A. B. Bubenik, 1990). Whether ephiphyseal growth could preclude this branched pattern is a matter for discussion. In giraffid ossicones external mineralization increases the diameter even after the cartilage is ossified whereas increase in length is prevented (Geraads, 1991).

The general similarities between the constructional patterns in the appendages of climacoceratines and lagomerycids explain why several authors have proposed relationships between the two groups. However, there are significant differences in the dentition and post-cranial skeleton which indicates a closer relationship of climacoceratids to the Giraffidae, as explained in the accompanying chapter on the systematics of *Orangemeryx*. However, the differences between the two appendages should not be neglected. The interpretation that the climacoceratine appendage is a lifelong structure with continuous growth and ramification by sprouting over the entire appendage and not limited to its distal part, could be related to the lack of regulation by sex hormones in the activation and growth of the appendage. This seems to be the case of the appendages developed by the different lineages in Bovoidea, in contrast to the Cervoidea. Thus, it could provide an additional argument for a close relationship between climacoceratids and Giraffidae. The absence of hormonal regulation could only occur if it originated in a tropical zone. In deer which inhabit non-seasonal environments near the equator the levels of hormones do not descend a great deal (not reaching the point where spermatogenesis is stopped) unlike those that survive in areas where seasonality is marked, such as the temperate zones. This means it could be due to a lack of sensitivity of hormonal receptors or because the differences between hormonal levels throughout the year are not so marked that mineralisation or growth would stop.

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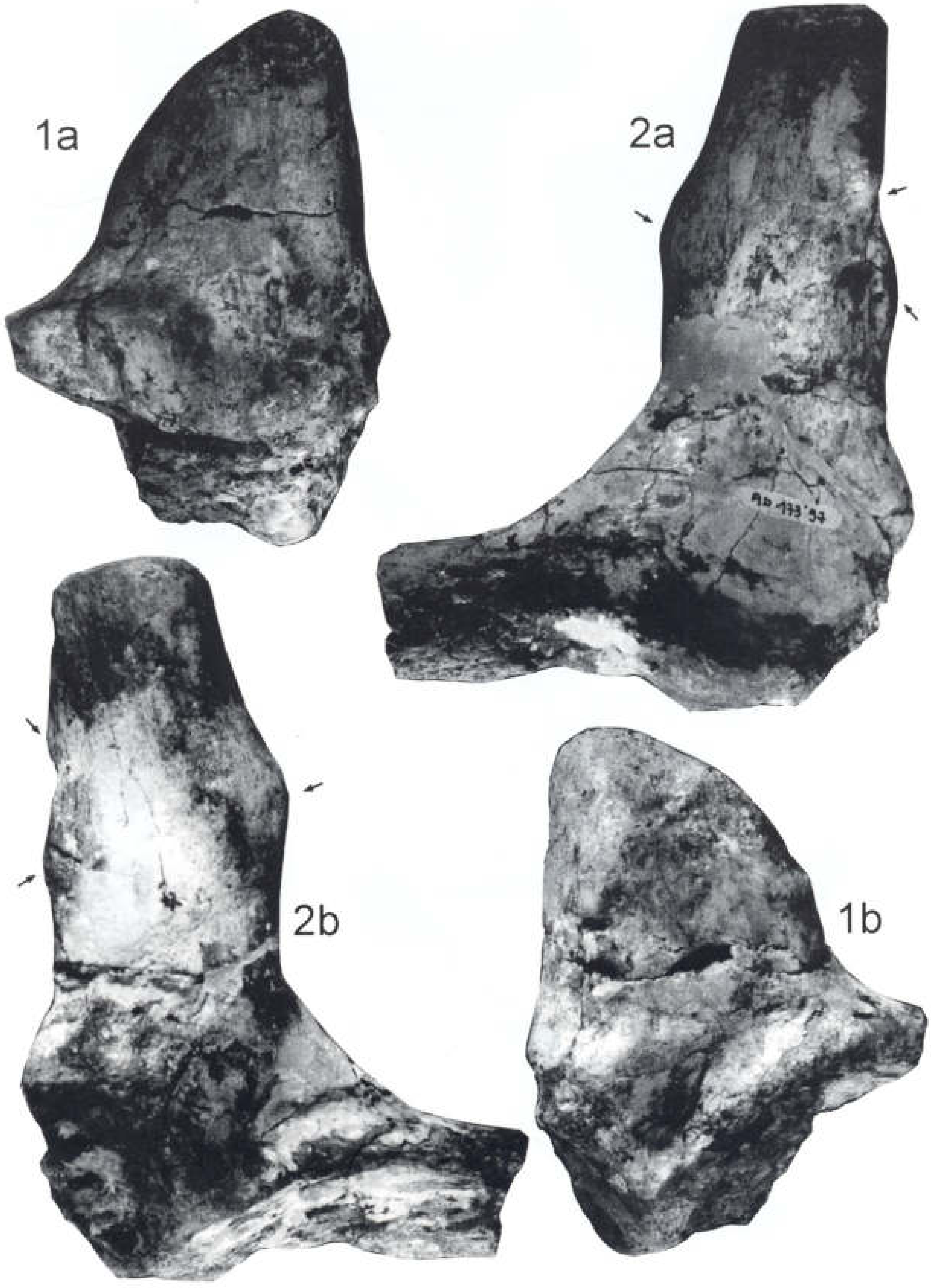

Plate 1: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD-600'98, fragment of left frontal bone bearing the basal part of the appendage; a) internal and b) external views. **2** AD-173'97, fragment of left frontal bone bearing the appendage broken at the middle of the proximal part; a) internal and b) external views. Note the presence of knobs on the basal part of the appendage. All figures are natural size.

Plate 2: Fragments of appendages of *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD-120'00, distal part of right appendage bearing three branches (broken) equidistally placed; a) internal, b) dorsal, and c) external views. Note the presence of a knob between the external and posterior branches. **2** AD-912'97, fragment of distal part of right appendage preserving only two of the branches which seem to branch off closer together and more distally than the missing branch; a) internal, and b) external views. **3** AD-413'98, branch. **4** AD-220'95, distal fragment of a branch. Note that the branches are long and with apices pointed and not polished. All figures are natural size.

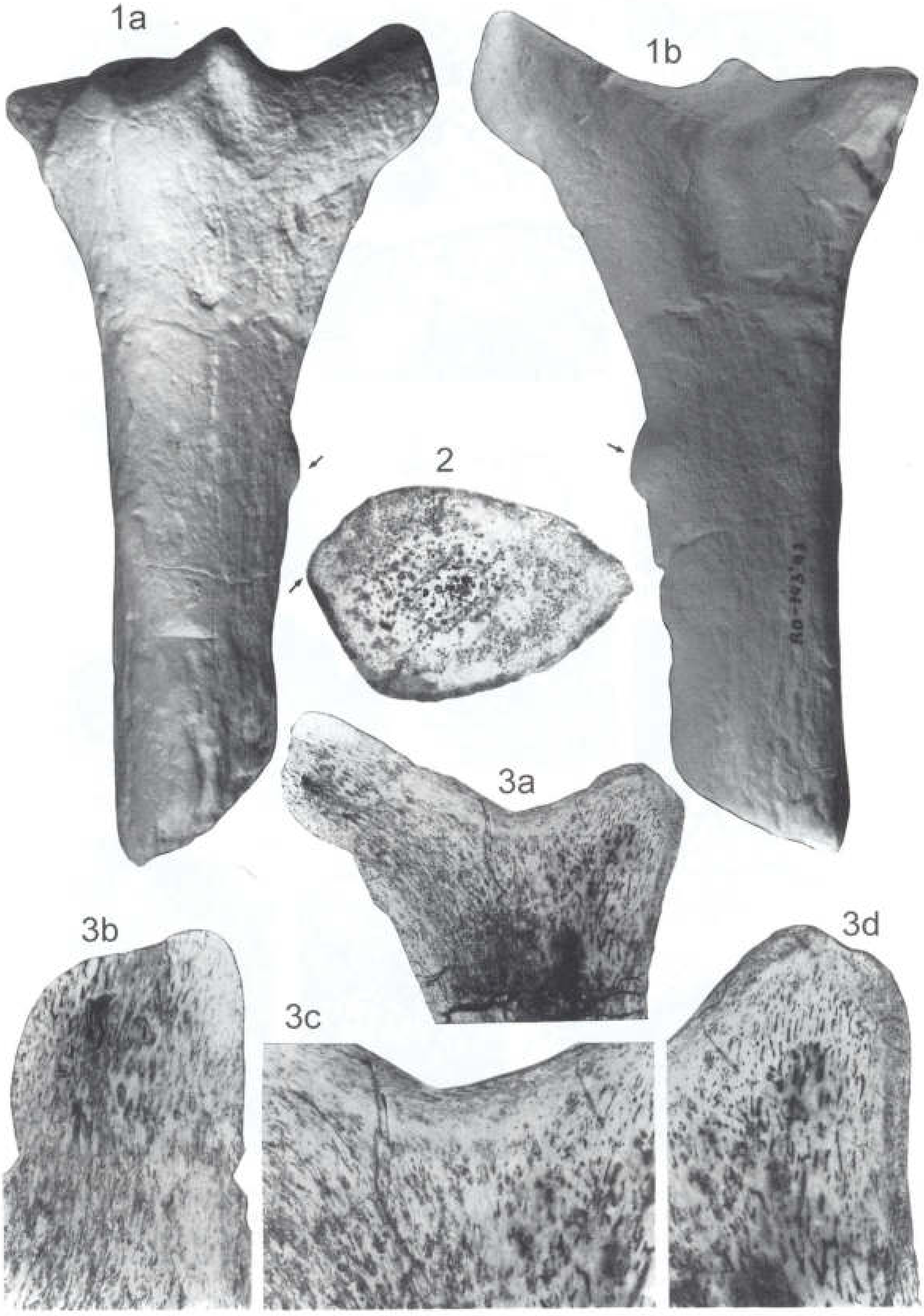

Plate 3: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** AD 743'97, (cast), fragment of left appendage bearing three branches (broken); a) external and b) internal views (x 1). Note the presence of a knob on the posterior margin of the proximal part. **2** same specimen, transverse section of the proximal part at the level of the knob (x 1,7). **3** same specimen, longitudinal section of the distal part; a) complete section (x 0,9), b) detail of the anterior branch (x 2), c) detail of the bifurcation area (x 2), and d) detail of the postero-internal branch (x 2). Note that there are several black lines just below the bifurcation. They do not indicate that the rejection of the distal part was in progress but correspond to the breakage of the appendage at this level.

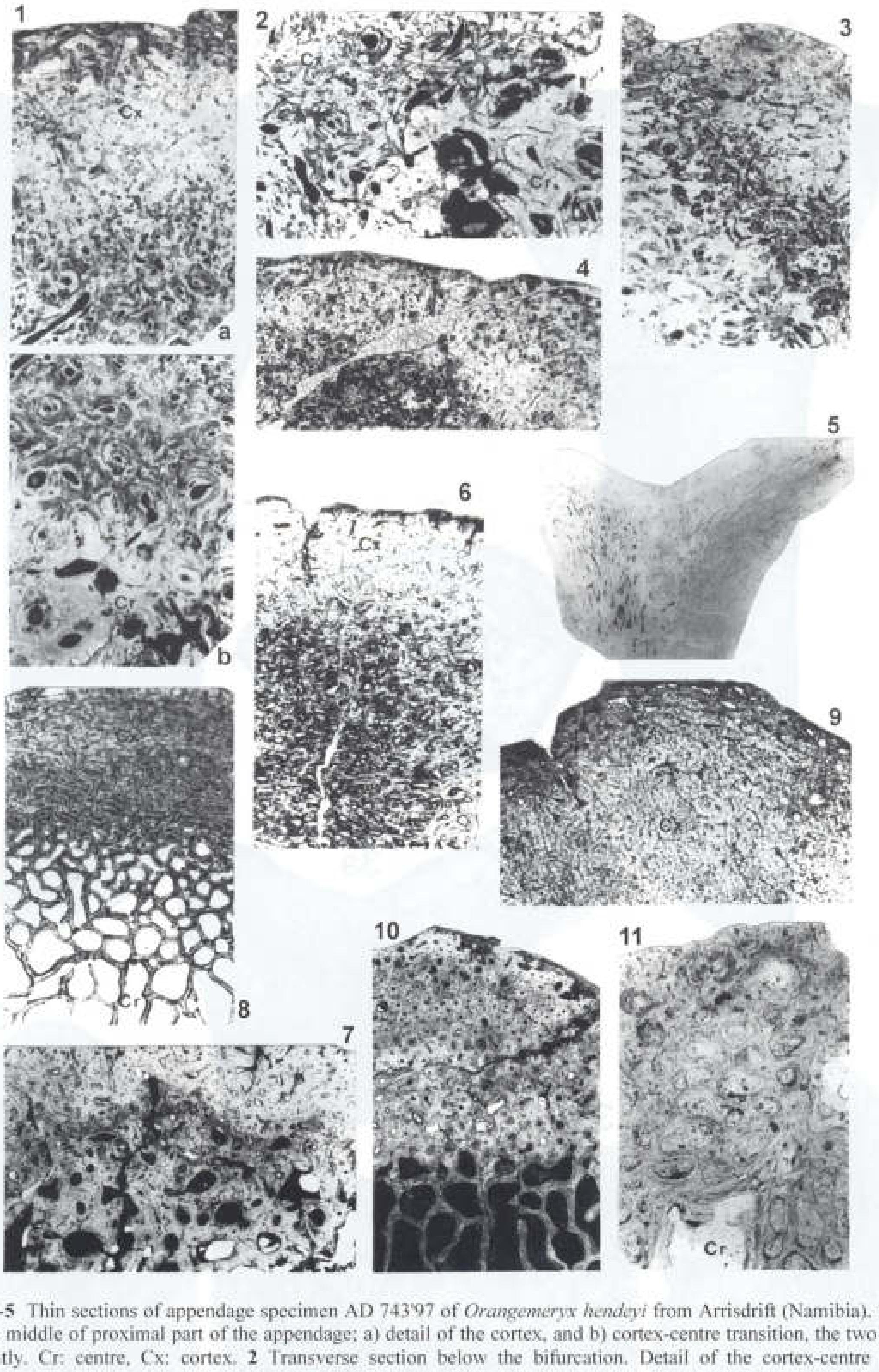

Plate 4: Figs **1-5** Thin sections of appendage specimen AD 743'97 of *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** Transverse section at the middle of proximal part of the appendage; a) detail of the cortex, and b) cortex-centre transition, the two photographs overlap slightly. Cr: centre, Cx: cortex. **2** Transverse section below the bifurcation. Detail of the cortex-centre transition. **3** Transverse section at the base of anterior branch. Detail of the cortex. **4** Transverse section at the base of the postero-internal branch. Detail of the cortex. **5** Longitudinal section of the proximal part.

Figs **6-7** Thin sections of protoantler specimen MNHNP/Fs295 of *Ligeromeryx praestans* from Pontigné (France). **6** Transverse section below the bifurcation. Detail of the cortex-centre transition. **7** Transverse section at the base of two branch. Detail of the cortex-centre transition.

Fig. **8** Transverse thin section at the base of a cast antler of extant *Cervus elaphus hispanicus*. Detail of the cortex-centre transition.

Fig. **9** Transverse thin section at the base of a protoantler branch of *Dicrocerus elegans*. Detail of the cortex showing peripheral layers.

Figs **10** Transverse thin section of a rib from Arrisdrift (Namibia) by its size probably belonging to *Orangemeryx hendeyi*. Detail of the cortex-centre transition.

Fig. **11** Transverse thin section at the middle of the horn core of domestic goat, *Capra*. Detail of the cortex-centre transition.Cr: centre, Cx: cortex. All figures are x 10 except figure 5 which is x 0.8.

Plate 5: *Orangemeryx hendeyi* from Arrisdrift (Namibia). **1** Positive print of a radiograph of specimen AD 743'97, figured in Plate 3. Note that the appendage is not completely mineralized and blood flow was still possible through the base up to the end of the apex. The dark area at the base of the proximal part and in the branching zone mimics heavy mineralization due to the thickness of the bone. **2** Positive print of a radiograph of specimen AD-912'97, figured in Plate 2, figure 2. **3** Positive print of a radiograph of specimen AD-173'97, figured in Plate 1, figure 2. All figures natural size.