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Indications of possible sexual dimorphism in the horn cores and certain cranial bone components of the insular, endemic ruminant *Myotragus balearicus*

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This paper examines possible indications of sexual dimorphism in the physical structure of the horn cores and certain cranial bone components of the extinct Pleistocene-Holocene ruminant *Myotragus balearicus* BATE, 1909 from the Cave of Muleta on the Balearic Island of Mallorca. Sexual differentiation in such components as the skull of *Myotragus balearicus* has been until the present impossible, especially as both male and female have similar horns and head shape, which by normal criteria are identical. The present paper proposes that certain visible structural differences can be seen in the vertical and longitudinal sectioning of horn cores as well as in the reinforcement of certain bones of the skull, as seen in cranial parasagittal sectioning.

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INTRODUCTION

Where the identification of sex in the skeletal remains of most mammalian species is relatively easy, the issue of sexual differentiation in *Myotragus balearicus* has been problematic and not at all a certain matter. There are a number of serious obstacles which have made sexual identification difficult, such as: (1) the lack of articulated skeletal remains in the cave deposits so far encountered, although individual specimens from some of these sources are remarkably well preserved; (2) the fact that both sexes of the species are in osteological appearance unusually similar, including such characteristics as superficially identical horn cores in both the female and

male and (3) to further complicate matters, there is a great variation in the size of full grown (adult) animals of both sexes (large males, small males, large females and small females). Hence, there are no clear sexual differences as are present in many species and that could make sexual differentiation a matter of course.

In fact, apart from the pelvis, neither conventional biometric measurement nor other statistical and biological analyses of bones have as yet been devised or found useful in determining sexual dimorphism in *Myotragus* (Waldren 1982). While there is still

a possibility that present findings may be a question of age or even dietary conditions, no research or analyses so far show these to be the case. There is, however, a programme in progress by the author which possibly can check the results observed here, as well as the question of diet and age on the structure of the bone by DNA tracking. In the meantime, this paper suggests that there may be some valid indication of sexual identification in the species.

In dealing with the problem of sexual differentiation in *Myotragus* certain theoretical assumptions have been made: (a) it is assumed that in the example of the horns, as reflected in the construction of the horn cores in both sexes, that their function, while similar, was at the same time distinctive and, thus, that sexual dimorphism and the function of horns should be identifiable; (b) the surface of the horns in the female strongly suggests an active role on the part of the female in the final choice of partners and that this may have been the function of the female horns; (c) an adaptation that may have possibly acted as a built-in population control, a mechanism particularly advantageous in an insular species of this kind; (d) in the case of the structure of the skull bone components, it is deduced that some differences between the sexes should also be discernible in the males of the species, due to the normal heavy competitive behaviour of the male during the rutting season.

Also, in the case of the Muleta specimens, the effectiveness of the horns and the way in which they may have been used during rut can be seen in examples of cranial wounds from the Muleta cave deposit (see Figs 5a and b; also Waldren 1982, where a fuller consideration of the behavioural posture and resulting wounds from jousting in evidence has been made). In these examples, ample proof of the severity and rigour of the rutting ritual in *Myotragus* can be clearly seen.

THE METHODOLOGY AND TECHNIQUE USED

The present research was inspired by the work of William M. Schaeffer and Charles A. Reed (Reed & Schaeffer 1972). In this paper, the value of parasagittal sectioning of the skulls of selected ovicaprine is evident and sexual dimorphism in sheep and goat well demonstrated in the species involved. In the present case of Muleta, the availability of a great number of detached and broken horn cores of *Myotragus* from the deposit of the Muleta cave has made such a sectioning experiment and study in the identification of sex of *M. balearicus* possible. The *Myotragus* materials used in this research all come from the Muleta cave. The sectioning and photographic work was done by the author and his assistant Mr Jaime Orvay in the Deiá Archaeological Museum and Research Centre, Deiá, Mallorca, Spain and the Donald Baden-Powell Quaternary Research Centre, Pitt Rivers Museum, University of Oxford, Oxford, England. The samples are on deposit in the Deiá Archaeological Museum and Research Centre, which is affiliated with the Museum of Mallorca and the Museum of Sabadell, Spain.

The present study demonstrates possible differences in sex in *M. balearicus* that can be observed through the vertical and horizontal sectioning of a series of unarticulated horn cores and the careful parasagittal sectioning of a number of skulls in an attempt to determine sexual differentiation in a second way. For the present, a cross-correlation study between the structure of the horn cores and that of the various bone components of the same skull has as yet not been carried out, although it is a course of study that is planned in the immediate future. All specimens have been cleaned with water, but in cases with severe adherent dirt or calcium carbonate a solution of 10% or less acetic acid (CH₃OOH) was used with subsequent baths for de-acidifying. Specimens have since been hardened using three different products,

partly in the desire to find the best bone preservative (mainly one that is reversible) and the result of the advancement in recent years of improved products. The three methods used are as follows:

- (1) a method suggested by the Department of Geology, University of Utrecht. This method employs a chemical solvent, xylene ($C_6H_4(CH_3O_2)$), in which chips of Styrofoam packing are dissolved, thus creating a solution of varying density. The specimen is emerged in this for up to half an hour, depending on the porosity of the bone and the viscosity of the solution. This process hardens as well as penetrates the bone, once the residue has dripped off and dried, leaving only the slightest of coating, which does not change biometric measurements. However, this method is not a reversible one and was eventually discontinued and replaced by a second method, unfortunately also irreversible, but with a lesser effect on the bone.
- (2) The horn cores used in the sexing of *Myotragus* by vertical and longitudinal sectioning were chosen at random from a collection of several thousands. These were sectioned after hardening in a product known as Santolite used in hardening sediments in the Geology Laboratory of the University of Oxford. The preservative has not proven as successful as xylene, but hardens especially porous specimens. The product also causes some difficulty in sectioning the specimens, as it adheres to the saw blade, and has a tendency to melt with the action and heated friction of the saw blade, and hence has been replaced.
- (3) The final method entails vacuum impregnation of the bone using the product Butvar, a plastic medium soluble in alcohol and hence reversible. This is done by placing the bones in a pressure chamber and removing the air, causing a vacuum which assists the natural porosity of the bone to draw the preservative into the hollow chambers of the bone on the return

to normal air pressure. This method is by far the better and has been adopted as normal hardening procedures, as it leaves little residue on the bone and is easily dissolved by alcohol when this is needed. The desired viscosity of the preservative is also easily managed.

THE HORN CORE TRANSVERSE AND LONGITUDINAL SECTIONING

In the 'transverse and longitudinal sectioning' of the horn cores, a short, 8 inch jewellers harp with a fine tooth, taught, 1mm, needle saw blade was used. As experimental materials, a large number (72) horn cores (an estimated 36 animals, although no pairing of the horn cores was carried out) were randomly selected for transverse and longitudinal sectioning from a collection of over 1000. These were divided into 3 series of 24 horn cores of random sizes, assumed to be representative in most cases of a variation of age and sex, although there is no guarantee of this being the case. Transverse sectioning of the first two series of horn cores was carried out so as to create a large number of 1 cm thick slab-sections along the full length of each of the horn core samples, beginning the first cut about 1 cm above the attachment of the horn core to the skull. Each slab-section was then polished on the flat ends in order to give the maximum of detail to the slab surfaces (Fig. 1). The use of such a large number of specimens was felt justified by the sheer number of detached horn cores from the Muleta deposit that otherwise have little scientific value other than what can be drawn from them analytically and statistically. The statistical count of these components has been the basis for estimates of the number of animals in the deposit. In turn, the horn cores were selected from every possible context in the Muleta stratigraphy to assure randomness. A few obviously immature specimens were also chosen and sectioned as a control. However, these young specimens show no apparent sexual differentiation.

As a result of the sectioning of the horn cores, distinct structural differences appear to be

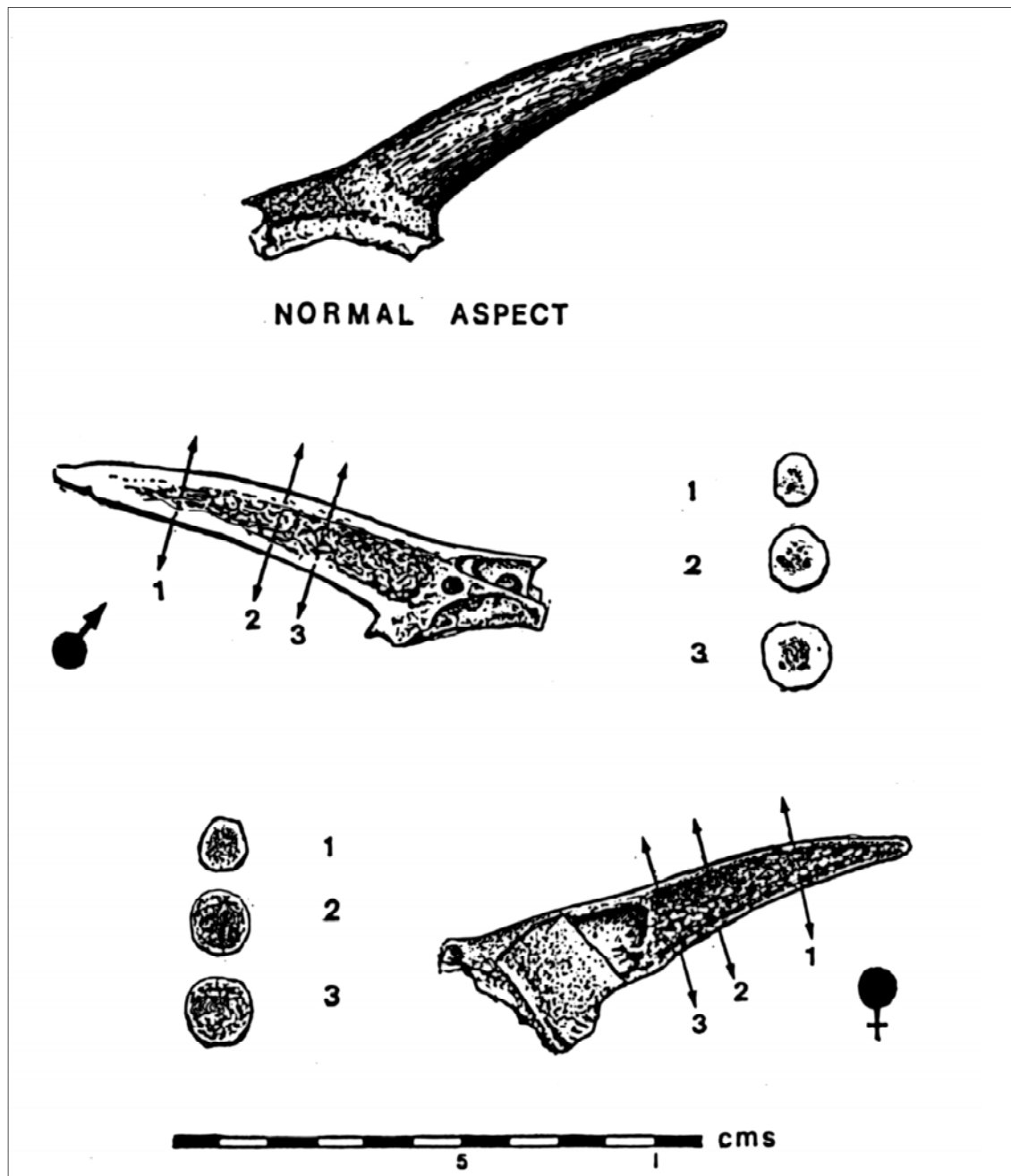


Figure 1 Proposed sexual differences in longitudinal and transverse sections of *Myotragus balearicus* horn cores. Top: normal aspect; Middle: male horn, longitudinal section and three transverse sections done at places indicated in the longitudinal section; Bottom: female horn, same sections.

discernible and can be divided into two categories in their structural and apparent compositional appearance (Figs. 2, bottom and 3, bottom). These two categories are believed to be sexually significant and not the result of

age or dietary conditions. Known behavioural and functional patterns normally undertaken by the male make it possible that some structural differences should appear in the physical make up of the horn core between sexes. For compa-

rative purposes, another series of 24 horn cores was treated and sectioned longitudinally, along the length of the arc of the horn core.

The results in all three series clearly show two distinct structural configurations: (1) a dense walled configuration with limited

spongiosa (male, Fig. 2) and (2) a thin walled configuration with extensive spongiosa (female, Fig. 3). The longitudinal sectioning was carried out resulting in two halves that equally demonstrate the same two classifications and configurations found in the transverse sectioning. They show identical structural composi-



Figure 2 Longitudinal (top) and transverse (bottom) sections of the male horn core.

tion made up of dense outer walls and limited spongiosa (interpreted as male, Fig. 2, top) and thin outer walls with extensive spongiosa (interpreted as female, Fig. 3, top).

THE CRANIAL PARASAGITTAL SECTIONING

The skulls used for 'parasagittal sectioning'

were selected for the maximum information they could give. They present a group of animals that were fully mature at the time of death, and whose dentition indicates they are approximately the same age. Consideration was also given in the selection of skulls for parasagittal sectioning as to the natural hardening of the specimens. This is to say samples

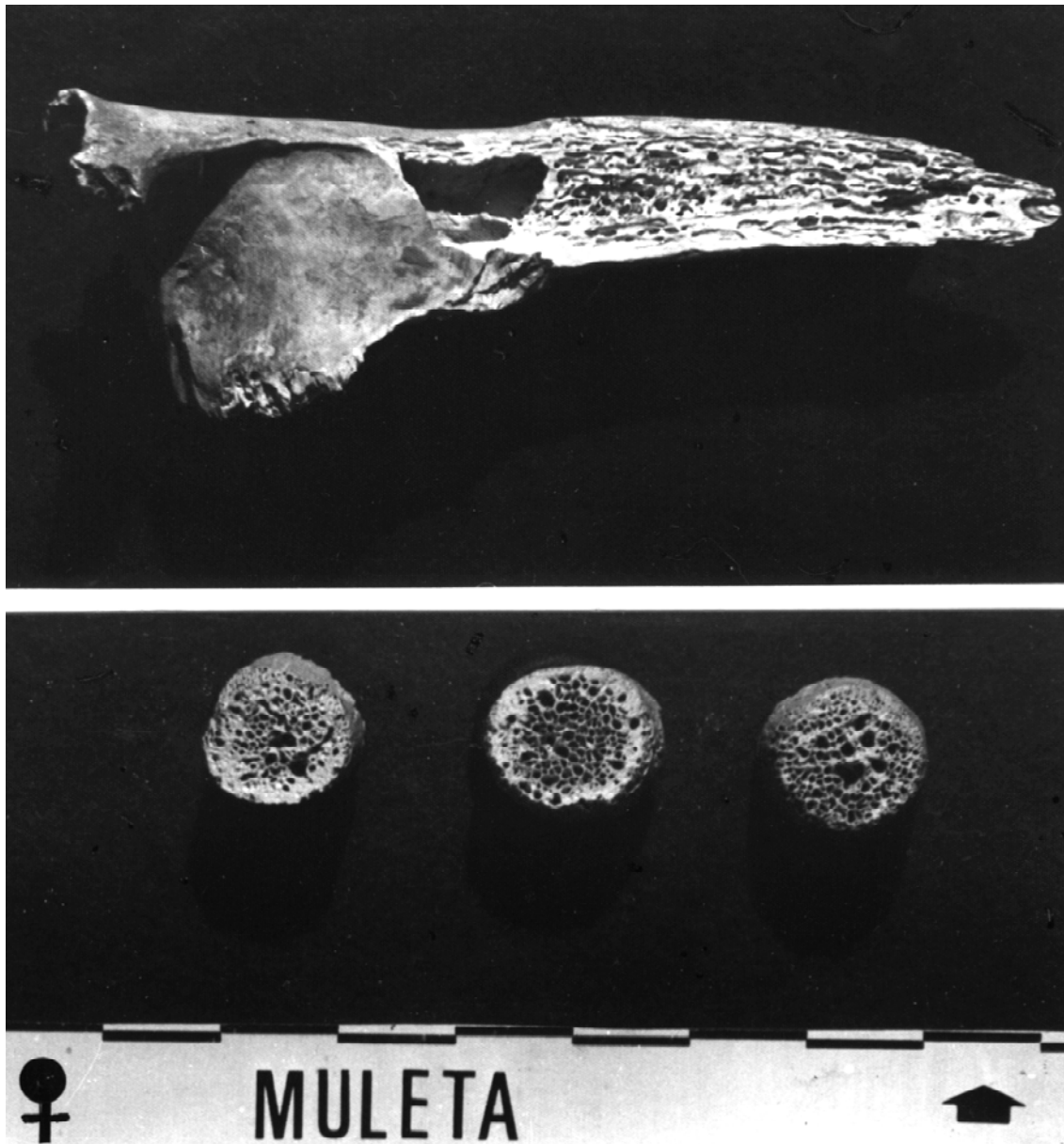


Figure 3 Longitudinal (top) and transverse (bottom) sections of the female horn core.

were used which had been hardened by natural replacement and coating of the craniums by calcium carbonate in varying degrees, but always sufficient to withstand the hazards of sectioning. This was done because it was found that a clearer cut could be made when there was no gummy coating of preservative or other substance which would adhere to the saw blade, preventing a clear cut. At the same time, not all specimens in their natural state have been or are suitable for sectioning because of their fragility. Some choice was made as to

what might possibly constitute a male or female, such as larger, splayed horns and broader facial feature. However, as pointed out earlier, there is no assurance that skull size or shape is a criterion of sex in *Myotragus*, so this selection was an arbitrary one. In the sectioning, a jewellers 12 cm long, fine tooth, carbon steel, needle saw blade of 1 mm thickness was attached to a harp saw with a height of 15 cm was used. The specimen was cupped in the hand of an assistant while being sectioned by the author (Fig. 4). In this way, the cut could be con-

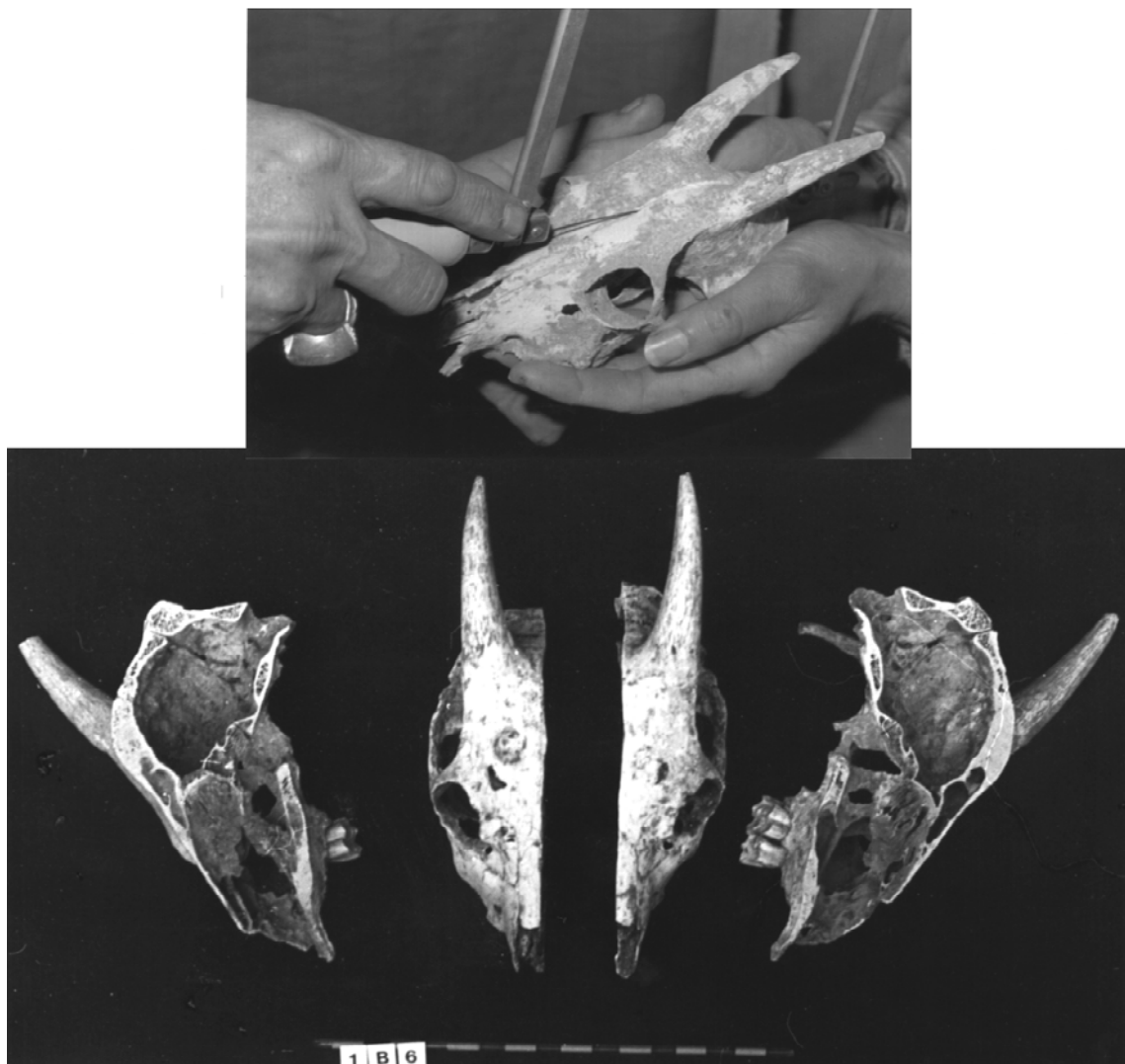


Figure 4 Top: photograph of the parasagittal sectioning of a skull from the Cave of Muleta; Bottom: two sectioned *Myotragus* skulls, one showing internal views (left and right), the other one (in the middle) in dorsal view, showing evidence of damage to the right frontal region of the skull incurred during combat.

trolled for maximum accuracy and minimised breakage. The sawing was kept approximately 3 mm to one side of the midsagittal suture of the skull in order not to damage the sinus chambers and to see them clearly. There has been a maximum of 1 mm loss between the halves of the skull, and they can be joined without damage to either part (Fig. 4).

In all events, the resulting sectioning has been both informative as to the various hidden characteristics of the inner structure of the skull, such as the reinforcement of certain bone elements of the skull as well as the structure of the horn cores, but also equally valuable, it is believed, in the question of sexual identification in the animal.

EXPLANATORY DRAWINGS

The drawings used in this study to demonstrate cranial characteristics were prepared in two different ways. In the first, the halves of the sectioned skull were photographed and tracings were made of the photographs, carefully tracing the details of the specimen with the palate surface parallel to a line drawn beforehand on the tracing paper. This horizontal line and its alignment with the palate plate of the maxilla of each half of the skull supplies a constant reference and alignment in each tracing from which subsequent calculations can be made (P1-P2 in Figs. 6 and 7). The second method, which does not necessitate the photographing of each specimen, is done by placing the section half, cut side down, on a slightly roughened transparent acetate sheet and tracing the outside profile. After this, the inner walls of the skull and other details are traced with a sharp pencil by reversing the acetate sheet. In turn, these are traced into standard sheets of tracing paper for reproduction. This method is a great deal cheaper and accurate as no details are lost or distorted by photography. Subsequently, angles and measurements can be accurately made from these carefully prepared and executed tracings.

DESCRIPTION OF THE DIAGRAMS AND BIOMETRIC CALCULATIONS

See Figures 6 and 7 for the indication of the position of the lines.

A1-A2 This is a line drawn as shown parallel to a line between the maximum extension of the nasal and frontal bones, through the intersection between CS1-CS2 and P1-P2.

B1-B2 This line is also created by its alignment with the frontal, parietal and supraoccipital bones and intersecting CS1-CS2 and P1-P2 lines, forming an angle B1-B2 and P1-P2.

C1-C2 This line is drawn between the two leading points on the occipital condyle and is extended to form the brain case rectangle (Waldren 1982: appendix 1E).

P1-P2 This is the calculated graphic line, aligned with the animal sample's palate and used as a standard for the specimen's horizontal orientation.

CS1-CS2 A right angle to P1-P2 used for the calculation standard in plotting Z1-Z2 and x and y.

x and y These are drawn as parallel lines to P1-P2 where CS1-CS2, touching the inner surface of the basisphenoid and frontal bones of the skull.

Z1-Z2 A horizontal line to P1-P2 plotted as the centre of x and y and the intersection with CS1-CS2. This intersecting point represents the centre of the calculation standard, although it varies in individual specimens.

O1-O2 This line is drawn through the most extended point of the occipital condyle and the supraoccipital bone as illustrated. It is drawn to intersect P1-P2 in order to calculate how far the angle of this intersection deviates from a right angle in both male and female specimens.

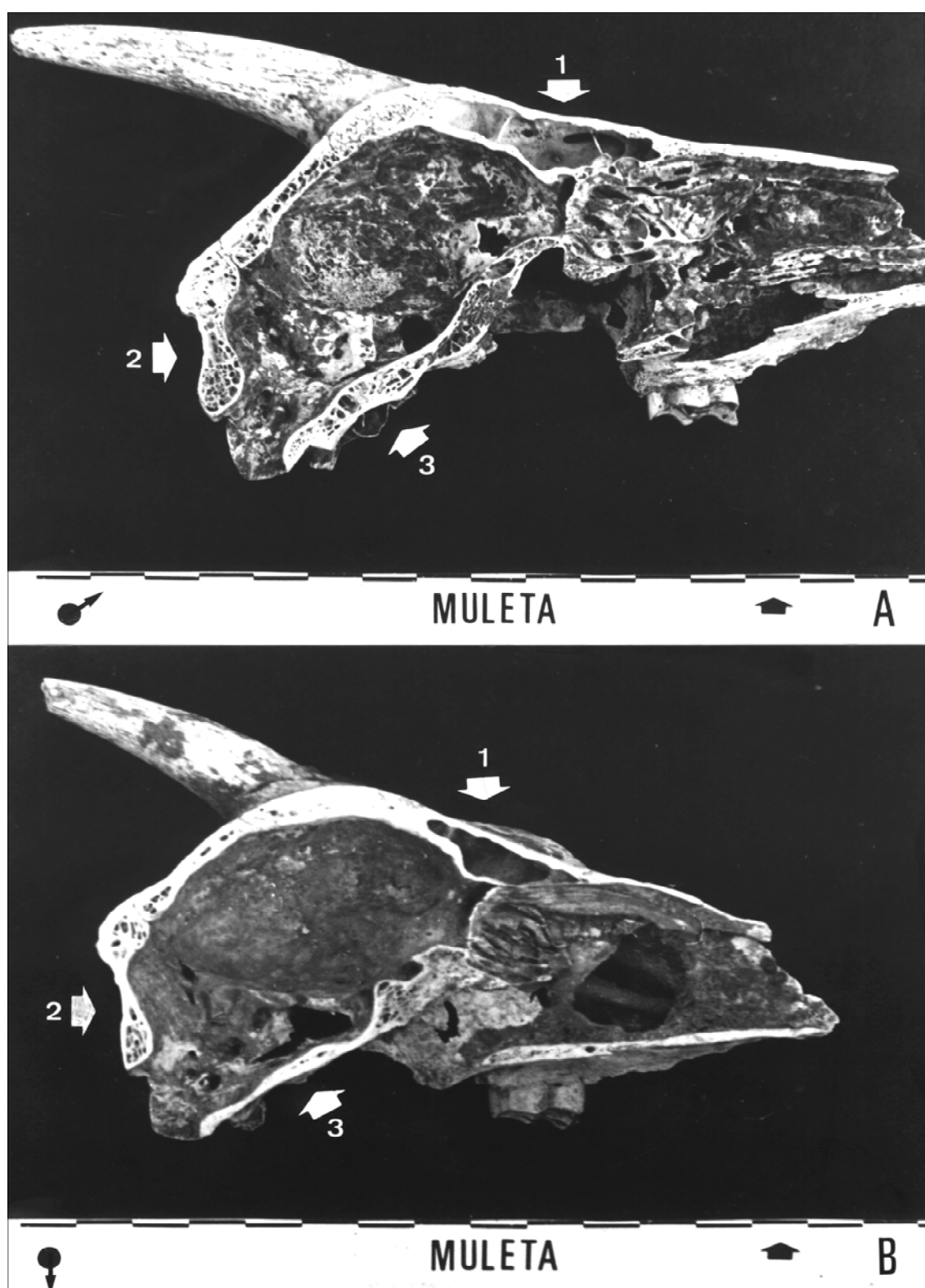


Figure 5 Two sectioned *Myotragus* skulls from Muleta. **A**: male; **B**: female; **1**: frontal and lateral sinus branches; **2**: supraoccipital; **3**: basioccipital and basisphenoid region. The structural difference between the sexes can be clearly seen.

OBSERVATIONS AND INDICATIONS OF CRANIAL SEXUAL DIMORPHISM

Sexual structural differences are remarkably clear in the parasagittal sections of the skulls (Figs. 6 and 7), as well as the many vertical and longitudinal sections of horn cores. It is apparent from the photographs and diagrams alone that all the bones of the basicranium show considerable differences, not only between the male and female *Myotragus*, but compared to other Rupicaprini, Caprini, etc., where competitive behaviour entails butting or wrestling and other head contact (e.g. Reed & Schaeffer 1972, Geist 1966a, 1966b). In the case of the male, there has been a considerable thickening of the supraoccipital, parietal, and frontal bones, as well as in the basioccipital and basisphenoid bones and occipital condyle. As in other Rupicaprines, sexual dimorphism is not as pronounced as in the Caprini. *Myotragus* appears to be more primitive than modern species in that the bases of its horns are quite far from the *foramen magnum*. The frontal sinuses are also more primitive, as they cover about one third of the anterior part of the brain and not most of it, as they do in modern genera. In the male, the frontal sinuses are larger and seem to be slightly more complex than in the female (Figs. 5-7).

The corneal sinuses are primitive in that they extend only to the base of the horn cores, whereas in modern species, as Reed & Schaeffer (1972) have pointed out, the corneal sinuses can reach as far as the tip of the horn core. The horn cores of *Myotragus* male and female show very little difference superficially. A mark of sexual dimorphism was first sought in the angle of splay of the horn cores as it occurred in individual specimens. A wide splay might have been characteristic of males as this would have seemed more effective in intraspecific combat. However, this does not seem to be the case as it seems from the evidence that males and females, when fully mature, both show great variability in the angle of splay. Sexual dimorphism

does show in the transverse and longitudinal section of the horn cores (Figs. 1-3). The outer layer of bone is considerably thicker in the male than in the female. Measurements of the base of the horn core of the male and the female do not show anything significant, other than the same variability of size. However, other less obvious differences in cranial morphology become evident when various angles and calculations are represented graphically. The most outstanding of these is the angle (between O1-O2 and P1-P2, see Figs. 6-7) plotted for the supraoccipital bone of male and female skulls. When the angles are calculated they differ considerably between the sexes, from 5° to 17°. In the case of the male, there is noticeably more variation of angle from near vertical to 17°, whereas the angle is more constant in the female (Table 1). However, the general robustness of the male supraoccipital is a further key in this respect. Another angle can be formed, which produces a schematic rectangle for the brain of male and female individuals. This is created by marking the proximal extensions of the occipital condyle (c1-c2), and extending a line so as to plot a right angle touching the top of the brain of the inner wall of the parietal bone. Then the same type of line is plotted for the junction of the basioccipital and the basisphenoid bones, and extending these lines until another right angle can be drawn intersecting the most distal point of the frontal part of the brain or frontal bone. The rectangles can then be measured for area, length and width and plotted (see Waldren 1982: table 12, diagram 3). In the specimens measured, there appears to be a difference between males and females, the brain rectangle is larger in area and longer in length in the male.

INDICATIONS OF COMPETITIVE BEHAVIOUR AS SEEN IN CRANIAL AND CORNEAL DAMAGE

In this section, for the sake of continuity and a better understanding of sexual differentiation, it is necessary to review briefly a few of the more important physical adaptations

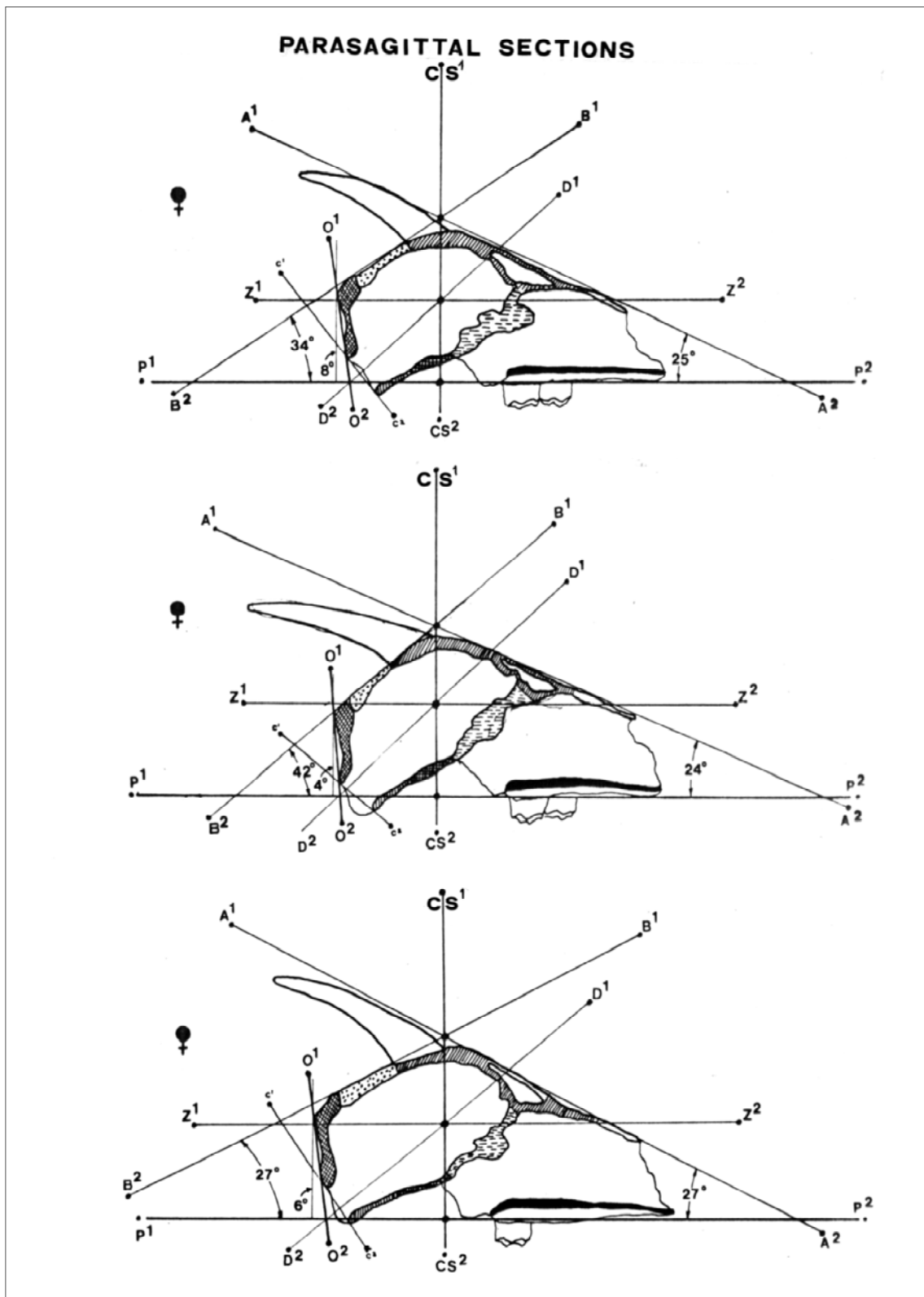


Figure 6 The diagrams and tracings of three female skulls; for explanations see text.

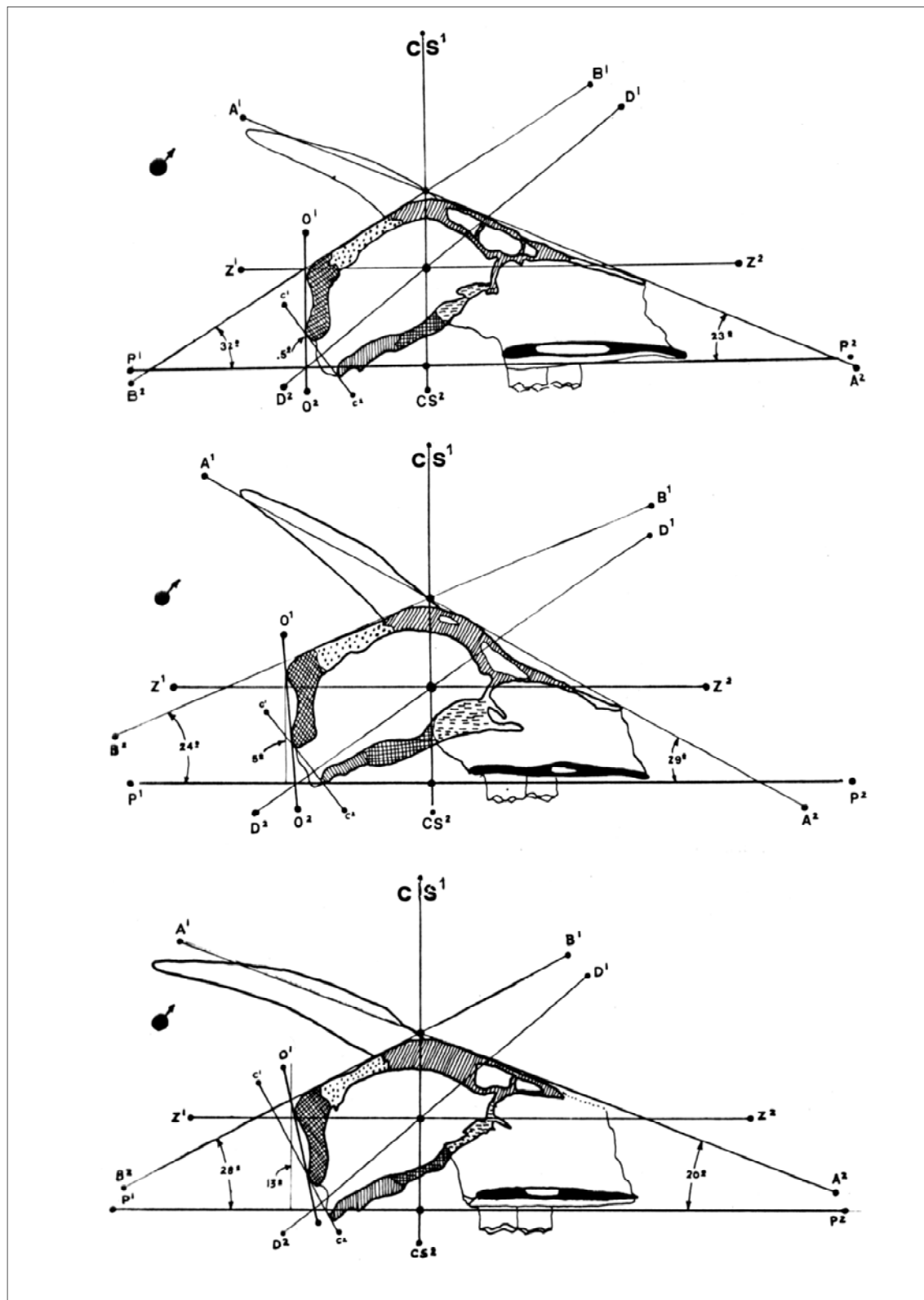


Figure 7 The diagrams and tracings of three male skulls; for explanation see text.

undergone by the animal in its evolutionary development and to examine how these may have direct and indirect relationship to social behaviour and sexual dimorphism itself. For example, the frontal position of the orbits is a peculiarity diagnostic of *Myotragus*. It is hardly necessary to point out that such a development drastically narrowed the animal's field of vision and undoubtedly would have had bearing on competitive and reproductive behaviour. Simultaneously such an adaptation would have made it easy prey to predators had any carnivores existed during its history and this would apply particularly in the final period of its coexistence with humans.

Developments in its lower dentition in the form of a reduction of the number of incisiform teeth from the four pairs normal in Artiodactyla, to a single pair of ever-growing, extra long and chisel-like incisors, along with a reduction in the number of premolars in both the upper and lower dentition, are related to available food, specialised feeding habits and the animal's geographic surroundings. This has a direct bearing on behaviour, especially when coupled with a shortening of

the limbs and fusion of the tarsal components. In turn, their fusion to the metatarsals or cannon bones of the rear limbs would suggest an animal with slow locomotion and little ability to change the direction of its forward movement.

Considerable evidence of injury caused by intraspecific combat among the male population has been noted in the better-preserved specimens of *Myotragus* from the Muleta deposit. The areas and type of wounds can give us some idea of the course that competitive behaviour took. These injuries concern mainly the cranial areas and the horns themselves; little other injury to the body proper is or would be discernible. The most severe marks of injury appear as wounds, which have healed or partially healed, made by horns on the frontal and parietal bones (Fig. 8). The extent and severity of these wounds suggest that the animal's opponent used considerable force during rutting activities. In several cases, the blows completely penetrated the frontal sinuses and the brain case in the parietal area. However, instant death does not seem to have occurred, as in all cases healing ridges have formed on the bone, and in

Table 1 Angle of the supraoccipital bone in *Myotragus balearicus* from the Cave of Muleta.

SEX	NO	ANGLE O1-O2	ANGLE P1-B2	ANGLE P2-A2
F	1A	-8°	34°	25°
F	1B	-4°	42°	24°
F	1C	-6°	27°	27°
F	1D	+12°	30°	28°
F	1E	-4°	32°	26°
M	2A	-5°	32°	23°
M	2B	-10°	26°	25°
M	2C	-17°	35°	24°
M	2D	-5°	24°	29°
M	2E	-13°	28°	20°
M	2F	-6°	31°	20°
M	2G	-25°	37°	24°
M	2H	-6°	37°	27°



Figure 8 Photographs showing wounds inflicted during the rutting ritual. Top: a wound in the frontal region; Bottom: two wounds in the parietal region.

some cases the wound to a frontal bone has completely healed (Fig. 4, bottom, middle). Healing also occurred in several parietal penetrations (Fig. 8, bottom, left and right) and although wounds do not appear to have led to instantaneous death, they may well have caused a belated one where the animals sought the protection of the Muleta cave.

The mode of movement in *Myotragus* during the rut is an intriguing subject and some clues to it may be given by morphological adaptation of its limbs and spine, where robustness occurs in both, and is especially exemplified in the animal's powerful neck. It is evident that all these aspects probably tied in with one another, the final result emerging during the actual competitive behaviour. For instance, the rigidity of the hind limbs in the region of the tarsals and metatarsals, as a result of their complete fusion in both male and female adults, would have made it difficult for the animal to shift in fighting off opponents during the rut. Such an adaptation would, however, give impetus to the male's drive as well as certain limits to its direction and movement in general. Supporting the animal's inability to shift direction in its hind limbs are the development of the robust cervical vertebrae and the high spines of the thoracic vertebrae which would have given the creature exceptional strength. Very powerful muscular development is evident in the neck and shoulders, and this strength would have come into play during competitive combat. The wounds present in the specimens suggest frontal approach and impact. Whether these wounds are the result of actions gone wrong during fighting is not altogether clear. Among *Oreamnus* (Rocky Mountain Goat), another mountain dwelling animal, no competitive combat exists (Reed & Schaeffer 1972). Body butting, head to head butting, and 'wrestling' with horns locked using the neck muscles are described by Reed & Schaeffer and many others. The damage done is also well described. The exact form that this competitive conduct took in *Myotragus* is not totally clear but the inflicted

injuries are observable and strongly support certain hypotheses.

The illustration here (Fig. 9) shows the only means by which certain types of wounds found in the frontal and parietal bones could have been inflicted. The angles are calculated from the postures of the two combatants, which are necessary for such injuries to occur. Even though the animals were to stand head to head, and in spite of the powerful makeup of the neck and shoulder of *Myotragus*, it seems impossible that the penetration of the horns into either the frontal or parietal bone could have taken place. The act of ramming is a more convincing explanation. This entails a standing off of individuals with a purposeful charge taking place, a frontal to frontal approach, and the resulting impact, are interesting in more than one respect. One of the peculiarities of *Myotragus* is the frontal position of its orbits, and at the most, its field of vision was not over 110°. Hence, it would appear that the animal would have been completely blind as to its opponent's position during the latter part of its approach and at the exact moment of contact. During the charge, its eyes would have been focused on a very narrow area of ground directly in front of its forelimbs. With horns that run almost straight back from its orbital region, its judgement of approach and impact during competitive combat must have been full of errors. If we link these factors with the rigidity of the hind metapodials, the shock at impact must have been considerable. Whether or not this was normally offset instinctively at the last moment in veering off by using the powerful neck muscles, is not known. What is apparent is the result of some kind of charge that at times was bone-penetrating, if the head-to-head encounter went wrong (Fig. 8). Such miscalculations during intraspecific fighting have been observed in modern species (Reed & Schaeffer 1972).

The differences and similarities within the species, as well as *Myotragus* to other

Rupicaprini, will undoubtedly become clearer when more biometric information is available. Meanwhile, the materials for this current study have been carefully selected to give the maximum of detail in their variety and preservation, as well as deciphering the question

of sexual dimorphism and some indications of morphology and competitive behaviour in *Myotragus*. Some of the details of the current research can be expected to change as only a portion of the Muleta materials have been used for this sort of research and none from

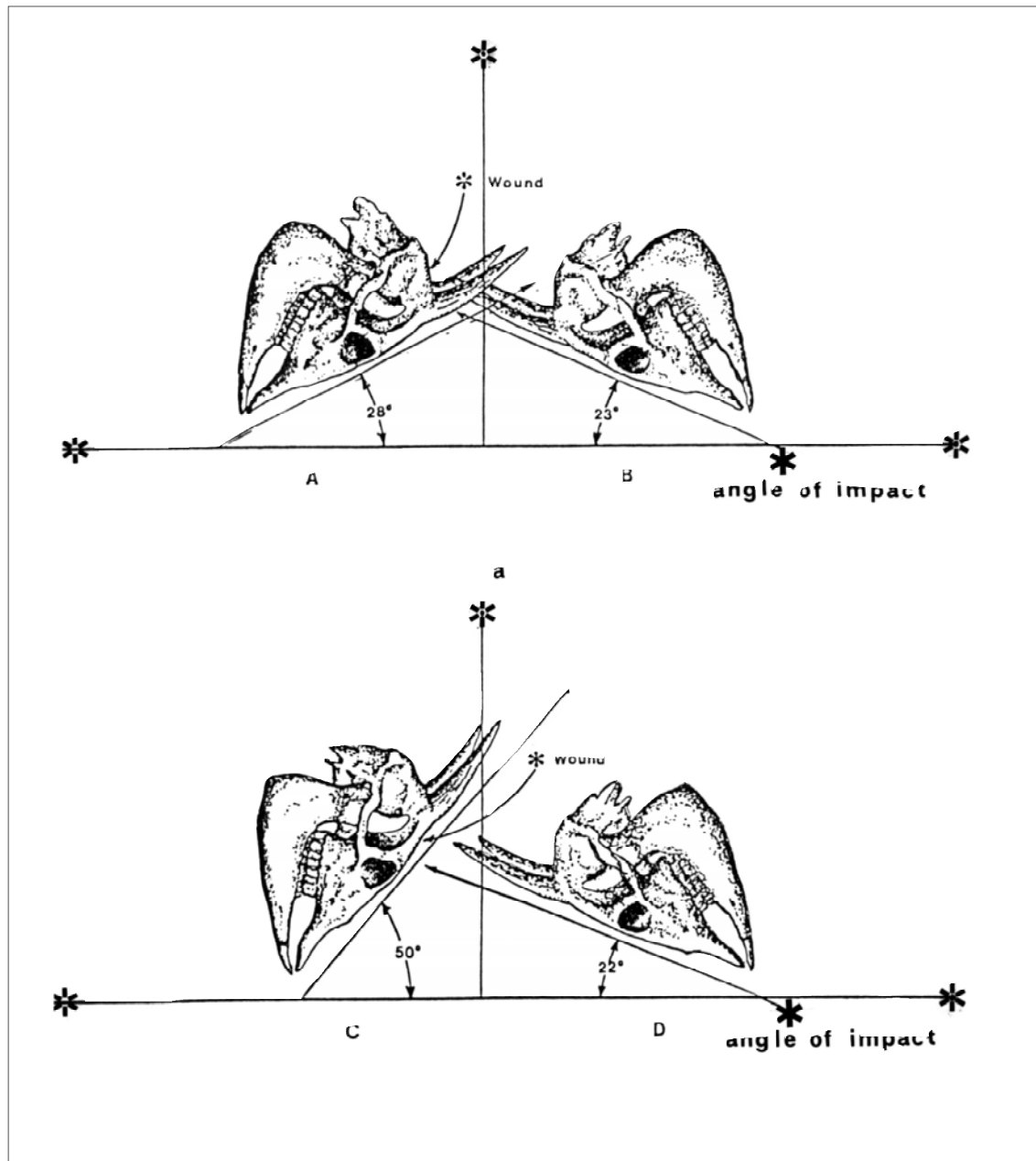


Figure 9 Two illustrations showing the hypothetical position of the skulls and the angle of impact of two adversary males during the rut. Top: posture necessary to inflict a wound in the parietal region of the skull; Bottom: posture necessary to inflict a wound in the frontal region of the skull.

other stations, which will have to be included when it becomes available in the future.

The value of this present research stems out of it being the first work done on the subjects in regard to *Myotragus* in an attempt to come to some conclusions on sexual differentiation in the species. There are many other considerations within the current work that can and should be enlarged upon, however as this is basically a preliminary study, such an enlargement is not possible at the present time. Nevertheless, the information found in both the graphic information and the text should be of some use and interest to paleontologists, and may serve as a beginning for a more comprehensive study.

The specialised nature of the *Myotragus balearicus* as an insular species with an isolated evolution for all of the Pleistocene and part of the Holocene periods in the Balearics, makes it of particular interest to many branches of science. Its aberrant and oddly developed characteristics, as well as recent evidence of its use and survival until the arrival of man and beyond is additionally important. Its extinction by man around 2600 cal. yBC gives a new insight into both the knowledge of the animal and the events as they transpired ecologically and culturally in this area of the Western Mediterranean.

CONCLUSIONS

The research into some of the aspects of sexual cranial dimorphism and competitive behaviour in *Myotragus balearicus* indicates certain characteristics both in morphology, social behaviour and sexual identification.

- (1) The research shows that the animal had primitive frontal sinuses, which cover approximately the anterior third of the brain, and appear to be slightly more complex in the males than in the females.
- (2) The corneal sinuses appear to reach only to the base of the horn core. There is no

significant difference in the diameter measurement of the base of the horn cores between the male and female specimens.

- (3) There is considerable difference in the thickness of the supraoccipital, basioccipital, basisphenoid and parietal bones of the skull: they are thicker in the males. This would be connected with competitive behaviour during rut.
- (4) There is a large variation in the angle of the supraoccipital bone of the male plotted as outlined in this study.
- (5) The rectangle of the brain, as plotted in this study (but not shown here because of available space), show that the male's rectangle is larger and longer.
- (6) There is no apparent relationship between males and females in the splaying of horns of individuals, which would be expected to be wider in the males for the effectiveness of the horns in intraspecific fighting. This may well be a clue to the animal's posture during combat, designating a frontal approach to the route of its charge.
- (7) The wounds perpetrated during competitive combat indicates the only possible posture of both animals at the moment of impact. When related to the rigidity of the tarsal-metatarsal complex, which indicates an inability to change direction quickly, this strongly suggests that the animal used a head-to-head posture during the rut. The severity of the wounds - whether accidental or not - show a forward charge of considerable force in order to effect a bone-penetrating blow.
- (8) The frontal positioning of the orbits and subsequent narrow angle of vision would have certainly caused considerable error judgement in competitive behaviour.

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