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THE OSTEOLOGY OF THE CRANIAL AND FACIAL BONES OF THE SAVANNAH BUFFALO

Syncerus caffer caffer (Sparrman, 1779)

by

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Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy
in Veterinary Anatomy.

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Date submitted : August 2002.

Dedicated to my
mentor in Veterinary Anatomy, Embryology and Histology,
the late professor H. P. A. de Boom.

ACKNOWLEDGEMENTS

I am indebted to the following persons and Institutions, without whose assistance this study could not have been possible at all :

THE UNIVERSITY of PRETORIA, as my employer, and with whom I have this postgraduate study registered. The Faculty of Veterinary Science gave financial and technical assistance. I would like to thank the following personnel in particular **:**

- Mr. D. J. Coetzer, for his assistance when collecting the material. I sincerely want to thank him for his continued motivation and for the enjoyable nights around the campfires in the bush. I also want to thank him for the use of the skull of a bull, used in various figures. I could not have completed this study without his superior technical skills and help.
- Mr. I. L. de Villiers and his personnel D. Baloyi, M. Ramatshela, A. Kekana and J. Sewatle.
- The late Professor J. M. W. le Roux, for his valuable guidance at the onset of the study.
- Biomedical artist C. D. Seegers, for the original monochrome illustrations.
- My colleagues, especially Prof. J. T. Soley, for his continued interest and encouragement.
- Prof. H. J. Groenewald for his arrangements in order for me to complete this study.
- Proff. R. I. Coubrough and Prof. N. J. Kriek, former and present Deans, for their patience and assistance in specific arrangements.
- Prof. N. J. van der Merwe as promoter.
- Librarians E. van der Westhuizen, A. Lourens & M. Nel; the IT team; Radiology Department for the radiographs and photographer C. Vermeulen for photos of the X-rays and the paranasal sinus model.

THE NATIONAL PARKS BOARD, with whom this project has been co-registered. I sincerely want to thank the Board for allowing me to collect the material on various occasions, and for their assistance in so many ways from the onset of the study. The Kruger National Park provided accommodation on all the occasions. The Park made available their staff and facilities, in order for me to prepare some of the material on site. I would like to thank the following personnel in particular **:**

- Drs V. de Vos, R. G. Bengis, D. F. Keet and J. A. Raath.
- Eric & Colleen Wood, Dan & Tessa Erasmus, At Dekker, Johan Dragt, Johan Malan, Johan Roelofse, Hugo van Niekerk, Piet Otto, Ian Whyte, Flip Nel, Johan Sithole and Dawid.

THE TRANSVAAL MUSEUM for supplying the skull of the immature cow, used in some figures.

Typing, photography, digital remastering and graphic arts was done by the author himself.

Lastly, I would like to thank everyone not mentioned above, who through the years have helped me knowingly and unknowingly - even in the least little bit - to continue with this immense task. In particular, I would like to mention Dr. F.E. Prins for his support over many years, and R.E. Manke for her assistance when building the model of the paranasal sinuses.

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By convention, anatomical illustrations are preferably left views, looking at the left side of the skull or the particular bone. Or, if it is a median section of the skull, then the right half is illustrated in left view. That is in an effort to always have the rostral end of the skull - or a part of the skull - directed towards the left of the page. Specific viewpoints are explicitly stated in illustrations to prevent orientation problems, especially for sectioned anatomical structures that may be difficult to interpret.

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SUMMARY

The Osteology of the Cranial and Facial Bones of the
savannah buffalo *Syncerus caffer caffer* (Sparrman, 1779).
by

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Zoologists classify the savannah buffalo under the Bovini Tribe. Osteologically, the skull differs from that of the water buffalo of Asia, inter alia, in that the vomer does not articulate with the palatine part of the osseus palate. This gross anatomical study gives a detailed description of all the bones of the skull, mandible and hyoid apparatus of the savannah buffalo *Syncerus caffer caffer* (Sparrman, 1779). These bones are similar in many respects to that of the domestic bovine. However, due to the robustness of the buffalo skull, many aspects pertaining to bones or parts of bones that are different or more pronounced, are of anatomical importance. The sum-total effect of all these features, gives the skull its typical macro-morphology that differentiates it clearly from the other genera in the Bovini Tribe. The more important characteristics that were found, are the following **:**

1. The skull of young animals retains basic embryonic reshaping potential till quite late in life. It can be seen as a remnant of Meckel's cartilage in the mandible as well as in prolonged remodelling in the regions of the orbit, dorsum of the nose, and most markedly, also in the lateral walls of the cranium. A subsequent temporary atypical fontanel can even leave an osseus scar in the temporal region.
2. Temporary canals, associated with the developing permanent premolars, appear in the maxilla and mandible.
3. A well defined biomechanical supporting pillar forms internally in the skull of the buffalo. It conveys pressure from the lingual side of the caudal molar alveoli, to the ipsilateral external lamina of the frontal bone in the region of the frontal fossa.
4. Apart from one small external segment, fusion of the perpendicular and basal plates of the ethmoid bone to the presphenoid bone, in the region of the orbital plate, makes ethmoid-related sutures the least visible sutures to see in all post-natal stages.
5. The retro-orbital position of the cornual process, and the presence of a nasoincisive suture, are some of the osteological features that are shared with the domestic goat.
6. Pneumatization of the nasal bone and dorsal concha may occur, as well as of the tympanic part of the temporal bone.
7. The detail of the sutures other than those of the ethmoid bone, may allow "fingerprint" identification of specific bones or complete skulls. Other applied aspects of the skull may be of importance to hunters and clinicians.

OPSOMMING

Die Osteologie van die bene van die Gesig en Kranium van
die savanne buffel *Syncerus caffer caffer* (Sparrman, 1779)
deur

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Dierkundig word die savanne buffel geklassifiseer onder die Bovini Tribe. Osteologies verskil die skedel van dié van die water buffel van Asia onder andere daarin dat die vomer nie met die verhemelte been van die monddak artikuleer nie. Hierdie studie in die makro-anatomie gee ’n gedetaileerde beskrywing van al die bene van die skedel, mandibel en hyoid apparaat van die savanne buffel *Syncerus caffer caffer* (Sparrman, 1779). Alhoewel hierdie bene in vele opsigte ooreenstem met dié van die gedomestikeerde bees, veroorsaak die ru-heid van die buffel se skedel baie verskille. Sommige daarvan is uitgesproke en van anatomiese belang. Die som-totaal van die verskille gee aan hierdie skedel ’n tipiese marko-morfologie wat dit onderskei van die ander genera in die Bovini Tribe. Ander belangriker kenmerke wat gevind was, is dievolgende :

1. Die skedel van jong diere behou vir ’n lang tyd hul basiese embriologiese vervormingspotensiaal. In die mandibel word dit gesien as oorblyfsels van Meckel se kraakbeen, en in die skedel as uitgerekte remodellering in gebiede van die oog, die neus, en mees opmerklik, in die laterale wande van die kranium. Gevolglik kan ’n verbeende letsel gelaat word in die temporale gebied weens ’n tydelike atipiese fontanel.
2. Geassosieerd met die ontwikkeling van die permanente premolare, kom tydelike kanale voor in die maksilla en mandibel.
3. ’n Goed gedefinieerde biomeganiese ondersteunings pilaar ontwikkel intern in die skedel van die buffel. Dit herlei druk van die linguale kant van die koudale molare alveoli, na die ipsi-laterale eksterne lamina van die frontale been in die gebied van die frontale fossa.
4. Behalwe vir een eksterne deel, is die versmelting van die perpendiculare en basaal plate van die ethmoid been met die presphenoied been, in die gebied van die orbitale plaat, intiem. Dit veroorsaak dat ethmoid verwante nate die moeilikste nate is om te visualiseer in alle post-natale stadia.
5. Die posisie van die horing proses agter die oog, en die voorkoms van ’n naso-incisive naat, is van die osteologiese kenmerke wat in die gedomestikeerde bok voorkom.
6. Belugting van die neusbeen en dorsale neusskulp kom voor, sowel as pneumatisasie van die tympaniese deel van die temporale been.
7. Die detail van nate, uitgesluit dié van die ethmoid been, kan “vingerafdruk” identifikasie van spesifieke bene of geheel skedels toelaat. Ander toegepaste anatomiese aspekte van die skedel mag belangrik wees vir jagters sowel as klinici.

CHAPTER ONE

GENERAL INTRODUCTION

(See figures **1.1 - 1.4**.)

GENERAL:

The savannah buffalo plays an important role in the epidemiology of various diseases prevalent in Africa. Some of these diseases may affect domestic animals [21] . Of these, Foot and mouth disease is probably the best known and most feared [18, 78 & 134] . Other diseases of veterinary importance to which the savannah buffalo of Africa either are susceptible, or can serve as carrier, are anthrax, brucellosis, tuberculosis, rinderpest, nagana and Theileriosis [19, 77, 97 & 132].

Except for solitary bulls, buffalos are typical gregarious animals [135] . The impact of healthy breeding herds on restricted areas such as a National Park, can be formidable. The biomass effect of the sum-total of animals on the vegetation of a restricted area can be determined scientifically. Precautionary steps can then be taken in management plans to control the number of animals [145] . Various options can be followed and larger numbers of excess animals can be either captured or culled according to scientific methods [17, 46 & 145] . Depending on the health status of animals, captured animals can be sold and relocated, or culled animals can be used as a source of food [57 & 152] . On private reserves, large bulls can be hunted individually, as they are sought after by big game hunters [80 & 151] . The monetary value of the savannah buffalo - especially disease free animals - became astronomically high in recent years [57] .

Considering the above only, the need for a detailed anatomical description of the head of the savannah buffalo does not appear to be justifiable. Especially, if it is only a study on the osteology of the skull. Therefore, at the onset of this study, representatives of various bodies involved with research of wild animals of South Africa, were consulted for their opinions as to which species of wild animals the anatomy might be more important to know than of others. Various opinions were weighed. Finally, motivated by a personal interest in the anatomy of wild animals of Southern Africa, and convinced by the Veterinary importance of the savannah buffalo [45] , this study on the anatomy of the head was decided upon.

INTRODUCTION:

It is firmly believed among most Veterinary Anatomists, that a description of the osteology of an animal should form the basis for any anatomical study. Ideally, it should be the basis for any scientific study of any animal, and a study on at least some aspects of the embryology should also be included. Information of the anatomy can be used not only by Veterinarians but also by Zoologists, Palaeontologists, Archeologists, Ostoe-archaeologists and hunters. A study on the osteology of the skull of the savannah buffalo - as a prime example of one of our larger Bovidae - can also fit in very well with a phylogenetic study of the evolutionary history of African mammals. Although not much has been documented on the osteology of the skulls of related fossil buffalos of Africa, or extinct relatives, the ecology and behaviour of the buffalo have been well-studied [26, 32, 33, 69, 72, 76, 88, 98, 112, 119 & 150] . Based on what is known, the savannah buffalo fits into the zoological system as follows [101 & 121] :

PHYLUM	:	CHORDATA
SUBPHYLUM	:	VERTEBRATA
CLASS	:	MAMMALIA
SUBCLASS	:	EUTHERIA (PLACENTALIA)
ORDER	:	ARTIODACTYLA
SUBORDER	:	RUMINANTIA
SUPER FAMILY	:	PECORA
Family	:	Bovidae [Cavicornia]
Sub-family	:	Bovinae
Tribe	:	Bovini

The Bovini, Boselaphini and the Tragelaphini are the only three tribes in the Bovinae Sub-family. Quoting from the key from Skinner J. D. & Smithers R. H. N. (1990) on the classification to the Bovidae family, the reasons for placing the buffalo in the Bovinae Sub-family are because "...pedal glands are absent or at most rudimentary", and because the horns of animals belonging to this Sub-family are ".... either more or less smooth throughout and present in both sexes, or spiral, usually keeled, and present or absent in females" . Also **:** The Bovini tribe is characterized by the following **:** "Size very large and form heavy; horns present in both sexes, not ridged; no face, pedal or inguinal glands; mammae two pairs; tail long and tufted; plainly coloured; no pre-orbital fossa or ethmoid fissure".

The Bovini Tribe has three genera viz. **:**

Bos - domestic cattle and the bison of Eurasia and North America,

Bubalis - the water and swamp buffalo of Asia, and

Syncerus - the buffalo of Africa. In the southern subregion of Africa, the subspecies found is the savannah buffalo *Syncerus caffer caffer* (Sparrman, 1779) [121] . This subspecies used to be referred to as the 'Cape buffalo' [72, 73 & 111] . 'Savannah' refers to the veld type in which this subspecies is typically encountered. Other non-domestic members of the Sub-family Bovinae in the southern African subregion, are the kudu, sitatunga, nyala, bushbuck and eland.

When one considers the available literature of the non-domestic large ruminants, it is significant to find that the osteology of the skull specifically, was usually excluded from studies [59 & 105] . The closest applicable anatomical descriptions that could be found, was one article on the osteology of the Egyptian buffalo, and one article on the paranasal sinuses of a *Bubalis* specie. The article on the osteology compares the skull of the domesticated Egyptian buffalo, *Bos [Bubalus] bubalis* L., with that of the native Baladi cattle breeds of Egypt [68] . The other article describes the paranasal sinuses of *Bubalus* and compares it with the domestic ox [115] . From these descriptions, and after considering some savannah buffalo skulls, it was noted that the gross external appearance of savannah buffalo skulls differs so much from the skulls of other genus types of buffalo and from the domestic bovine species (both *Bos taurus* L. and *Bos indicus* L.) that it would be incorrect to extrapolate information directly from these species. From the literature, only basic Zoological and Palaeontological information is available on the skull of the savannah buffalo. That literature lacks the detail to be of much use when an anatomical description of the soft tissue structures has to be done. Also, taking some measurements for Palaeontology in the prescribed way - as based on the bovine - cannot be applied for the savannah buffalo [143] . Thus, without applicable data on the anatomy of the skull of the savannah buffalo, a comprehensive descriptive study on the osteology could be justified. A detailed study of the embryological development of the skull in the savannah buffalo was however not undertaken to support all the gross osteological findings, as it forms a study on its own. To compensate for this, available literature on the embryological development of skulls of man and animals were therefore extensively reviewed [7, 23, 34, 51, 54, 60, 70, 84, 94, 95, 102, 106, 113, 127 - 129, 141, 146 & 154] . A limited number of young skulls of calves were however studied. Studying the skulls of these young animals together with all the others, did reveal some aspects of importance of the ontogenetic development of the skull of the savannah buffalo. These aspects are mentioned where applicable in the text and are taken up in the **Discussion**, chapter four.

FURTHER JUSTIFICATIONS FOR THIS STUDY:

The rationale for such an elaborate study as this, is based on three more criteria **:**

Firstly, one cannot properly describe the dentition, and therefore the splanchnology of the head of the savannah buffalo, if the osteology has not been described in detail yet, and vice versa. And, aging buffalo - by using the dentition without due consideration to aspects of the osteology of the skull - makes age estimates less accurate. Presently, savannah buffalo are roughly aged on various morphometric parameters such as general body size and the shape of the horns on a herd basis. And in individuals, if at all possible, also by considering essentially the protruding parts of teeth [56, 107, 125, 133 & 142] . Because of the interrelationship that exists between the teeth and the skull, the matter had to be readdressed in this study under the **Applied Anatomical aspects of the teeth of the savannah buffalo**. (See section E, chapter three.)

Secondly, the author has a personal interest in the topography of the viscera of the game animals of Africa. That interest is shared by many others, and articles on the topic have appeared not only in scientific publications but also in the lay press [47, 148 & 149] . For the African buffalo, at least one scientific publication describes the topography of the organs of the body in general [64] . Descriptions are also found of the position of the brain including a more technical one. That description appears again in a reasonably abbreviated form in this work under the section on the **Applied Anatomical aspects of the skull** [64 & 65] .(See section E, chapter three.) Big game hunters that intend to shoot savannah buffalo might find the Applied section of value and therefore the topographical aspects renders further justification for this study.

Thirdly, and purely from a Veterinary Anatomist's point of view, this study can also pave the way for a wider study of the gross anatomy of the head. Indeed, it was originally intended to include not only the osteology but also the blood vessels, nerves, muscles and splanchnology of the head of the savannah buffalo in one encompassing study. Such a complete study can eventually form a monograph on the head of this species.

Hopefully, this study on the osteology might serve as a template along which the osteology of the skulls of other non-domestic Bovini can be based.

TERMINOLOGY AND NUMERICAL SYSTEMS USED:

Except for the terms used in the section on **Craniometric data**, the terminology used in this study conforms to the internationally accepted terms for Veterinary Anatomy [53] . These terms are listed in the fourth edition of *" Nomina Anatomica Veterinaria "(N.A.V.)* ***** [1] - see the first footnote below. Although the savannah buffalo is a non-domestic animal, it is lately regarded as a game ranch animal in the African context [6, 19, 37, 49 & 99] . Therefore, even though the terminology as indicated by the *N.A.V.* is almost exclusively compiled for use on domestic animals, it could and should be used by all disciplines when non-human anatomy is described. Many terms are in use by Zoologists and Palaeontologists and have in fact been used in earlier publications [105, 115 & 121] . It is understandable however that due to the large size and the well defined osseous components of the skull of the savannah buffalo - or even other wild animals for that matter - one can expect to find many imperfections in the *N.A.V.* terminology as it is now. Additional terms have been proposed previously [115] and many others terms are also

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1 A copy of the *N.A.V.* can be obtained from **:** The Dept. of Anatomy, College of Veterinary Medicine, Cornell University, Ithaca, N.Y. 14853. (See **Frewein J., Habel R.E. & Sack W.O.** under **List of References**.)

proposed in this study. For example, in the savannah buffalo, particular bones involved in different sutures - or aspects pertaining to it - cannot adequately be described by using existing terms and explanations alone. That is because the existing official terms deal with much smaller domestic animals that do not present such grossly enhanced characteristics of so many osseus structures as the savannah buffalo of Africa. Therefore, standard *N.A.V.* terms that are either confusing, or that could cause severe misinterpretations, are indicated by an asterisk that is followed by a footnote number ***** [2]. Explanatory comments on the specific term, are then made in that particular footnote. Similarly, structures that are found in the savannah buffalo but which are totally lacking in the standard *N.A.V.*, are addressed by allocating terms. These newly allocated terms are also explained under footnotes. The asterisks and the footnote numbers are in **superscript** and **bold black**. All the footnotes in the text are numerically numbered from 1 to 191, and forms one of three numerical systems that is used in this text (vide infra).

To encompass many problems in the semantics of descriptive osteology, a specific numerical system was introduced for the nomenclature of existing and newly introduced terms in this work, to assist all readers with the complexity of the subject. In line with the approach of the *N.A.V.*, the main bones that make up the cranium and those that make up the facial part of the skull, are orderly arranged in 22 subheadings in this study. Then, each term that is used to describe an osteological feature, is allocated the same number as the specific subheading of the skull bone under which it falls. The subheading numbers for this numerical system of all the terms, are typed in **bold red** and in the same font size as the rest of the text. The official term linked to this numerical system, appears in *italic* font, and starts with a capital letter. Official terms are always preceded by the Anglicised term which in turn is printed in **bold black**. The order in which terms appears in that particular subheading, is further denoted by another numerical system shown by a superscript number. The subheading number (in **bold red**) and the superscript number (not bold typed or red lined), therefore relates each term that

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2 Terms that do not appear in the *N.A.V.* but which are in general use by anatomist, are also marked by an asterisk ***** throughout the text. The meaning of terms indicated by an asterisk only, are generally well known despite the fact that they are not listed as such in the *N.A.V.* They are therefore not discussed further under footnotes, except where really necessary. Those readers who are unfamiliar with both the official and the unofficial terms used in Veterinary Anatomy, should consult the **Glossary of terms** at the end. Each term taken up in the Glossary is described by a short definition, and asterisks clearly differentiates the unofficial from the listed *N.A.V.* terms.

describes a structure, not only to the specific bone of the skull it belongs to, but also to where it is discussed in the context of that particular subheading. In cases where terms need further subdivisions, these subdivisions are denoted by dash signs. If that needs further clarification or subdivision (only three exceptional cases), it is denoted by alphabetic letters. These exceptions - printed here in a condensed form - can be used to explain the system : **7**$^{41`` \mathbf{a\ \&\ b}}$, **7**$^{41``` \mathbf{a\ \&\ b}}$ and **11**$^{3` \mathbf{a,\ b\ \&\ c}}$.

Official terms are printed in *italics* only once, and that is under that specific subheading where that official term is used for the first time. Elsewhere, when reference is made to that same term (structure) under other subheadings, the number (and superscript number) is printed in ordinary fonts. It is then usually preceded just by the Anglicized term. Or, the number (and its superscript number) can either follow or precede the official term (in ordinary print) when the Anglicized term is not specific enough. This numerical system for all the terms should be used to link related aspects throughout the text as it functions as an index. In cases where official *N.A.V.* terms are amiss, the best suitable Anglicised term is used and numbered. That number is then also printed in **bold red** and once only. Other categories of structures are those for which non-official terms do not exist, and where even Anglicised terms would be either unsuitable or inappropriate. These structures also have to be identified. That is done but then only by a number (in **bold red**) with a superscript number. This has to be done because it also gives identity to those (unnamed) structures and secondly, to be able to explain it where necessary under a footnote. Because structures in the last category are described - or at least having a number allocated to them, and given a numerical 'place' in the text - they can be referred back to from elsewhere in the text by just using the number. Printing the numbers in bold red not only increases the visibility of all the numbered terms when perusing the text but also helps one to find non-official terms or unnamed structures, as they never appear in italic fonts. Only in exceptional cases was it necessary to allocate two different numbers to one and the same structure. Such duplication only occurs in the following eight instances **:**

- **(a)** the major palatine canal (numbers 13^{33} and 19^{21})
- **(b)** the osseus nasal septum (numbers 11^{14} and 13^{11})
- **(c)** the supraorbital canal (numbers $10^{22`}$ and 13^{29})
- **(d)** the infraorbital canal (numbers 13^{32} and 16^{28})

(e) the ethmoidal foramen (numbers 11[12] and 13[27])

(f) the interalveolar margin (numbers 16[4] and 21[15])

(g) the infraorbital margin (numbers 15[10] and 20[4])

(h) zygomatic arch (numbers 1[8] and 20[1]).

Although avoidable, this duplication occurred during the compilation of the text, as *Nomina* also lists these structures in more than one place. It is understandable that terms for the nasal, orbital and palatine surfaces in the different regions of the skull - to which more than one bone can contribute - may become duplicated.

In two exceptional cases, it was found best not to conform to the heading under which the official term is placed in *Nomina*. In those cases, the term was used in the italic font in the subheading where it seemingly belongs best **:**

(a) In the *N.A.V.*, the *Processus tentoricus* is listed under the parietal bone. In this study, it is listed under the interparietal bone because it seems justifiable not to consider it as part of the parietal bone, but as the remains of an interparietal bone. This was done even though no embryological study was done to confirm the ontogenetic development of this process.

(b) The auditory ossicles are discussed in a subheading of their own, following that of the temporal bone, and not under the sensory organs as in *Nomina*.

Attention must be given to the way the terms themselves (and not the numbers) are shown **:** Anglicized terms are always used directly before all official *N.A.V.* terms. Only Anglicized terms that precede official *N.A.V.* terms (in *italic* fonts), are printed in **bold black**, but are not bold typed elsewhere. Terms in *italic* are always used in the singular declension. However, in some rare instances, the plural is used to indicate that the structure is always either paired or multiple. In those cases, both the Anglicised term and the official term are then used in the plural, for example the intrasinal lamellae of the frontal sinuses (9[12]), or the paired ethmoidal fossae (11[10]).

The fact that the bones of the skull can be either paired or unpaired bones, needs special consideration when interpreting the text **:** When an aspect of a paired structure is considered, only that part on the one side is discussed at a time. Yet the reader has to realize that both **antimeres** (right and left opposites) are mirror images on either side of the median plane. And automatically, both are actually referred to even when just the one is discussed. Rarely however, the antimeres on both sides of the median plane have to be considered together when they form a single concept. Those instances are clearly pointed out to the reader in the text. Logically, in the case of unpaired structures - which lies on both sides of the median plane - the two halves of that structure are then considered as the antimeres.

The complexity of the sequence of events along which this study progressed, and the subject matter (the skull, being a product of ontogenetic development that occurred before), dictates that the text is written in the passive voice. The fact that the antimeres of paired and unpaired structures have to be described the whole time, supports a passive voice approach too.

Square brackets [-] indicate terms that have fallen into disuse. Although some of them might sound more familiar, or are linguistically more correct, or could explain something better, they should preferably not be used. Four square-bracketed terms are used in this text because of their convenience **:** They are the [neuro-]cranium, [viscero-]cranium, the [hyoid bone] and [prae-]sphenoid(-ale). In the case of the hyoid and the prae-sphenoid bones, the brackets have fallen in disuse, and the latter term is conveniently also converted just to presphenoid / presphenoidal / presphenoidale / rostrum presphenoidale, whatever the case may be. In many instances in this text, the term [prae-]sphenoid / [prae-]sphenoidal /[prae-]sphenoidale is preferred, when some more emphasis on the rostral part of the presphenoid bone is intended. Therefore, in this text, both these variations for the presphenoid and the rostrum presphenoidale are interchangeably used.

Terms listed in the *N.A.V.* are not applicable for all the different domestic animals. Therefore, not all the listed *N.A.V.* terms would be encountered in this study, purely because some of the structures are not found in the skull of the savannah buffalo. These should not be interpreted as omissions as it is unlikely that any structures have been completely missed in this study.

TERMS AND PLANES, POSITION AND DIRECTION, CRANIOMETRIC ASPECTS, THE GLOSSARY OF TERMS AND THE FOOTNOTES:

THE DATUM PLANE AND OTHER TERMS THAT INDICATE POSITION AND DIRECTION:

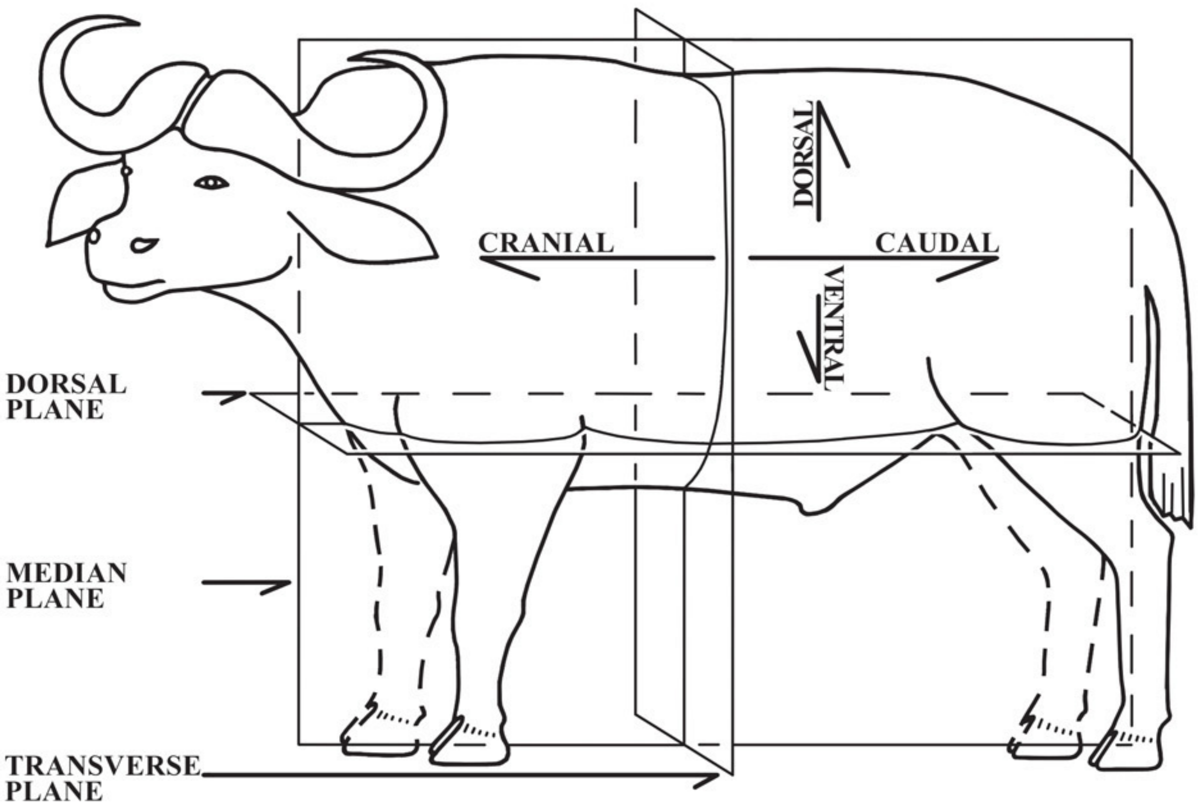
Terms that indicate topographic orientation or various planes, and direction, are according to the *N.A.V.* and standard anatomical usage. The "datum plane" however is not listed in the *N.A.V.* but is a convenient term taken from human anatomy [8]. It needs to be addressed at this point **:**

The **datum plane** for the skull of the savannah buffalo has to be established first because the spacial orientation of a prepared skull - as a scientist would have it on his or her table - is not necessarily the same as the head is kept in the living animal. The datum plane is determined by placing the skull (with or without the mandible) on a horizontal surface. The longitudinal axis of the skull is afterwards determined by drawing an imaginary line from the centre of the apex of the skull caudally, to intersect the caudal aspect of the skull on a median point. In the case of the savannah buffalo, the skull must be adjusted so that the line comes to lie parallel to a second line that lies horizontally on the dorsal level of the nose or nasal bones. With the skull tilted - in order to meet the prerequisite that both lines have to be horizontally oriented - the first line would then form the horizontal axis of the skull. The spacial orientation of the skull would then be in the required **datum plane**. Figures 1.1 - 1.4 should be studied (vide infra).

It has to be noted that the longitudinal axis has to be distinguished from the axis of the skull base. It must also be noted that the concept of the datum plane has to be properly understood to interpret the use of the orbital axis under the **Applied Anatomy** section. (See figure 3.74.) The introductory illustrations supplied in the text become very helpful also for the non-anatomists, especially when reading the section on the **Applied Anatomical aspects** at the end.

FIGURE 1.1 : INTRODUCTION

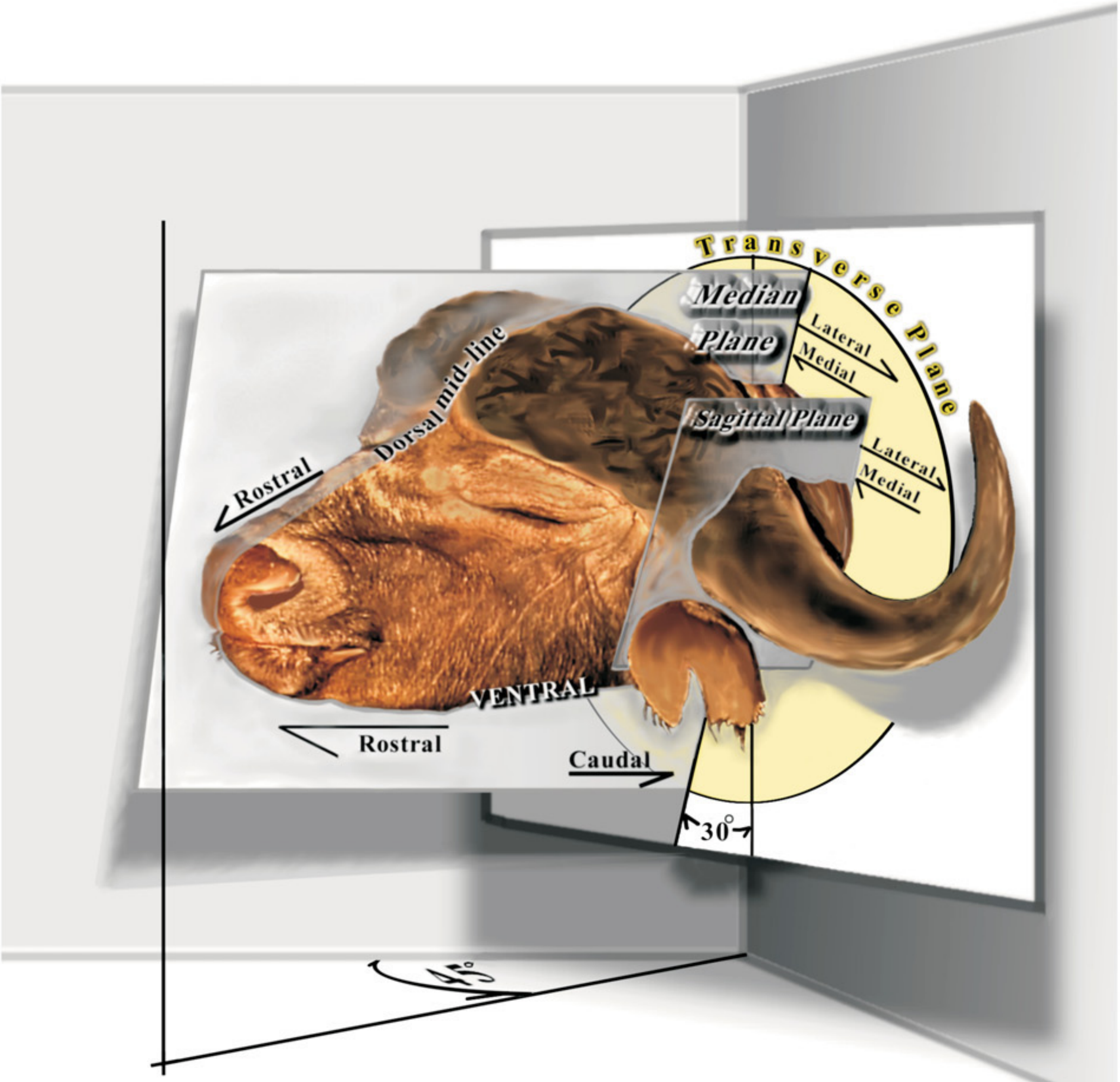
PLANES AND DIRECTIONAL TERMINOLOGY FOR USE IN TOPGRAPHICAL ANATOMY :
THE ANIMAL IN THE NORMAL STANDING POSITION



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 1.2 : INTRODUCTION

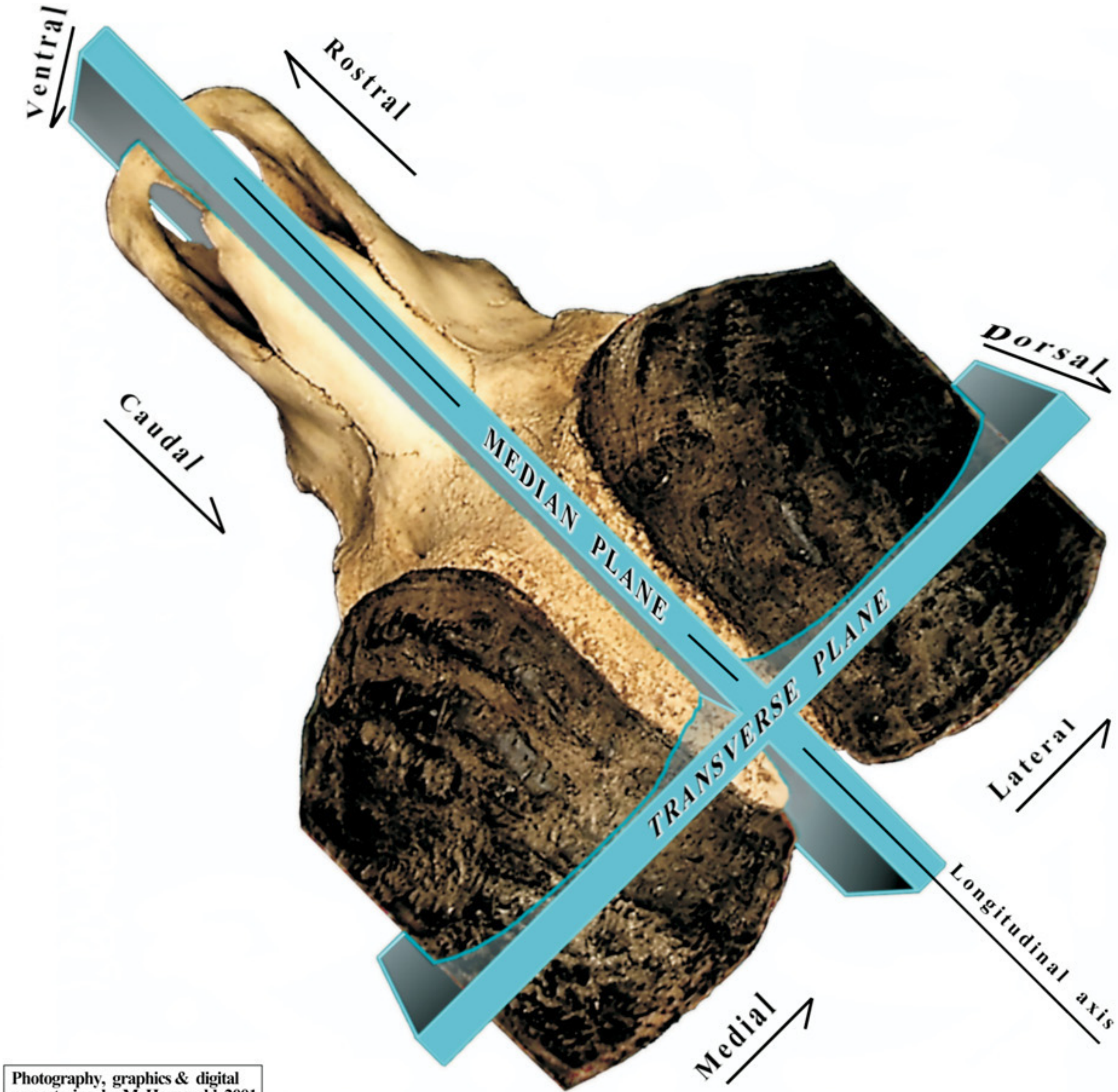
PLANES AND DIRECTIONAL TERMINOLOGY FOR USE IN TOPGRAPHICAL ANATOMY :
THE HEAD OF THE SAVANNAH BUFFALO IN OBLIQUE ROSTRAL VIEW



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 1.3 : INTRODUCTION

PLANES AND DIRECTIONAL TERMINOLOGY FOR USE IN TOPGRAPHICAL ANATOMY :
THE SKULL IN DORSAL VIEW



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 1.4 : INTRODUCTION

PLANES AND DIRECTIONAL TERMINOLOGY FOR USE IN TOPOGRAPHICAL ANATOMY : MEDIAL VIEW OF THE SKULL IN THE DATUM PLANE, INDICATING AXES I - III, THE LONGITUDINAL AXIS, AND ANGLES FORMED BETWEEN AXES

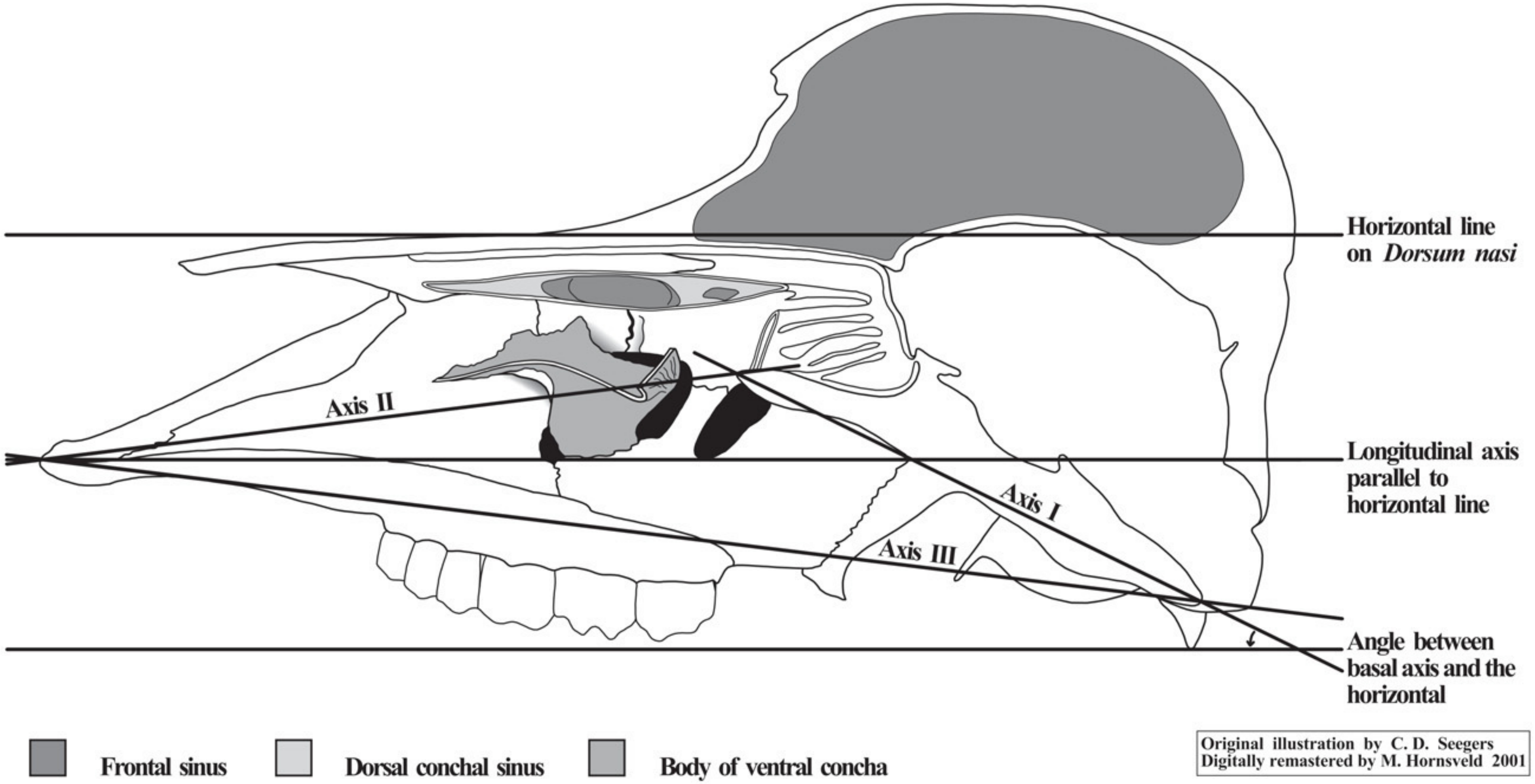


FIGURE 1.4 : INTRODUCTION

PLANES AND DIRECTIONAL TERMINOLOGY FOR USE IN TOPOGRAPHICAL ANATOMY : MEDIAL VIEW OF THE SKULL IN THE DATUM PLANE, INDICATING AXES I - III, THE LONGITUDINAL AXIS, AND ANGLES FORMED BETWEEN AXES

GLOSSARY OF TERMS, CRANIOMETRIC ASPECTS, AND COMMENTS ON THE FOOTNOTES:

It is realized that terms commonly used by Veterinary Anatomists to indicate position and direction, needs to be defined for those who are not so familiar with these terms. Also, terms used in the section on **Craniometric data** (vide infra), can be foreign even to many Veterinary Anatomists. Therefore, apart from all the illustrations, a **Glossary of terms** is included right at the end.

Ideally, when reading the text of any anatomical study, the *N.A.V.* should be consulted on a continuous basis. Usually, only purist Anatomists would do that. In this work, because the Anglicised terms for anatomical structures are descriptive enough, and having a Glossary at the end, it is not necessary to have the whole *Nomina Anatomica Veterinaria* available for every reader when perusing this work. In the Glossary, terms used in the section on the **Craniometric data** (those that do not appear in the official Veterinary Nomenclature), as well as other non-official terms found elsewhere in the text, are indicated by an asterisk (*). The system by which these terms are indicated, is therefore the same as in the 22 subheadings under section A (chapter three), except that the terms - in section A - are further explained by numbered footnotes. The section on the Applied Anatomical aspects of the skull specifically, would be difficult to understand for the uninitiated without the help of a **Glossary of terms**.

In the Glossary of terms, and in the section on the **Craniometric data**, the following additional comments on terms and footnotes should be kept in mind **:**

To distinguish the network system of **bold red** numbered terms - indicating *N.A.V.* terms, non-*N.A.V.* terms and all other numbered structures - the terms for **Craniometric data** are indicated by a hash sign # * [3] but are not numbered. This distinction is made because these terms are used mostly by Palaeo-anatomists and often they are used in the abbreviated form only, as is apparently customary in that specialized field (vide infra). Also in the **Craniometric data** section, proposed additional measurements - as suggested

3 Osteo-archaeological terms for specific use in the subheading on **Craniometric data**, are marked by a hash sign # because they do not appear in *N.A.V.*

by this author - are indicated differently by using the typographic sign - § * [4] .

Some basic terms in everyday use among Veterinary Anatomists - that are also not listed in the *N.A.V.*, but which are handy terms - are marked just by an asterisk in the Glossary as in the text.

Official *N.A.V.* terms in the section on **Craniometric data** (and even in the Glossary if it is used there for the first time) appears in italics in exactly the same way as in the text (section A). New terms proposed in this text (as discussed in the footnotes under the specific subheadings where they belong best), are not taken up in the **Glossary of terms**.

To make it more convenient for those who read the text, even lengthy footnotes are sometimes duplicated instead of referring the reader back to the original footnote where the topic was discussed first. Rather repeating a footnote, is also deemed necessary in many instances, because a slight shift in emphasis is sometimes needed even though the wording of footnotes covering that same topic, might seem the same. A **List of footnotes** is provided at the beginning of this work.

PROBLEMATIC DESCRIPTION OF THREE-DIMENSIONAL STRUCTURES:
THE NEED FOR A PARADIGM SHIFT AWAY FROM CONVENTIONAL APPROACHES**:**

The sizes of the paranasal sinuses of the skull of the savannah buffalo are in proportion to those parts of the skull in which they are found. In the savannah buffalo, the paranasal sinuses and the enclosed spaces in the conchal bones, are relatively much better developed than in other small and large domestic ruminants [87 & 147] . Therefore, the external and internal layers of the skull bones in which they occur are further separated. This plays a determining role in the perceived "thickness" of the skull bones, especially if one realizes that the size of a full grown savannah buffalo skull, can be up to half a metre long. The extent to which skull bones (and conchae) are pneumatized, and to which the inner and the outer layers of a bone are

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[4] Additional terms proposed by this author for used in **Craniometric data**, are marked differently - § - because they also do not appear in *N.A.V.*

dispersed from each other, calls for additional terminology as well as unconventional approaches to improve three-dimensional concept formation for readers. Additional terminology and an unconventional approach is needed in order to grasp not only the topography of the sinuses but also the different facets of the bones that are involved in suture formation. Typically, three facets or parts of each bone, are involved in sutures between pneumatized parts of skull bones. These parts are the internal and the external lamina, and the third part - often referred to as the partition or septum in this work - that connects the former two parts (layers). The partition 'adheres' to the similar partition (or septum) of the adjacent bone to form the suture. What is more, is that even in non-pneumatized parts of the skull, hardly any suture can be regarded simply as either "flat" or "serrated" in the traditional two-dimensional meaning of the term. The concept also of "squamous" bones gets a total new meaning when one considers the bones that make up the roof of the skull of the savannah buffalo. Thus, additional terms - some of which are proposed in this work, others not yet even thought of - might condense lengthy explanations. The following is an example of such a problematic case to describe the real situation of all the facets involved **:**

> The lamina externa of a bone like the maxilla, has a large external surface (which forms the facial surface of the facial part of the skull) but it also has an extended internal surface (that is of that same lamina), which lines the maxillary sinus on the lateral side. The internal lamina of the maxillary bone also has an "external" surface - which lines both the nasal cavity and the oral cavities on the inside - as well as an internal surface that is almost as elaborate, lining the maxillary sinus medio-dorsally and medio-ventrally.

Therefore, a clear distinction should be made between the different surfaces of each lamina, as they rarely remain supported by spongy bone, not even at the partitions or septa between adjacent bones and adjacent sinuses. The following serves as good example as it follows the previous example well **:**

> The suture (the partition or septum) between the palatine process of the maxilla and the horizontal part of the palatine bone, is approximately 25 mm "thick". That is because the

palate as a whole, is greatly pneumatized. A major part of this suture - consisting out of two such partitions or septa - separates the two components of the palate. The suture therefore appears as a double layered septum that extends between the nasal and oral surfaces of the palate. Each septum consists of compact bone, and also has two sides **;** one side faces the suture and therefore the septum on the other side of the suture, as well as having a free inner surface that faces the sinus.

The traditional meaning of an infraorbital canal, cannot be applied in the case of the savannah buffalo. That is because spongy bone is absent between the internal and the external lamina over large areas, due to the large sinuses. Why a paradigm shift away from conventional approaches is needed, can be seen clearly when the infraorbital canal is considered. It also follows the previous two examples well **:**

The inner aspect of the infraorbital "canal" - that part which is traditionally understood when one refers to this canal - is surrounded by a tubular wall that exists on its own, i.e. it is not embedded in spongy bone. Due to this fact, and due to it connecting the pterygopalatine fossa at the one end and the facial surface of the skull at the other end, the outer surface of the "canal" can also be seen when the maxillary sinus is opened. When seen from within the sinus, the "canal" lies as a separate entity in the maxillary sinus as a pipe-like structure because it is not embedded in spongy bone. It is of such a magnitude that it even plays a role in mechanically strengthening that region of the skull. This "canal" is therefore much more than just an intra-osseus conduit that conveys nerves and blood vessels from the pterygopalatine fossa to the facial surface of the maxilla.

The above examples should stress the need for a paradigm shift - especially in the minds of small animal Anatomists - to realize just how much different the skull of the savannah buffalo is. Without regard for these tricky three-dimensional aspects, the reader probably cannot comprehend all the implications of what is described in the text. The concept of "antenasal", and "antepalatine" surfaces are introduced under the palatine and zygomatic bones to elucidate such descriptive problems as discussed in the above. (See footnote 147 under the palatine bone, and 20[9] under the zygomatic bone.)

THE NEED FOR A PARADIGM SHIFT AWAY FROM CONVENTIONAL TERMINOLOGY:

To accommodate a larger audience but also to put purist Veterinary Anatomist at ease, the following has to be said as it differs rather from Veterinary Anatomy convention **:**

In this text, it is generally stated that a bone is 'fused' to another bone at a suture and not that it articulates with another bone. (Not included in this generalization, are the articulations between the bones of the hyoid apparatus. These articulations, as well as the temporo-mandibular joint, will be addressed further below.). However, 'fused' does not always mean that these sutures are ossified yet. But, because in most cases the sutures do ossify later in life, it is better to use the term 'fuse' instead of 'articulate', as it should strictly be. The reason for preferring the term 'fuse' is also because some of these sutures - or at least part of them - can permanently or temporarily be incomplete to form permanent or temporary fissures. Or, part of a suture might also incorporate a fontanelle which can involve "defects" of ossification of cartilage. What is more, is that these "defects" can even enlarge temporarily. Obviously, neither the term 'fuse' nor the term 'articulate' would describe these situations exactly. Therefore, when a suture (or part of a suture) ossifies earlier or later than expected, it is specifically mentioned in the text. When a suture does not ossify as expected but rather forms a temporary or a permanent fissure, or a fontanelle, it is also clearly stated. Temporary fissures or fontanelles may eventually fuse completely by ossification, or remain incompletely or only partially fused to the complementary bone or bones. Such variations to the theme are explicitly mentioned. But because so many permutations of the final outcome may occur, the term 'fuse' is used initially. Afterwards, details are then given as to the different phases through which the suture can go. Thus, when bones 'fuse' to other bones as it is used in this text, it infers the following **:**

- **(a)** Typically, a bone starts off by 'articulating' with another bone at a suture. Then eventually the two bones fuse with each other to such a point where no suture between the original bones remains at all. It has therefore 'fused by complete ossification' by the time maturity is reached. This is the default meaning of 'fuse'.

Or, one or more bones can 'fuse' to others at a suture, meaning to **:**

(b) 'articulate' via an un-ossified cartilaginous part, to ossify only partially in late life, or never in a complete way. In other words, it remains in 'articulation' with the other bone via cartilage. This is also the traditional meaning of 'articulate', and also the meaning for which this term is reserved for in this study. It therefore 'fuses' in the sense that it remains in articulation or partial articulation, via a cartilaginous interface. As stated before, what 'fuse by articulation' obviously exclude, are the true synovial joints between some components of the hyoid apparatus, as well as the temporo-mandibular joint.

Or, 'fuse' can mean

(c) a bone 'articulates' at a specific suture with another bone or bones that form the other complement of the suture, but in an incomplete or aberrant way, to result in either a temporary fissure, a fontanelle, a temporary atypical fontanelle, or a permanent fissure. In the latter case, no cartilage is involved at all, and no fusion by ossification ever takes place. In the case of an atypical fontanelle, the amount of cartilage actually increases temporarily before it ossifies (partially, completely, or in an aberrant way) with age.

The terms 'fuse' and 'articulate' must be distinguished from yet another term namely 'unite'. Fortunately, 'unite' is rarely used, and then only with a special purpose in mind in this text **:**

(d) For descriptive purposes, it is sometimes necessary to describe different parts (usually surfaces) of the same bone separately and in different paragraphs. Describing different parts of the same surface in such a way, are only for the ease of the description. That occurs typically when two surfaces of the same bone lie in two different planes. Where these different parts are actually ongoing with one another, it will obviously occur along an imaginary line. As contradictory as 'unite' may sound, 'to unify' two parts and surfaces of a single bone in this way, helps to surpass a technical problem in the semantics of detailed descriptions where no suture or fissure of any kind is involved.

The different bones of the hyoid apparatus 'articulate' and 'fuse' by means of all possible types of articulations as found in Veterinary Anatomy. These include synchondroses (cartilaginous joints), true synovial joints, lose fibrous joints, dense fibrous joints (syndesmoses) or even fibro-cartilaginous joints (symphyses). With one possible exception, synchondrotic joints - not just of the hyoid but of other bones of the skull too - ossify later in adulthood, forming synostoses as are expected. Examples found in the skull are the synchondrotic ‘articulations’ between the bodies of the occipital, sphenoid and presphenoid bones. (See subheading 2, 4 and 5 respectively.) Syndesmoses and symphyses of the hyoid and skull bones do not ossify. However, what is unexpected, is that what appears to start off as a loose fibrous joint between the ceratohyoid and the epihyoid of the hyoid apparatus (see subheading 22), clearly becomes a true synovial joint later in life. The various permutations of ‘articulations’ that occur between the components of the hyoid apparatus, therefore clearly differ from the general pattern [25, 55, 101 & 114]. That also prompted the unconventional approach to use the term ‘fuse’ instead of articulate. The intermandibular joint is the one possible exception referred to in the above of a synchondrosis that may not fuse by ossification. If it does ossify, then it is only partially so, and only late in life. The temporomandibular joint is an example of a typical synovial joint that articulates in the true meaning of the word.

USING THE ILLUSTRATIONS AND THE TABLES:

Ample illustrations are provided in the different chapters because it is a well-known fact that anatomical descriptions are notoriously difficult to follow. Low readability of anatomical text is an unavoidable consequence of the three-dimensional nature of the work. It must therefore be comprehensible that descriptions of anatomical structures are more difficult to read than story books. In this case of the savannah buffalo, an additional fourth dimension has to be taken into account too. The fourth dimension, is the reshaping that takes place in the morphology of the skull as the animal ages. One prime example to consider, is that of the cornual process. In young animals, the cornual process starts as a small structure, but eventually it becomes a massive part of the skull. This reshaping (the fourth dimension), is also sexually linked, which complicates the whole matter.

Figure 1.1 means the first figure in chapter one. Figure 4.4 means the fourth figure of chapter 4. The numbering of illustrations under chapter 3, follows the same rules, except that they are further denoted by the sections in which the chapter is divided **:** Section A deals with the **Osteology**, section B is for **The Skull as a whole**, C for the **Skull cavities**, D for **Craniometric data** and section E for the **Applied Anatomical Aspects**. Ideally, it would be best if the text could be studied in conjunction with actual specimens that are marked. Modern audiovisual aids would also obviously make it easier, but such aids falls beyond the scope of this study. Relevant figures are referred to at the commencement of each chapter and each subheading. The most relevant figures referred to, are marked in bold.

By convention, illustrations are left views of anatomical structures, looking at the left side of for instance the skull or the particular bone. Or, - as it is done in this study - if it is a median section of the skull, then the right half is illustrated in left view. A **List of illustrations** is provided at the beginning of this work.

Although it is impossible to annotate every structure in the illustrations, it has been done in such a way that a reader equipt with a basic but sound knowledge of anatomy should be able to follow the text. Only six structures are not visible and could therefore not be annotated in any of the illustrations. In the text, they are marked 'not illustrated'. They are the following **:**

- **(a)** An enlarged fourth endoturbinate (11 [26]). Although the normal fourth turbinate is shown, the enlarged one could not be illustrated. To do it would require another illustration.
- **(b)** The large central foramen (10 [22]) that leads to the supraorbital canal. (Although the foramen is visible in figure 3.78, it is not annotated there because that figure does not fall under the descriptive Osteology section.)
- **(c)** The small but permanent lacrimoethmoidal fissure (15 [14']). This fissure can only be seen after all the ethmoidal conchae have been broken away. The position of the fissure - where it would occur on the lacrimoethmoidal suture (15 [14]) - is however shown in figures 3.37 & 3.40.
- **(d)** The facial crest (16 [7]), as seen in lateral view in old bulls, when it is more prominent.

(e) The medial ridge ($16^{21`}$) on the nasal surface of the maxilla.

(f) The intermediate ridge ($16^{21``}$) on the nasal surface of the maxilla.

It is recommended to use the numerical system - under all the subheadings of section A - as a cross-linking method, in order to make the descriptive, illustrated and systematic anatomy easier to follow.

Tables 3.1 to 3.4 summarize the findings of the **Craniometric data** and the Applied anatomical aspects of the dentition of the savannah buffalo.

RATIONALE FOR A SECTION ON CRANIOMETRIC DATA:

INTRODUCTION:

Craniometry used to be part and parcel of anatomical descriptions of the skull of domestic animals [30]. Unfortunately however, this practice has fallen into disuse for many years despite the fact that Craniometry is a well-established section in descriptive human anatomy [144]. In the meantime, Palaeontologists and Zoologists have been making use of this descriptive technique with much success. Recently, some attempt was again made by Evans (1993) to highlight the essentials of canine Craniometry for use by Veterinary Anatomists. In that work, more emphasis is put on the differences between dolichocephalic, mesaticephalic and brachycephalic dogs, than on pure osteomorphology per se. However, it does illustrate the beginning of the return of the practice into Veterinary Anatomy. Standard Osteo-archaeological terms from Palaeo-anatomy as well as some terms from human Craniometry - most of which do not appear in the *N.A.V.* - had to be adopted and adapted for this study [8,51 & 144]. The standardized method for analysing the skull and mandible of the domestic Bovine as described by von den Driesch (1976), is used as basis in this study. The advantage of a chapter on **Craniometric data** for this study, is that it would make the information on the gross anatomy also available for comparison to other large ruminants of the Bovini tribe and can serve as basis for other studies on Osteomorphology [103 & 105]. The results of the **Craniometric data** are condensed in tables 3.1 - 3.3.

RELATIVE VERSUS ABSOLUTE SIZE**:**

Morphological variations among the different breeds of domestic animals are known to be great, with the variations in size and shape among domestic dog breeds probably the widest of them all. Buffalo is said to have the greatest intra-species morphological variation among the wild mammals of Africa [121] . Because intra-species morphological variation also appears to be reflected in the skulls of the savannah buffalo studied, it was deemed necessary to distinguish between relative and absolute sizes **:**

To give some relevance as to the massiveness of the skull of the savannah buffalo, and to the absolute sizes of a few structures, dimensions are given at various places in the text as part of the anatomical description, as well as in the section on the **Craniometric data**. Various criteria were originally used to determine the age estimates of the animals when they were collected. Of these, the eruption and wear of incisors were probably the most important. In the case of immature and mature animals, body size was also important. And in animals of all ages, other external features of the head, such as the size and shape of the horns, were heavily relied on [107] . Even though all these criteria were considered, it became apparent in this study that the growth rates of young savannah buffalo could vary a lot. Despite the fact that many of the skulls used for this study was also sculptured to expose the teeth (to determine the ages more accurately), the ages - and therefore the skull sizes - are not absolute values. That is because the exact birth dates of none of the animals are known.

A condensed section on basic **Craniometric data** of some specimens used in this study was therefore added to accommodate the size aspect of the skull of the savannah buffalo. (See section D.) It is written according to standard palaeontological prescriptions as stated above [143] . Incorporated into that section are also some new measurements or new approaches, that was found to be necessary to suit the specific needs of the savannah buffalo.

It must be noted that the dimensions of the skulls used for the Craniometric section, is included to assize the material that was used in this study only. It is therefore not intended to serve as reference for a complete morphometric or osteo-archaeological study on the skull of the savannah buffalo. A detailed study on that topic should rather be done by specialist Archeologists, Palaeontologists or Zoologists, or by a multi disciplinary team of experts and on a larger sample. The Craniometric section was also intended to widen the scope of readers beyond the field of Veterinary Science. Thereby, this study can accommodate other specialists into this more modern approach of a detailed gross anatomical description, as approached by a Veterinary Anatomist.

Of possible importance to some readers might be the length of the cornual process, which was omitted for one good reason only, and that was not to damage the prime specimens of adult skulls that happened to be used in the Craniometric section. Obviously, overall horn length and the length of the cornual process are related to each other, but it is not the same thing. The lengths of the horns are not generally recorded by Anatomists and therefore falls outside the scope of this study, especially because there is more than one standard or method to measure horn lengths as used by trophy experts [57 & 138]. Furthermore, because National and International hunter associations keep records of maximum horn lengths, there is no need to do it in this study. The elongation of the cornual processes and the reshaping of the frontal bone are however anatomical issues. For the purpose of this study, these aspects serve as an example of disproportionate growth in the skulls of savannah buffalo. They are normal for the buffalo, and are typically associated with aging and gender. If a section on the Craniometry was not included in this study, it would have been extremely difficult for uninitiated readers of anatomy, to follow the extent of disproportionate growth in specific areas of the skull. Another example of disproportionate growth can be found in the widest point of the skull where the width of the zygomatic arch is compared to the width of the retroarticular process of the temporal bone. The tuberous enlargement of this process in old bulls has a marked effect on calculated indexes when the maximum width of the [neuro-]cranium is used as one of the criteria in the formulae.

The anatomical and the applied anatomical importance of the above aspects are also analysed in the **Craniometric data** section. It gives a more thorough perspective of the topic, and stresses the difference between relative and absolute size, some of which have more applied value than others.

SEXUAL DIMORPHISM AND INDEXING OF CRANIOMETRIC DATA:

Sexual dimorphism in skull morphology is clearly evident in this species. Gender differences of anatomical value - or aspects that might be of potential value to other specialist groups - are pointed out in the text under the 22 subheadings of section A. And obviously, it is also evaluated in the section on **Craniometric data**. Although some of these gender differences are salient, a few basic indexes could be computed for that section. However, because this study was done on a limited number of skulls, and with a different intention, the values of these indexes are questionable for any purpose other than for this anatomical study. Computing indexes based on **Craniometric data** compiled from many skulls of both genders, can help to elucidate the large intra-species variation as seen in the savannah buffalo. A detailed analysis of all the traits that show sexual dimorphism in the savannah buffalo, falls outside the scope of this study and should rather be a study on its own.

APPLIED ANATOMY OF THE SKULL OF THE SAVANNAH BUFFALO:

The **Applied Anatomical aspects** of the skull, has been incorporated into this study under section E. Applied aspects related to hunting, dentition, aging and the longevity of savannah buffalo are addressed. A dental chart for the dentition of the savannah buffalo is given in TABLE 3.4. Serious attention is also given in the **Discussion** (chapter four) to some other theoretical aspects on the skull with possible application for the savannah buffalo.

ALTERNATIVE APPROACH TO THE TRADITIONAL OVERVIEW OF "THE SKULL AS A WHOLE":

Typically, in Veterinary textbooks, the descriptive anatomy of the bones of the skull is rounded off by a lengthy review on the skull as a whole. The external configurations of the skull are then once again reviewed from all sides and the mandible and the hyoid bones are included in such an overview. And finally, the cranial, the nasal and the paranasal cavities are pondered over for a last time. In this work however, consideration to **The skull as a Whole** and **Skull Cavities** (see sections B & C) are done very briefly, as there is no need to repeat everything that has been said in the detailed description of the text. Nor does it make any sense to summarize conclusions at that point. Rather, without having done embryological studies, the **Skull as a Whole** is considered in that respect in the final chapter under the

Discussion. There, amongst other discussion points, it is speculated over whether the ontogenetic development of the skull of the savannah buffalo is in par with the norm or not. Reconsidering the embryology under the **Discussion** is necessary to evaluate the fissures, sutures, fontanelles and other differences that are found in the savannah buffalo. This was found to be necessary because these structures are just that much different from what has been described for the skulls of other large ruminants like the domestic bovine.

THREE NUMERICAL SYSTEMS ALL IN ONE:

When referring to other literature in scientific work, it is done according to prescribes rules - stemming mostly from convention - as a pattern is formed on how there has been published on the topic [1 & 109] . The references consulted for this study, are therefore listed in alphabetical order and numbered from top to bottom at the end of the text in a complete **List of references** * [5] . The numbers allocated to each cited authority, are therefore indicated in a numerical system in all chapters but that for the Results. These numbers appear in superscript and correspond to the numerical position in the alphabetical list of the references. The numerical system in superscript for cited authors has to be clearly distinguished from the numerical system that forms the network for the anatomical terms as well as from the numerical system for the footnotes. For convenience sake, the systems are once again summarized in the following paragraph **:**

> The most important numerical system is the one that was specifically introduced into this study to increase the visibility of anatomical terms by letting them stand out in **bold red** in the same sized font as the rest of the text. The numerical system for footnotes is indicated by a **number in superscript**, preceded by an **asterisk,** and both the asterisk and the number are in **bold black**. The Harvard system for authors that were cited (in superscript and bold) is not used in chapter three (Results) where the other two numerical systems are used. Therefore, even though three numerical systems are used in this work, they can easily be distinguished from each other. Terms for Craniometry (designated # or §), are not numbered and do not form an additional numerical system.

[5] The Harvard system.

SUPERSTITION AROUND THE SKULL OF THE SAVANNAH BUFFALO VERSUS SCIENTIFIC METHOD:

The following is quoted from *East African mammals, An atlas of evolution in Africa* by Kingdon (1982) when referring to the skull and horns of the savannah buffalo **:**

> "The horns are very popular symbolic trophies. As whole heads mounted on shields, or as sheaths, carved and stuffed with vegetables, earths and bits of animals, buffalo horns serve the common purpose of symbolising virility or fertility. In Buganda they are known as *jembe* in traditional witchcraft, being regarded as an appropriate home for the *mayembe* spirits which influences the success of both procreation and the harvest and so buffalo horns are a common artefact in the paraphernalia of witchcraft. However, witches and diviners do not compete over the size of their horns in the way the trophy hunters do".

Anatomically speaking, the mandible, the hyoid apparatus and the skull of the savannah buffalo, is made up of 47 different bones. That is, as they appear in the adult skull. Some of the unpaired bones could have started off as paired bones in the young embryo and if these (excluding a theoretical rostral bone in the muzzle) are all counted, they could add up to 51 bones maximally. It is better to consider the bones of the skull individually and more scientifically, than to speculate over the potential witchcraft power of the skull of this beast of Africa.

SUMMARY OF THE AIMS OF THIS STUDY:

The first and primary objective of this study, was to establish a detailed osteological description on the skull of the savannah buffalo. Also, the osteology of the skull, mandible and hyoid apparatus of the savannah buffalo had to form the basis of a descriptive study of the anatomy of the head of this species because that of the domestic bovine cannot serve that purpose. This descriptive work also has to form the basis from which Internationally acceptable terminology - not yet incorporated in the official lists - can be developed from. That would be necessary in order to suit specific needs when the anatomy of other wild animals are also described. Even though the similarities with the domestic animals are striking, and are used to base descriptive anatomy on, the dissimilarities become problematic aspects when the general gross anatomy has to be described. The anatomy of the elephant serves as the extreme example. Therefore hopefully, this descriptive work on the osteology can pave the way for a complete descriptive work on the muscles, blood vessels and nerves of the savannah buffalo.

A second aim of this study was to establish a complete reference work which can be used with ease by anyone to compare the osteology of skulls of other wild ruminants as found in Southern Africa. The numerical system for the terms was specifically introduced so that anyone with a basic knowledge of anatomy can follow the description although it remains a daunting task - even for Veterinary Anatomists - to comprehend what one sees when an unfamiliar skull is studied for the first time.

Thirdly - without having had the intention originally - it could clearly be seen from the literature that this study can also serve to bring all Veterinary Anatomists, Zoologists, Archeologists and Palaeontologists on par with International standards of the Nomenclature of Veterinary and Human Anatomy.

A fourth aim - which was only realized when the detail of the skull was exposed - was to study the development, eruption and wear of the teeth to determine the ages of the specimens more accurately as these were only estimates at the time of collection. (See **Materials and methods**.) Ideally, a study on the Dentition of the savannah buffalo could be included in a study on the osteology of the skull. That is because the teeth forms such an integral part in the development of the skull bones - more particularly the maxilla and the mandible. What is more, is that a sound knowledge on the dentition is so important in aging the specimens correctly. The dental arches are only briefly discussed under the maxilla and the mandible and illustrations on the occlusal pattern of cheek teeth are supplied. (See figure 3.44.) Apart from that, detailed aspects of the teeth have been excluded from this thesis as it is already voluminous. A purist anatomist would also know that the teeth actually - and traditionally - falls under the Digestive System. After having studied the tooth bearing parts of the skull and mandible, and after the literature on the Dentition of wild animals was studied, it was concluded that the Dentition of the larger wild ruminants could be revised, especially because savannah buffalo are commercially bred since recent years [99] . Having done all the work already, the intension is to eventually publish a section on the Dentition of the savannah buffalo.

The essence of the applied anatomical aspects - gained from this thorough study on the skull of young and old savannah buffalo skulls - was not an original aim, but it developed into a valuable part. Many of the important aspects of the applied anatomy might become sought-after information for Veterinarians and game rangers that work with these animals on farms and National Parks. Hopefully, big game hunters can also find the applied aspects of the anatomy useful.

Finally, the educational value of the detailed anatomy of an animal can be used at a higher cognitive level by specialist Veterinary Clinicians, who in zoos and Veterinary Facilities all over the world, deal with wild animals of Africa. At a more basic level, the educational value that the anatomy of wild animals may have for children, is hugely underestimated. For those who are interested in what lies underneath the skin, there are much more to an animal than taking a picture of it.

CHAPTER TWO

MATERIALS AND METHODS

(See figure **2.1**.)

INTRODUCTION:

Forty-seven heads of male and female savannah buffalos of different ages, were collected by the author for a study on the gross anatomy of the head of the savannah buffalo. The age and gender composition of the collection was based on an original protocol registered at the University of Pretoria. The protocol was compiled for a comprehensive study on the muscles, the blood vessels, the nerves, the splanchnology (including the teeth) and the osteology of the head and neck of the savannah buffalo. The original protocol (see footnote 10) required that at least eight specimens had to be studied for each of these sections. That explains why so many heads were collected. Obtaining the material had to be synchronised with yearly culling programmes as executed by the National Parks Board in the Kruger National Park. The culling programme of the Parks Board is based on sound ecological and managerial studies and executed according to strict protocols [145] . After concurrent registration of the project at the National Parks Board, the material was collected during the culling seasons of 1986, 1988 and 1992. The collection and transport of the material were subjected to State Veterinary requirements. These are essential measures to prevent the spread of foot and mouth disease virus [18,78 & 139]. The Kruger National Park supplied the accommodation during these collection times. Essential initial processing of material could also be done in the Park before transportation the material to the University.

THE CULLING PROCESS:

Briefly, the standard culling procedure for buffalo was as follows **:** A group of approximately 30 individuals was separated from a much larger herd, by using a helicopter. From the helicopter, animals are individually darted at close range. Scoline was used to initiate chemical euthanasia * [6] . Death followed due to respiratory failure within approximately

[6] Succinyldicholine

fifteen minutes [75 & 145]. Euthanasia by fatal brain shot with a large calibre rifle, was executed in cases where animals were not dead by the time that work on the darted animals had to start. Such animals were obviously automatically excluded from this study. After the death of the last animal in the group was confirmed, and the person in charge declared the area safe for all workers to enter, the throats of all culled animals were sliced. Exsanguination was standard procedure when these specimens were collected because the remaining parts of the carcasses - as well as all the other intact carcasses - were intended for human consumption. All carcasses were subjected to post-mortal inspection at an abattoir. When a carcass was condemned, it was processed into carcass meal.

INITIAL SELECTION OF ANIMALS FOR THIS STUDY AT THE POINT OF CULLING:

Animals could only be selected for this study after the culling process had advanced to the point where the animals had already been exsanguinated. Selection of the specimens was based on gender and rough estimates of age. Ages were guesstimated by looking at the size of the animals and the size and shape of the horns. The external morphological features demanded a sound knowledge of the expected size of peer group animals from the same calving seasons of previous years. Except for the animals intended for this study, the cheeks of all the other cropped animals were incised at the culling site to expose the cheek teeth also. That was done as part of an ongoing National Parks Board study on the population dynamics of the specie. The ages of animals - other than those intended for this study - were therefore more closely estimated by a person experienced in aging buffalo by also looking at the cheek teeth. The cheeks of the animals intended for this study, were not incised. That was in order to preserve the complete and intact heads for future anatomical needs. They were therefore only aged by looking at the eruption sequence and wear of the incisors (apart from the morphological features of the body). Aging buffalo on body size, horns, and teeth had been well studied in Western Uganda, Zimbabwe and in the Kruger National Park [46, 56, 107 & 133]. Studies by this author further complemented these criteria for aging. These studies were done on the various stages of development of the enamel organs of the permanent (yet un-erupted) incisors and cheek teeth. Material for the study on the enamel organs was specially collected and dissected (vide infra under ADDITIONAL SAVANNAH BUFFALO SKULLS

STUDIED). Aging on dentition for this study was compared with other studies on the eruption sequence and wear of teeth, and on the development of teeth of a variety of domestic and wild animals as well as in man [2 - 5, 10, 11, 15, 56, 58, 62, 81 - 83, 85, 86, 92, 100, 117, 118, 123 - 125, 130, 133, 140 & 142]. Only after that, could apparent conflicting age interpretations - as was seen in the material used for this study - be understood. One explanation is that the developmental stages of enamel organs - and also tooth wear in similarly aged animals - can vary a lot more than what was previously regarded as the norm. Minor age corrections could be made to some of the 47 specimens that were collected, but that did not affect this study. Detail of the study on the dentition do not form part of this thesis.

At the time of collection, individual heads were identified and discerned from others by code marks cut into the horns. The right horn was used for bulls and bullocks and the left horn for cows and heifers. An ordinary hand saw was used to cut the marks * [7]. Subsequently, each head was also labelled with a tag and tied by a rope for easier recognition. A register for all the animals was compiled and photos were taken of each individual head. The approximate age range of the animals that were collected varies between approximately two or three months to 15 years. The heads were severed from the carcasses shortly after death. The exact time of severance varied between approximately two and five minutes to twenty minutes, after which processing for preservation immediately commenced. Knives, wire saws and hand saws were used to decapitate the animals as quickly as possible. The level of decapitation was approximately at the level of the second or third cervical vertebra. The selection, decapitation and processing for embalming, took place in field conditions at a priority level lower than the culling procedure itself. Due to various other sound reasons - of which ambient temperature and safety aspects for the helicopter and its crew were but two - all procedures were done in the late afternoon. Before dusk, the author, aided by one technician, could collect and embalm a maximum of four or five specimens per day.

EMBALMING THE MATERIAL:

Embalming whole carcasses of large domestic animals by means of intravascular injection

7 Of a type used for cutting wood.

with a formalin solution - as well as other admixtures added to it - has been done since 1901 [120] . Embalming solutions and methods that have standardized over the years have been used and even developed further in this Department [22, 35, 61, 63, 71, 104 & 136] . Water buffalo too, have previously been embalmed by intravascular injection, but the chemical composition of the embalming fluid as recorded in that description cannot be approved at all [67] . Embalming only a head and neck of a wild animal with formalin, has also been described for gazelles [63] . Personal experience on embalming decapitated heads showed that one can get results at least as good - if not better - than embalming the complete corpse of a large domestic animal, euthanased and exsanguinated specially for that purpose (vide infra). The extensive collateral supply of anastomosing vessels on the arterial and on the venous side of the circulation of the head and neck region, renders separated heads exceptionally well for embalming. The technique and equipment for embalming, had to be customized further to suit the needs for the extensive field conditions in which it had to take place (vide infra under EQUIPMENT AND SETUP). Apart from the normal embalming procedures with a 10 % formalin solution, State Veterinary prescription also required a 24-hour post-fixation-submersion of the collected heads in the same strength formalin solution * [8] . The embalming

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8 The 10 % formalin solution was made up by using a saturated formaldehyde solution, quantified by the manufacturer as a 38 % solution. Being fully saturated, such a solution is regarded as a 100 % formalin solution, equal to a 4 % gaseous solution of formaldehyde. It was diluted at a ratio of 1 to 9 with tap water. It was imperative that all biological material was indeed fixed properly in formalin to comply with the State Veterinary requirements for the control of Foot and mouth disease virus. These requirements specify that specimens (savannah buffalo heads) had to be embalmed by intravascular perfusion fixation, with a 10 % formalin solution. And subsequent to fixation, the specimens also had to be submerged in a 10 % formalin solution for 24 hours as external virocidal agent and fixative. The latter requirement was in order to denature any possible biological matter that could adhere to the outside of the specimens (on the skin and horns). The Kruger National Park supplied the facilities to submerge the heads. All specimens were brushed with soap and running water before and after the submersion procedure. Besides removal of attached biological matter, washing the specimens after the submersion treatment also helped to decrease formalin vapour exposure to those who had to handle the specimens. It must be noted that these specimens were taken from a Foot and mouth endemic area and the savannah buffalo is known to be a carrier of the disease. Only after the full treatment regime, could the heads be transported under a special permit, out of the Kruger National Park, and to the destination. Collected heads were transported by trailer as well as on the back of the vehicle (see **footnote 13**), via non-endemic and non-quarantine areas, directly to the Faculty of Veterinary Science, Onderstepoort, Pretoria, South Africa. Onderstepoort lies in a non-Foot and mouth region but adjacent to a Foot and mouth vaccine laboratory. Prior to transport, the specimens were wrapped in thick gauge plastic. The plastic was in the form of a tube on a large roll. Knots were made at each end of individually wrapped heads. Wrapping in plastic ensured the following benefits **:**
(a) Dehydration would be limited during transport.
(b) Less formaldehyde vapour exposure to people during loading, transporting and offloading the specimens.
Although most of the work was done in the field in non-enclosed spaces, the exposure levels to formaldehyde had to be restricted at all cost for health reasons. The plastic was removed at the destination.
Since collection, the specimens have been kept immersed in 10 % formalin, in specially designed reservoirs. These were custom made for the long term preservation and handling of all large and small anatomical specimens in the Department. Complete chemical fixation of mammalian tissue for histological purposes is said to take one to two weeks at room temperature. It is however unknown how long it takes under the ambient temperatures as experienced in the Kruger National Park, but it can only be much shorter as evidenced in the field **:** Visually, complete denaturing of muscle proteins could be seen within 12 hours, and the consistency of the muscle turned rubbery at the time of pervascular fixation. No literature was searched to obtain references on the virocidal effect of formalin solutions, as it falls outside the scope of this study.

fluid used, was therefore free from other additives usually used in embalming cadavers intended for academic purposes. The rationale behind additives is inter alia to lower the exposure of toxic formalin vapours to dissectors. Volatile oils, often added to embalming fluids, can make the smell of dissections also more acceptable. To compensate for the extensive conditions in which the work had to be done, the embalming process was preceded by irrigating the heads first with a "normal" saline solution * [9] . No literature for this method could be found but it is based on facts of the circulatory system, clinical experience and a sound knowledge of basic physiology. The technique was incorporated into the protocol * [10] . This was done to accomplish proper fixation of all tissues to meet not only the requirements of the State Veterinarian - in order to prevent the survival of all possible virus particles - but also to obtain the best preserved anatomical material

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9 The saline solution was made up by dissolving approximately 9 gm of salt per litre of water, that is 225 gm in 25 litres of water. Large crude crystals of sodium chloride (NaCl) were used. The crystals were of a less refined standard than what is usually used for human consumption. Water used, was ordinary drinking water from a tap, obtained from the nearest camp site with hot water facilities (in the Kruger National Park). The saline solution was taken as an iso-osmotic 0.9 % or "normal" saline solution. This "home made" solution served as a cheap medium to irrigate blood components that remained in the circulatory system after exsanguination. It was immaterial if small variations in the osmolarity of the saline solution caused either crenation or lysis of red blood cell as it was not expected to significantly affect the accuracy of a study of this magnitude on gross anatomy. It was also not expected to affect either the musculature or the skulls. The saline solution was made up daily before culling commenced. The normal saline solution was transported in 25 litre containers to the culling sites. The temperature of the solution was judged lukewarm by hand feeling and not by using a thermometer. Later in the afternoons - when it was used - the temperature of the saline solution was still approximately body temperature.

10 The protocol portrays the procedures to be followed in any research project as was approved by both the Research and Ethical Committees of this Faculty.

possible * [11] .

EQUIPMENT AND SETUP:

The following equipment was used **:**

Catheters **:**

Various sizes (diameters) of used disposable dog urinary catheters were used. These were collected beforehand from clinical departments at this Faculty. The catheters were custom trimmed to lengths of approximately 100 mm and given a bevelled end, using scissors. A range of supplies was kept to choose from, as the length and size of the catheters that were needed depended largely on the age and size of the specimen to be embalmed. The coupling end of the catheter served as the receiving (or "female") end for the syphons. This end was equipped with the more modern type of "Leuer" coupling

[11] Historically, since the first attempts to preserve specimens for anatomical studies, many chemicals have been used and different techniques developed to embalm biological material. Apart from all the variations in the formulae and methods, the techniques have all been marked by only one thing and that is that they were customized to personal preferences. Before the discovery of formalin, any technique could apparently be written up as an anatomical technique. Many others then essentially followed blindly. Since the discovery of formalin in 1863 by August Wilhelm von Hofmann, fixation by chemical denaturing of proteins became important, and not the detail of the techniques or the different additives that were concocted. Literature on formalin solutions varies a lot regarding the concentration levels advocated, whether in combination with other chemicals or not. Scientific evidence for calculating the minimum concentration of the formalin that is necessary to embalm or fix material is not clear, as long as it can at least sterilize the particular specimen, and as long as it could coagulate the proteins. Advocated concentrations vary between 5 % and 25 %. Obviously, specimens like fetal material would behave differently chemically, and factors like age and fat contents also play a role. Syringes and syphons were traditionally used to administer the fixative solution. Reference as to the height of the containers for syphoning - which determines the magnitude of the hydrostatic pressure - varies from 1.2 to 1.8 metres above working level, to between 2.5 and 6 metres high. Hydrostatic pressure created from a height of approximately 1.4 metres above the ground, is roughly equal to the normal systolic blood pressure of man (120 mm of mercury). That height can mathematically be calculated from the chemical formula of water. (See **footnote 14**.) The blood vessel walls of healthy and "fresh" individuals, can sustain higher pressures compared with senile individuals or those in which decomposition has taken place. As "a rule of a thumb", the hydrostatic pressure should just be less than the pressure that would rupture the walls of more delicate vessels. When cadavers are fixed in toto, the pulmonary vessels are the most sensitive to excessive hydrostatic pressures. In geriatric or semi-decomposed cadavers, it is even more important to keep pressures down. Literature also states that when a part of a cadaver - as in this case the separated head only - has to be embalmed, the "freshness" and specific age of the specimens (apart from flushing it with saline), apparently plays a more important role to embalm it successfully, than any other scientifically calculated prescription, apart from being intravascularly applied. Fortunately, variations in methods and formulae to preserve specimens have stabilized over the years into a standard technique that was essentially also applied for this study. Having preserved this savannah buffalo material in 10 % formalin (and not 5 % or 25 %) by pervascular perfusion, was therefore more than adequate. Initially - for this study - it was reasoned theoretically that heparin should be added to the saline irrigation solution at a concentration of 5000 i.u. per 25 litres. The idea behind it was to prevent further blood clot formation. However, the regime was discontinued within the first day or two. There were four reasons for ending the heparin regime. Firstly, no clear-cut advantages could be seen at that stage (even though it was prior to having done any dissections). Secondly, much more irrigation solution (and heparin) was used than anticipated and the cost of the heparin was too high. Thirdly, it was experienced that factors like the time lapse between the time of darting, order of darting, order of death and time till decapitation, until the end of the irrigation process, was more important than the theoretical effect of using heparin too. Irrigation commenced between two and twenty minutes after death. Fourthly, administering heparin after death and after clots could have formed anyway, with so many factors not under control of the author, did not warrant the continuation of the heparin regime. As it did not form part of the State Veterinary prescriptions or the original protocol, it was of no concern to stop it. Practical experience after the first day already showed clearly that the quality of the preserved savannah buffalo material was beyond what was needed for gross anatomy purposes. It was therefore clearly evident that the specimens were collected and processed soon enough after death, to give extremely well preserved material.

system that fits on all modern syringes without the need of any adaptor * [12] . The coupling end of the catheters could be closed off as each one had its own cap permanently attached to it.

Syphons :

Syphons were custom made from flexible plastic tubing with inner and outer diameters of 7 mm and 10 mm respectively. Tubing walls were 1.5 mm thick, elastic, formalin resistant and transparent. The tubing was cut into lengths of approximately 5 metres long. Each piece was fitted permanently with a connecting piece, the probing (or the "male") end of the "Leuer" coupling system. The other open end of the tubing was permanently attached to a rigid medium-sized bronze brazing rod that gave that end of the syphon some handling rigidity. The brazing rods were approximately three to four mm in diameter and 0.75 metres long. The tubing was affixed to the brazing rod by thin copper wire at intervals of approximately 50 - 100 mm. These wires were attached to the rods and the tubing so that they would not slip from the rod or occlude the lumen of the tube. Approximately 4 mm of the rod projected beyond the open end of the syphon to prevent occlusion of the tube against the bottom of the container. At the height of the rim of the container, the rods were bent at an angle of approximately 40 degrees. Some extra length of tubing was allowed in the region of the bend in the rod to prevent collapse of the tubing. The rod and the tube allowed free movement of the syphon in all directions once inserted into the container. The simplicity of the equipment also allowed unobstructed installments of more syphons into the containers. The mere weight of the rods kept the open end of the syphons 4 mm away from the bottom of the container. This assured a continuous flow of fluid, once syphoning was initiated. Apart from keeping the tube always in an immersed position, the purpose of the bend in the rod was also to help redirect the syphon from the higher altitude - from the top of the cabin of the vehicle where the container was placed - to the working area below. The length of the syphons allowed a work area at ground level with a radius of approximately 2 metres. Twelve syphons were made, as up to six sets of syphons were sometimes used simultaneously.

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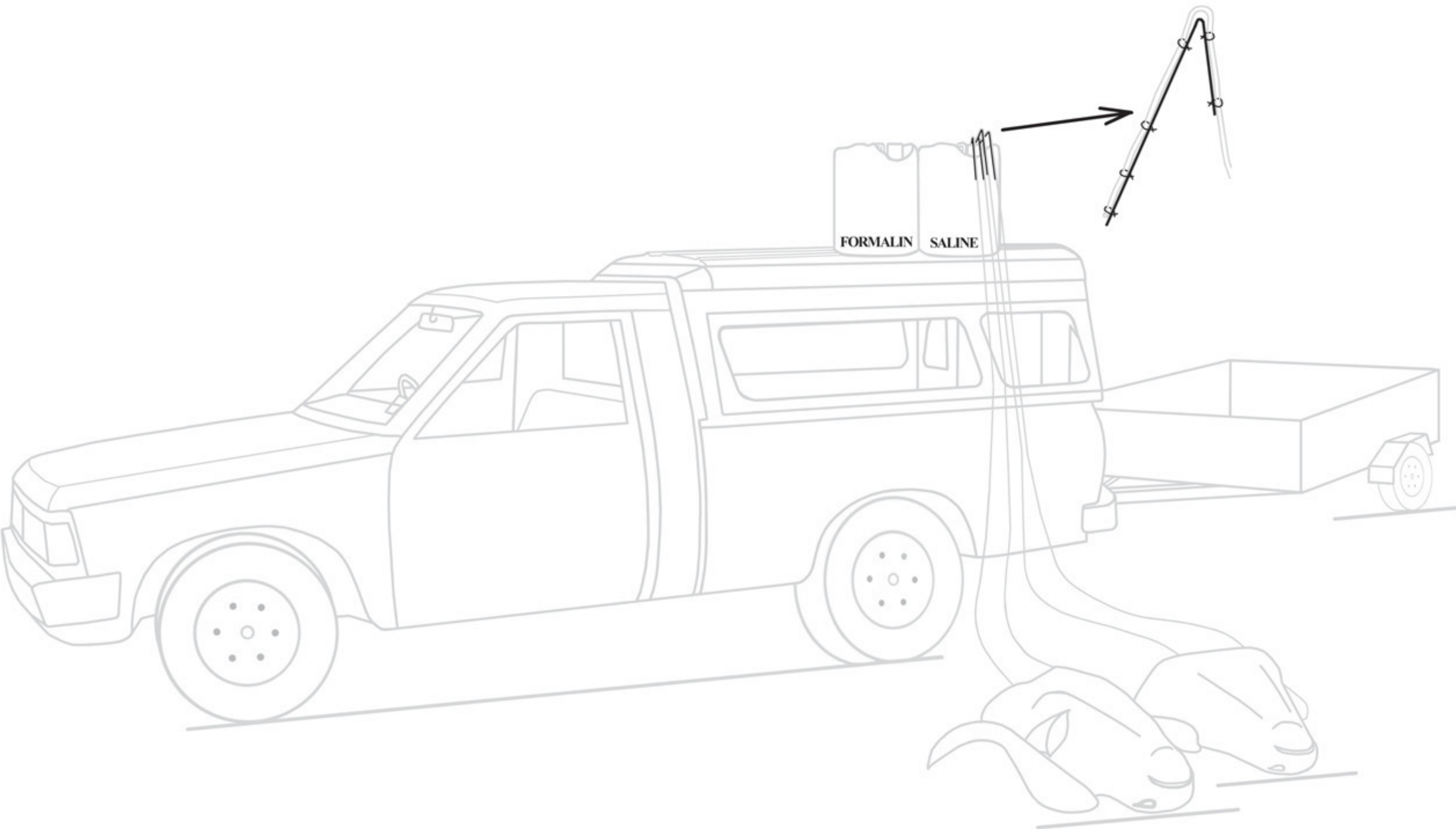
12 For the sake of clarity, the other - and older - system was the "Record" locking system, which needed special adapters before it could be connected to modern syringes or needles.

FIGURE 2.1 : MATERIALS AND METHODS

SCHEMATIC ILLUSTRATION OF EQUIPMENT USED FOR FLUSHING AND EMBALMING HEADS UNDER EXTENSIVE FIELD CONDITIONS

FIGURE 2.1 : MATERIALS AND METHODS

SCHEMATIC ILLUSTRATION OF EQUIPMENT USED FOR FLUSHING AND EMBALMING HEADS UNDER EXTENSIVE FIELD CONDITIONS



Photography, graphics & digital remastering by M. Hornsveld 2001

Containers to keep and transport larger volumes of fluids :

Six to eight, semi-disposable but durable, 25 litre plastic containers were used. These containers were of a lightweight type, equipped with top-fit handle grips and with sunken screw-on tops. They could be stacked on top of each other for transport. The tops sealed well enough to eliminate the risk of any leaks due to the rough handling conditions. The quality of the plastic they were made of, made it possible to transport water and saline as well as formalin solutions over bumpy off-road terrain in wilderness areas where the specimens had to be collected. The openings of the containers varied in diameter between 70 - 80 mm, depending on the model. These openings were large enough to handle six to eight syphons simultaneously.

Sundries :

A supply of the following was always kept ready in a crate before departing on any trip to collect material :

< Concentrated formalin for embalming, kept in smaller plastic canisters of 5 litres. Each canister contained enough formalin to make up 50 litres of a 10 % formalin solution. Three or four 5 litre canisters were always kept ready for daily collection of savannah buffalo heads.

< Crude, unrefined salt kept in pre-weighed sachets of 225 gm each, enough to make up 25 litres of a “normal” saline solution per sachet. A large stock of sachets was always available.

< A roll of ordinary cotton string, disposable gloves, cotton wool, scalpels handles (nr 4), blades (nr 23), wood type hand saw (cheaper than proper Post mortem saw), wire-saw (embryotomy type), water (150 - 200 litres or more per day), approximately 30 artery forceps of various sizes (from the small “mosquito” type to large ones), syringes of various sizes, liquid soap in pump action containers for washing hands, paper rolls for drying hands, pliers, thin copper wire and the whole collection of catheters and the custom-made syphons. Latex (for intravenous and intra-arterial injections), colouring pigments for the latex, glacial acetic acid and ammonium solution were not taken out on daily excursions but were kept at the base camp. (See footnote 15.)

A vehicle :

In operations such as culling procedures in the field, independent but highly mobile transport for the researcher is indispensable, as vehicles have to serve as sole transport medium to and from collection sites in the bush. These sites cannot be predetermined for comfort and researchers work totally independent from the transporting system of the culling team. A vehicle suitable to be used in wilderness areas was used to transport the equipment, the author and one technician. The vehicles used, had ample space at the back for all the equipment that had to be transported, and for all the heads collected each day * [13] . Due to the formalin vapours released from the collected specimens, it was found best if the vehicles were not equipped with a canopy in order to allow free movement of air. The roof of the cabin of the vehicle (- or the roof of the canopy when one was fitted as in Fig. 2.1 -) served as the standard elevated level from which syphoning could take place in field conditions. Depending on the terrain, the cabin or canopy roofs were for all practical purposes between 1.4 and 1.8 metres above ground level. The ground always had to serve as working surface and it served well to absorb all excess embalming fluids.

INSTALLATION OF CATHETERS:

The catheters were inserted into both the common carotid arteries near their severed ends. Prior to insertion, each artery was first separated from the accompanying (ipsilateral) vagosympathetic trunk to expose the arterial wall properly. Inserting a catheter was achieved by making a small incision with a scalpel blade in the wall and into the lumen of the artery, near its severed end. The bevelled end of the catheter was then inserted via the incision and directed towards the head. Each catheter was semi-permanently attached to the wall of the artery, using some string that was tied tightly around the arterial stump. Tying the catheter to the arterial wall, also prevented leakage of fluids between the catheter and the artery. Such leakage was to be prevented when positive hydrostatic pressure was applied to the circulatory system. Untying the strand allowed temporary removal of the catheter when needed. The

13 Vehicles used, were usually either an “LDV” (or “light delivery van”) type, or an all-terrain vehicle. The latter were preferred because they come equipped with four-wheel-drive and tow-bars. The vehicles were also used to transport all the heads collected from the culling sites in the Kruger National Park to their final destination in Pretoria (South Africa). Ordinary or heavy duty trailers were used, depending on the weight of the freight they had to carry.

severed ends of both the external jugular veins were also exposed and checked at the onset of the procedure to ensure that the venous stumps were indeed patent and free of larger blood clots. The catheters served the purpose as permanently installed connecting points to the arterial system. By this means, the natural circulatory system of the neck and the head could be used to perfuse - under positive hydrostatic pressure - all tissues simultaneously at capillary level.

RATIONALE BEHIND IRRIGATION OF SEVERED HEADS PRIOR TO FIXATION:

Fixation (or embalming) by perfusion was preceded by irrigating the circulatory system first, using a 'normal' saline solution. This was done to reduce the chances of blood clots blocking capillaries or larger vessels, and to enhance the results of the embalming process. The temperature of the 'normal' saline solution was approximately body temperature.
The rationale for irrigating the circulatory system first, is as follows **:**

Time-dependant formation of blood clots can be expected to occur when blood remains stagnant in the circulatory system of decapitated heads. That is aggravated when the blood comes into contact with formalin. It is also a known fact that tissue starts to become turgid when embalming is started. That is considered undesirable for perfusion, because plasticity of tissue would tend to retain the clots that could have formed. In this case of collecting savannah buffalo heads under extensive field conditions, exsanguination of heads was expected to be incomplete. Also, the time from death until embalming could be started, was not under the control of the author, and that time varied between approximately two and five minutes to twenty minutes.

The irrigation process itself could be done in a matter of minutes, much shorter than the embalming process. That ensured that the embalming process itself could be done in the absence of stagnant blood in the capillary beds, as well as in the larger vessels. The duration of the irrigation process varied slightly from animal to animal, depending on various pre- and post mortal factors individual to every animal. Irrigation was continued until return of the normal saline via the jugular veins was not tinged red by blood. Irrigation of heads was done while they were still warm and prior to elasticity loss. That prevented to a large extent many of the potential problems that one could expect to experience under such extensive conditions. It also ensured a much quicker and a more effective embalming process that guaranteed the quality of the embalmed material, as it was a once-in-a-lifetime opportunity.

CALCULATION OF THE MAGNITUDE OF HYDROSTATIC PRESSURE FOR PROPER FUNCTIONING OF THE SYPHONS:

Positive hydrostatic pressure - approximately equal to an anticipated systolic blood pressure of 120 mm of mercury, but created by gravity in a syphon - is adequate to ensure a continuous flow of fluids through the circulatory system of the heads intended for this study. The pathway of the fluids was from the containers, placed on the roof of the vehicle, via the syphons and catheters into the left and right common carotid arteries, and via the capillary beds to the veins of the venous system. Excess fluids drained from there onto the ground. For syphoning, the containers were raised between 1.4 and 1.8 metres above working level (depending on the terrain). This was found to give more than adequate hydrostatic pressure ever needed under all working conditions and in all individual cases. The exact hydrostatic pressure for a water column of 1. 4 metres is equivalent to 125.73548 mm of mercury, and a water column of 1.8 metres is equivalent to 162.45 mm of mercury * [14] . As the syphoning tubes were transparent, real flow of fluids in each syphon could be determined by visual inspection. The whole system was planned to work in field conditions, where electricity and modern equipment is not just absent but impractical. From experience gained at previous occasions where preservation of material for anatomy purposes was done under equivalent extensive conditions, it was known that not having any technologically involved equipment is best. All that had to be done was to place the brazing rod with the one end of the syphon into the container. Containers (one marked ‘normal saline’ as irrigation fluid, and the other marked ‘formalin’ as embalming fluid) were placed on the roof of the cabin of the vehicle. As the containers weighed more

14 Exact hydrostatic pressures can be calculated **:** The molecular weight of water - H_2O - is calculated by adding the molecular weight of its atoms. That of hydrogen is 1.0079 x 2 = 2.0158, plus oxygen at 15.9994, totals 18.0152. The molecular weight of mercury - Hg - is 200.59. (These figures can be obtained from any periodic table of elements.) The molecular weight of mercury is divided by the molecular weight of water **:** 200.59 ÷ 18.0152 = 11.134486. This gives the converting factor to convert mm of Hg into mm of water. If a systolic pressure of 120 mm Hg is presumed to be a norm, then 120 mm of mercury X 11.134486 = 1336.1383 mm of water. A height of 1.4 metres therefore gives a hydrostatic pressure still in excess of what is anticipated as the upper limit of a systolic blood pressure (of man). Obviously, when clots obliterate the system, higher pressures (therefore placed up to 1.8 metres high) could be called for. Never was a higher pressure than 162.45 mm Hg (i.e. higher than 1.8 metres) needed in the collection of the material for this study.

than 25 kg when full, picking them up to that height did need some effort, but at least the platform created by the roof of the cabin was always available. Syphoning was initiated by oral suction at the connector end of the syphon. Although the transparent nature of the tubes helped visual regulation of suction force, one stood a change to get a mouth full of saline or formalin solution. It was a small price to pay compared with all the other advantages of the system. Adjustable clamps - set conveniently near the connecting ends of the syphons - were added additionally to some syphons, to have more control over the pressure and flow of the fluids. These clamps could be set delicately enough to adjust the final hydrostatic pressure at the "male" end of the syphon according to specific need. Usually, only a removable artery forceps was clamped over the tube. A forceps clamped over the tube had the disadvantage that it stopped syphoning altogether. Two syphons were always simultaneously used on every head by connecting a separate syphon to each common carotid artery. This was to ensure that the system would work even in those rare cases where a blood clot could occlude one common carotid artery. Or, even if one syphon were to become non-functional, for whatever reason, the system would still work across the arterial system of the head. Larger clots that still remained despite irrigation could be washed out by temporary disconnecting one or both catheters, in order to flush out the vascular system (vide infra). The ratio of syphon size to the diameter of the container openings, was favourable enough so that one container could easily handle up to eight syphons at a time. The intra-vascular perfusion fixation (embalming) always followed the saline irrigation and was never done alone. Containers going empty, were immediately replaced to prevent repeated syphoning initiations. The above apparatus and technique for embalming under extensive conditions were highly effective as it was near failure free, unbreakable, and quick to assemble. Disassembly and transportation were also without any fuss. The time it took to irrigate and to embalm a daily collection of heads was less than two hours. Larger heads took longer to preserve than smalls ones. Heads collected for this study weighed from 5 kg for the young calves, to nearly 90 kg for the big bulls.

IRRIGATING VERSUS FLUSHING THE CIRCULATORY SYSTEM:

In some cases, the passive method of irrigating with 'normal' saline did not produce the required results soon enough. In those cases, a method of flushing was quickly resorted to, if flow through the vascular system was felt to be too slow. (Where necessary, it was also applied during the embalming process.) Although the two terms - irrigation and flushing - apparently mean the same thing, they are not synonymous with each other. For convenience sake, perfusion is also discussed here, although as part of the embalming process it belongs under the next heading. For the purpose of this study, these three terms therefore mean the following **:**

Irrigate refers to the flow of 'normal' saline through the vascular system. But it can refer to the flow of embalming fluid when the saline solution again has to be rinsed out of the system. In the former case, stagnant blood becomes diluted by the irrigation process and in the latter case, the 'normal' saline solution is gradually replaced with the embalming fluid. Saline irrigation was continued until the return of the saline - at the cut ends of the jugular veins - were free from all blood clots and tainted saline. When this was not accomplished soon enough, the following technique of flushing was applied **:**

Flushing refers to the technique of running one of the fluids (either the saline or the formalin solution) under variable positive pressures through the blood vessels but not necessarily in the normal direction. That meant that the circulatory system first had to be 'pressurized' or slightly overfilled, to an adequate level with the appropriate fluid. To obtain that, large sized artery forceps were applied to the jugular vein stumps while syphoning was allowed to continue. Visual dilation of the jugular veins served as good indicators of the status quo of the intra-vascular pressure. It could also be checked by digital palpation of the distended jugular veins if they were not visible. Re-opening one or both the jugular veins by removing one or both the clamps (with the syphons still running), created an increased flow especially in the venous system. That caused the flushing out of blood or clots from the distended blood vessels. And when embalming, also to flush out the normal saline that could cause a dilution of the formalin solution. Unilateral flushing of the venous system, sometimes gave better results than unilateral flushing. To flush the arterial system, the jugular veins were kept occluded by a clamped artery forceps to each side, and then one or both catheters were disconnected from the common carotid arteries. That was also after adequate pressure was allowed to build up first in the circulatory system. The latter method caused the saline (or formalin solution) to run out of the artery or arteries in a reversed direction. Or, sometimes, both the arterial and the venous system could be opened up simultaneously. That was done to augment flushing with manual massaging of the heads without the fuss of all the syphons in the way. Flushing with or without manual massaging, usually dislodged the most persistent clots in the circulatory system.

Perfusion (vide infra) is when the embalming fluid is irrigated over an extended period of time through the larger blood vessels and the complete micro-vasculature. That allowed formalin to permeate through the capillary walls, and to diffuse into the tissue at cellular level. Chemical fixation of all tissue could then take place with time. (Obviously, the ‘normal’ saline actually also perfuse through the vascular system and capillary networks during irrigation.)

After the irrigation and flushing processes obtained a certain satisfactory level - learned from experience - a large removable plug made from cotton wool was inserted into the vertebral canal. This often required quite some force to effectively block off the drainage of saline (and embalming fluid) via the venous routes in the canal. Venous drainage in the vertebral canal is via the ventral internal vertebral plexus and its complex system of branches. It seemed similar to that of the domestic bovine. The cut surface of the neck also revealed many other vessels from which fluids either squirted out (arteries) or leaked out (veins) or oozed out (from capillary beds in the muscles). Only the major arteries from which fluids squirted were closed off by applying an artery forceps. That caused the intravascular pressure to increase sharply and was used when enhanced flushing was necessary. The rate of oozing from cut muscle surfaces was much slower than the rate of inflow, and was of no concern. Oozing - even in the pressurized state of the vessels - declined rapidly, and after the first day hardly any oozing occurred from the cut surface. The vertebral artery and vein in the transverse canal were sometimes problematic to close off. Either small artery forceps clamps, or cotton wool plugs, or both, did the trick to stop them from leaking. Small insignificant vessels - usually from the cut surfaces of the muscle or from vessels between muscles - were ignored as long as it was apparent that the inflow of syphoning fluids exceeded the total loss of fluids. That state of affairs could be evaluated by looking at the extent to which the jugular veins remain filled. By this means also, the intra-vascular pressure could be maintained at a satisfactory level.

Before the embalming process began, it was made sure that the head-neck junction at the atlanto-occipital joint was in the extended position. That was usually automatically achieved by placing the heads upside down on the ground when all the tissues were still pliable and prior to the onset of the irrigation process. Apart from being the only way that heads with such big horns can be put firmly on the ground, it was also the most convenient position to get the common carotid arteries exposed.

EMBALMING BY INTRAVASCULAR PERFUSION:

Perfusion - to embalm the heads - always immediately followed the irrigation and flushing processes as described above. For embalming, a 10 % formalin solution was used and applied via the same route, technique and equipment as was used in the preceding procedures. Only the syphons were changed from the one container with the saline solution to the other container with the formalin solution. Prior closure of the tube (by either bending it acutely or applying a clamp), prevented interruption of syphoning temporarily. The temperature of the formalin solution was - as for the'normal' saline solution - approximately body temperature. Within a few minutes, the skeletal muscles of the heads started to contract in a pulsating way before they became turgid, indicating the onset of chemical fixation. Pulsating muscles were considered as a good indicator of an open circulatory system that was sufficiently irrigated and flushed, giving good embalming expectations. The specimens obtained a semi-rubbery consistency within a few minutes. The colour of the muscles also immediately started to change although it took a few days of embalming at chemical level, before they obtained their final well-preserved colour. Administering a continuous flow of formalin solution was continued for as long as time and circumstances allowed in the afternoons before dusk terminated the day's work. Thereafter, the syphons were disconnected and the caps of the catheters applied. That was to prevent dust and dirt to enter the circulatory system during travelling back to camp. No problem was ever encountered that could have been ascribed to air entering the circulatory system as was found by other workers [63 & 136] . All material was transported back to the resident camp on the open back of the vehicle. Upon arrival at the camp, the catheters of all specimens were re-attached to syphons in formalin solution, and kept connected overnight (usually for another eight to twelve hours). A fair amount of "swelling" of the heads was observed especially in younger animals by the following mornings. That was due to what can be described as "hydrostatic oedema" because of an excess of embalming fluid administered. It was most notably seen as peri-orbital swelling and as a slight protrusion of the tongue tip. It caused no concern, as within a few hours, the "oedema" would go down upon disconnection of the syphons. A slightly overfilled head, actually served a dual purpose **:** Firstly, the excess embalming fluid served as a reservoir to counteract evaporation loss as high ambient temperatures were experienced during the days. Secondly, having the blood vessels undergoing progressive chemical fixation under distended conditions, were intentional **:** Vessels fixed like that in the dilated state, eased the intra-vascular injection of latex that followed the embalming process of heads selected for that purpose * [15] . Syphons were disconnected in the mornings to be available for use on new specimens to be collected. Approximately every eight hours, additional formalin was administered again to all previously collected specimens. That counteracted degrees of fluid loss due to oozing and evaporation from the cut surfaces of the neck muscles. It also reassured that enough formalin was present for chemical fixation.

SELECTION AND PROCESSING OF MATERIAL FOR THE OSTEOLOGICAL STUDY:

Of the 47 irrigated, flushed and formalin fixed specimens, **seven heads** were chosen to form part of the osteological study. A **further four heads** - which were previously obtained, prepared and formalin fixed in a similar way during a culling programme in 1966 - was also chosen for the osteological study. The latter four specimens were the heads of older bulls collected by the same technician that helped with this collection. However, these buffalo

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15 Latex injection of selected heads was intended for another part of the study on the blood vessels."Revultex" latex was used to fill the arterial and venous sides of the circulatory circuit. Each component was done separately. Blue pigmented latex was used for the venous system, and red pigmented latex for the arterial system. Pigments used were "Vulcanosol blue -BASF 5704815" and "Heresa universal red stainer". The venous system was filled via the angular occular vein after a small skin incision was made just rostral to the medial angle of the eye. The arterial system was filled via one of the common carotid arteries. The pigments were first dissolved in a 25 % ammonium solution before it was mixed into the latex. Latex injection of the venous system was done more than a week after field collection, whereas the injection of latex into the arterial system was done the next day when the arteries were still more pliable. Topical glacial acetic acid was used to cause instant setting of the latex that oozed from capillary networks, or even when leaking from small or larger vessels. Six latex injected heads (2 arterial & 4 venous) were dissected as "wet" specimens to study the development of the enamel organs, as discussed under ADDITIONAL SAVANNAH BUFFALO SKULLS STUDIED.

heads were not flushed with saline when they were collected. The seven heads of the one group and the four heads of the other group (**adding up to 11 complete skulls**) were selected according to age and gender criteria to obtain a wider spectrum of features for the study on the osteology. All the remaining heads were stored permanently by keeping them submersed in a 10 % formalin solution.

Except for two more skulls of young animals of approximately three to four months old (vide infra), the following was done to prepare the skulls and mandibles for the osteological study **:** After skinning, larger chunks of muscle and soft tissue were cut away by using knives and scalpels until hardly any connective tissue remained on the skull and mandibles. After some hyoid apparatuses were damaged, the hyoid bones were removed in toto when the musculature was removed piecemeal (vide infra). The skulls and mandibles (but not the hyoid bones) were then boiled in water and prepared according to proven methods [35 & 61] . Wherever possible, prolonged boiling was carefully monitored, to avoided de-calcification of especially the teeth. Each skull and mandible was treated individually. The skulls and mandibles were boiled in voluminous pots. The pots are the same type used by large catering companies, and custom installed for that sole purpose for this Department * [16] . The pots have oil-immersed electrical elements with loose-fitting lids. Because no pressure can build up, the boiling temperature (at the altitude where these institution lies) is approximately 96 degrees Celsius. In some larger bulls, the horns had to be cut off before boiling, to be able to fit into the pots. Having the horns cut, also prevented them from being stolen, as some were of hunting trophy quality. Experience learned that the older the animal and the longer the specimen had been kept in formalin, the longer they had to be boiled. In the case of one of the very old bulls that were collected in 1966 - and kept in formalin for more than 20 years - it had to be boiled vigorously for 76 hours before the connective tissue was soft enough to be manually removed.

After manual cleansing, the fat contents of the skulls were lowered by chemical means, using trichloroethylene in a specially designed de-greasing plant, that was also custom installed

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16 “Marlin Catering Equipment”

for this Department * [17] .

The skulls of the two young animals of approximately three to four months old - vide supra - were prepared differently **:** After allowing 24 - 48 hours of rinsing in running water to get rid of excess formalin vapours, the skin, muscle and all soft tissue were carefully removed by standard dissecting technique. That included the removal of the periosteum to expose the bone proper. Because the skulls of these two animals were so young, they were not boiled, as boiling would have ruined the cartilaginous and fibrous components of the skull and hyoid. The two specimens were subsequently stored by keeping them submerged in a 5% formalin solution. They were kept in small plastic containers, separate from the larger collection (**totalling 13 complete skulls with matching mandibles**).

Additional to the above thirteen skulls prepared from formalinized specimens, three other skulls - but al three without mandibles - were also obtained for temporary use. Only one of these could effectively be used for this study **:** The first one was a magnificent hunting trophy of a bull of uncertain origin, with the only history that it was from somewhere in central Africa. It was only used in a comparative way when the skulls of the other old bulls with known histories were studied. Because it was of unknown origin (and therefore of unknown subspecies), it was not counted as part of the material for this study. The second skull was a trophy-sized skull from a farm next to the Kruger National Park. It could only be used for superficial study, and although it could be counted as that of a savannah buffalo specimen, it was not. Both hunting trophies were well cleaned by the time they were borrowed. Nevertheless, because they were slightly stained, they were also properly cleaned by boiling in water and trichloroethylene in the same Departmental facilities. The third skull was obtained from the Transvaal Museum, Pretoria. It was certified as the skull of a female savannah buffalo, numbered TM 3313. As it was a museum specimen, it could also only be

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17 "Proctor Industrial Cleaning Systems", fulfilling AECI recommendations. The plant was custom installed for this Department, based on the same principle of industrial de-greasing plants for removing oil and grease from mechanical components. Complete skulls and mandibles were partially immersed in the boiling (86-88 ° C) trichloroethylene, and partially kept in the vapours of it. Depending on the fat content of individual skulls, this process extended over a period of a week or more, based on visual inspection and experience. It became clear afterwards that some yellow fat still remained undissolved in the spongy bone of the occipital and petrous bones. The trichloroethylene de-fatting regime that was followed, and the equipment used, was therefore not 100% effective to get rid of all oils and fat from the bones of such large skulls.

used for superficial study and could not be cut up, to reveal internal structures. The skull of this immature cow was however selected for illustration purposes - to serve as an example of a skull of an immature cow - and is counted as part of the material for this study (**totalling 14 skulls, but only 13 mandibles**). An uncounted number of other hunting trophies were compared on a regular basis as the study progressed.

HYOID BONE COLLECTION:

The hyoid bones (hyoid apparatuses) were recovered from the selected formalinized heads before boiling as stated above by careful dissection. The following hyoid apparatuses were collected **:** The complete hyoid apparatus of one mature bull, one very old cow, and one bullock of approximately three to four months. The right half only of two more animals - a mature cow and a heifer of approximately three to four months old - were also studied. The right halves were taken as representative of the complete hyoid apparatus. The hyoid bones (uni- and bilateral halves) were manually cleaned and kept in 5% formalin solutions in a glass container with a tight fitting lid. The hyoid apparatus of the mature bull was used for the schematic illustration. Hyoid apparatuses of a further two more animals were dissected as part of special dissections on the pharyngeal and laryngeal regions of the savannah buffalo. The 'in situ anatomy' of these two hyoid bones and their articulations were exposed and studied. These specimens were kept in 10 % formalin in large stainless steel tanks (**totalling 7 hyoid apparatuses**).

THE CORE COLLECTION OF BONES USED FOR THIS STUDY:

The **14 skulls, of which 13 had matching mandibles, and the hyoid apparatuses of 7 animals**, were therefore effectively obtained from animals that used to belong to the one or other herd of buffalo of the Kruger National Park. The Park lies within the Gauteng Province, formerly known as the Eastern Transvaal part of South Africa. The species of buffalo represented by the skulls used in this study is therefore representative of the savannah buffalo of the southern subregion of Africa, *Syncerus caffer caffer* (Sparrman, 1779) [73,111 & 121]. These specimens were used as the **core collection of bones** to study, describe and illustrate the osteology of the cranial and facial bones.

ADDITIONAL SAVANNAH BUFFALO SKULLS STUDIED:

The statistical number of skulls used for the osteological study, was increased further by confirming some osteological aspects on 18 more animals. These were also collected from the same National Park. Only the left side of the dental arches were collected as part of a special study on the dentition of the savannah buffalo * [18] . The development of the enamel organ and the development, eruption and wear of permanent teeth were studied in these specimens. The embedded parts of the teeth were exposed by sculpturing away all overlying bone. The study had a dual purpose **:** Firstly, it was done to confirm the ages of specimens collected for this study as some minor discrepancies were found. Secondly, the dentition had to be studied in an effort to understand the formation of temporary osseus openings in the tooth bearing parts of the maxilla and mandible. These openings - referred to as gubernacular canals - are associated with the development of the permanent premolars prior to eruption. (See **Glossary of terms**.) The study on the dentition established parity between what is seen both externally of the clinical crowns of teeth as well as internally of the embedded parts of teeth over the whole age spectrum of savannah buffalo. All these aspects have to be considered when aging skulls and when studying the osteology. Although they were not complete skulls, the additional 18 skulls that were used to study the dentition, effectively increased the number of animals on which this study is based (**totalling 32 skulls, 31 with matching**

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[18] The study on all the teeth of the dentition of the savannah buffalo, forms part of an envisaged splanchnology part of the project as originally planned. Material for the study on the dentition was collected during the culling programme of 1992. The collection represents animals of ages that varies between four months and approximately twenty years. These specimens were collected at the specially equipped Parks Board Abattoir in the Kruger National Park. Material for this study on the teeth, was collected approximately 8 to 12 hours after culling. Selection of specimens was based on age information that accompanied each carcass. Recording age and morphometric data for each culled animal is standard procedure in the Park. Ageing of the animals were done at the culling site the previous afternoon by a person having experience in doing so. Incisors and also the cheek teeth were considered, after buccal incisions were made. However, the priority level for collecting and processing research material in that part of an abattoir - at the end of the carcass dressing line - is, as can be expected, not high. Because the carcasses were intended for human consumption, meat inspection procedures on the heads and carcasses had to be done first. Only the left side of the tooth bearing parts of 18 skulls were collected for this study on the dentition. The procedure was as follows **:** The horns were cut off by using a hydraulically operated press of the abattoir. The press was fitted with a special cutting blade, used for trimming the skulls and other parts of the carcass intended for carcass meal processing. Circumstances beyond the control of the author, rules those parts of an abattoir, and unfortunately, information on the gender of the specimens could not be retained. Approximately eight hours later (in day-light time the next day), the external laminae of the tooth bearing parts of the maxilla and the mandible were cut away to expose the embedded parts of the teeth. Various tools were used, some of which was custom made on site. Tools used included the following **:** a hacksaw, hammers, chisels, scalpels, forceps, all sizes of screwdrivers, etc. The teeth and the enamel organs were exposed by sculpturing away all overlying bone. After removal of all soft tissues too, the specimens consisted only of bone and teeth. Specimens were then preserved and stored by immersion in a 10 % formalin solution for a week. Specimens were kept in tight-sealing glass containers. These were then transported under a permit from the Kruger National Park to Onderstepoort, Pretoria, South Africa, where the specimens were removed from formalin. After air drying, final sculpturing was done with an electric bone cutting saw (see **footnote 21**) and customized tools. The study on the dentition made further critical evaluation of the ages of the specimens for the osteological study possible. The special part of the study on the dentition made it possible to interpret changes that take place in the tooth bearing parts of the maxilla and mandible. (See **gubernacular canals**, subsections 16 & 21.) Detail of the study on the teeth per se, is excluded from this thesis.

mandibles, and the hyoid apparatuses of 7 animals).

Finally, findings on the development of the enamel organs and how they relate to the gubernacular canals in the tooth bearing parts of the maxilla and mandible, were confirmed by dissecting **six more "wet" specimens that were injected with latex**. (See footnote 15.) The following specimens were dissected **:** Two very young male animals in which the arterial system was filled with latex. Their ages varied between two and 3½ - 4½ months respectively. In the four other specimens, the venous system was filled with latex. Three were of male animals of 4 months, 12 months and 12 - 16 months of age respectively. The fourth specimen was that of an immature cow of approximately 2 - 3 years of age. Although the development of the enamel organs was primarily studied and not the osteology, they also form an integral part of this study as they rendered information on the tooth bearing parts of the skull and mandible. If all the specimens accounted for in the above descriptions are counted, it gives a grand total of **38 skulls, 37 with matching mandibles, and 7 hyoid apparatuses**.

PHYSICAL EXPOSURE OF INTERNAL ASPECTS OF THE SKULLS:

A band saw * [19] was used to cut off larger sections of skulls - like the horns - and to split skulls in the median plane. This had to be done for the sake of easing up the handling of some larger and heavier specimens * [20] . Smaller parts of the skull were cut away in a more precise way with an electrically operated hand-held type of oscillating saw * [21] . This saw made it possible to expose the detail of deeper laying structures that could not be exposed by using the band saw.

19 A locally manufactured band saw that is commonly used in well equipped butcheries **:** "OKTO Mark 2"

20 To give readers some background information, the following weights may help one to realized aspects of size and weight of savannah buffalo that should not pass unnoticed **:** The complete unskinned head of a mature bull with horns, weighed approximately 90 kg. The dried skull of an old bull, with intact horns, but without the mandible, weighed in at 15 kg. The weights of two other skulls of bulls taken randomly, in which part of the horns were cut, but which included the mandibles, weighed 10 and 14 kg respectively. These measurements should illustrate the physical effort involved in handling such heavy specimens.

21 "Desoutter Oscillating Saw type DGOS". This saw is actually made to cut Plaster of Paris casts. Interchangeable disc-shaped blades of various diameters and grades of tooth roughness were used. Blades of different sizes made it possible to get into most of the internal parts of the skull, cutting bone with a fair amount of ease and accuracy.

SKULLS EXAMINED BUT WHICH DO NOT DIRECTLY FORM PART OF THIS STUDY PER SE:

Three more non-savannah buffalo skulls - or parts of skulls - were also studied even though they do not directly form part of this study. They were used to gain insight into the general osteology of the skull of Bovini. The skulls referred to, were kept in a neglected condition in this Department and as far as could be established, they were obtained approximately in 1950 from an unknown source.

- The first specimen was the broken skull and matching mandible of an old animal that could be identified as most probable that of an Egyptian Buffalo (*Bubalus bubalis*). Even though this skull and mandible were of unknown origin, it could be identified on general shape of the skull, the cornual processes and horns as well as on the vomer's fusion (articulation) to all three the components of the boney palate [68, 98 & 116] . It could only be used as a worthy contribution and as additional material that aided the author to understand more about the comparative osteology of the Egyptian Buffalo.
- The second skull could be identified only as probably that of a Water buffalo of a *Bubalus* type. Identification was based on the horns, the general shape of the skull, and the partial fusion of the vomer to the nasal crest. Lacking more detail - but with enough accuracy - it can only be specified further as not the skull of the Egyptian type, but most probably that of an Asiatic type. The skull was even less complete than the Egyptian buffalo skull, and it lacked a mandible.
- The third specimen was the cornual processes, Calvaria and part of the occiput only (no mandible) of a Water buffalo, most probably belonging to the *Bubalus* type. It was of a young animal of less than approximately one year of age. Although incomplete, the specimen was important to consider as it also showed a temporary sphenoidal fontanelle, similar to what is seen in savannah buffalo juveniles. (See footnote 42.)

The Egyptian Buffalo skull and the two other Water Buffalo type skulls - representing *Bubalus* species - and all the other savannah buffalo skulls (**thirteen skulls purely for osteology plus eighteen more on the dentition plus 6 more wet specimens for the enamel organs and one skull without a mandible**) representing *Syncerus* species - were collectively used for this study. They were also compared with an uncounted number of skulls of local breeds of the domestic bovine (both *Bos taurus* and *Bos indicus* breed, as well as crosses between these). The skulls of the domestic animals formed part of a larger collection of skulls collected over many years in this Department for general academic use.

From all the material referred to above, a wider concept of the differences and similarities between skulls of "Buffalo" (*Bubalus* and *Syncerus* types) and "domestic bovine" (both types of *Bos*) could be formed for the purpose of this study.

COMMENTS ON THE LITERATURE THAT WAS READ:

The official terminology list (the *N.A.V.*), textbooks, articles, dissection-guides on gross Veterinary Anatomy of domestic animals, and other literature covering many more aspects of osteology, were intensively scanned for this study [9, 16, 20, 24, 27 - 30, 36, 38 - 44, 48, 50, 51, 53, 55, 66, 93, 96, 100, 101, 108, 110, 120 & 153].

Complementary to this study, the basic gross anatomy of the osteology of the skull and mandible of other large - but not related - wild animals, was also studied [89, 122, 123 & 137].

Biomechanical aspects from Veterinary Anatomy literature had to be studied too, in order to understand some of the structural reinforcements found in the skull of the savannah buffalo [12, 13 & 14].

Anatomical aspects, which are not well described in Veterinary Anatomy, had to be studied in the literature on gross human anatomy [8, 31 & 126].

Because literature across four languages (German, French, English and Afrikaans) was used, and due to the Latin based official terminology, dictionaries of these languages had to be consulted too [8, 52, 79, 90, 91 & 131].

MICROSCOPIC ANATOMY:

No histology was done on the sutures to distinguish fibrous or cartilage content, or to determine stages of ossification, to proof or disprove (or differentiate) *synchondrosis*, *symphysis* or *synostosis* respectively, as it falls outside the scope of this macroscopic study.

TYPING & LAYOUT OF MANUSCRIPT, DIGITAL REMASTERING OF ILLUSTRATIONS, AND ANNOTATIONS:

After choosing representative skulls and mandibles, and selecting the best views, hand drawn illustrations in monochrome were made by the biomedical artist that used to work at this Faculty. For possible future clinical use and comparison with the bovine, radiographs of an intact formalinized head of an immature animal, but the skull of a mature animal, are included. As it compares well enough with that of the bovine, no discussion on the radiology is given as it falls beyond the scope of this study [74] . Viewing of radiographs is ruled by conventions that are not the same as for anatomical illustrations. However, the rules applicable for anatomical illustrations were applied for the lateral radiographic view of an immature animal.

The purpose of all the anatomical illustrations, the digitally remastered photos and the radiographs, is to capture not only the detail but also most of the variations that were seen in this study on the osteology. Schematic and semi-schematic illustrations were made in order to create additional visual material as an adjunct to the text. That was also the purpose of the paranasal sinus model. The photos of the radiographs were done directly digitally, but all the others slides were scanned first (analogue-to-digital) by the author. All the illustrations, including the monochrome illustrations and the radiographs, were digitally remastered and annotated by the author. Typing and the layout of the manuscript was also done by the author. The computerized work and the physical measurements taken of the skulls, were done by using standard computers, computer graphics software and standard measuring tools * [22] .

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22 Various models of computer hardware and different version of software were used over the years of the study. The software included the following **:** "Corel Photopaint 7" (by "Corel Draw 7"), "Corel Word Perfect 8", "Adobe Acrobat 5.0", "Snappy" (an image grabber, used with a "Sony CCD" video camera, fitted with a "Canon" 8 - 80 mm zoom lens), a "Pentax ME super" reflex camera with various lenses, and a "HP S20" scanner. A "HP Deskjet 820 Cxi" printer was also used. The last computer used was a "Mecer" personal computer, fitted with an "Intel Pentium III" processor. The auditory ossicles were studied using a "Nikon SMZ 10 " stereo-microscope, fitted with a "Nikon HFX II" aperture setting system. A slide gauge with vernier scale, a set of curved callipers, and metric rulers were used for taking measurements for the section on **Craniometric data**. Household silicon was used to build the paranasal sinus model.

CHAPTER THREE

RESULTS

A : THE BONES OF THE SKULL

1. INTRODUCTION TO THE CRANIAL BONES (*OSSA CRANII*)

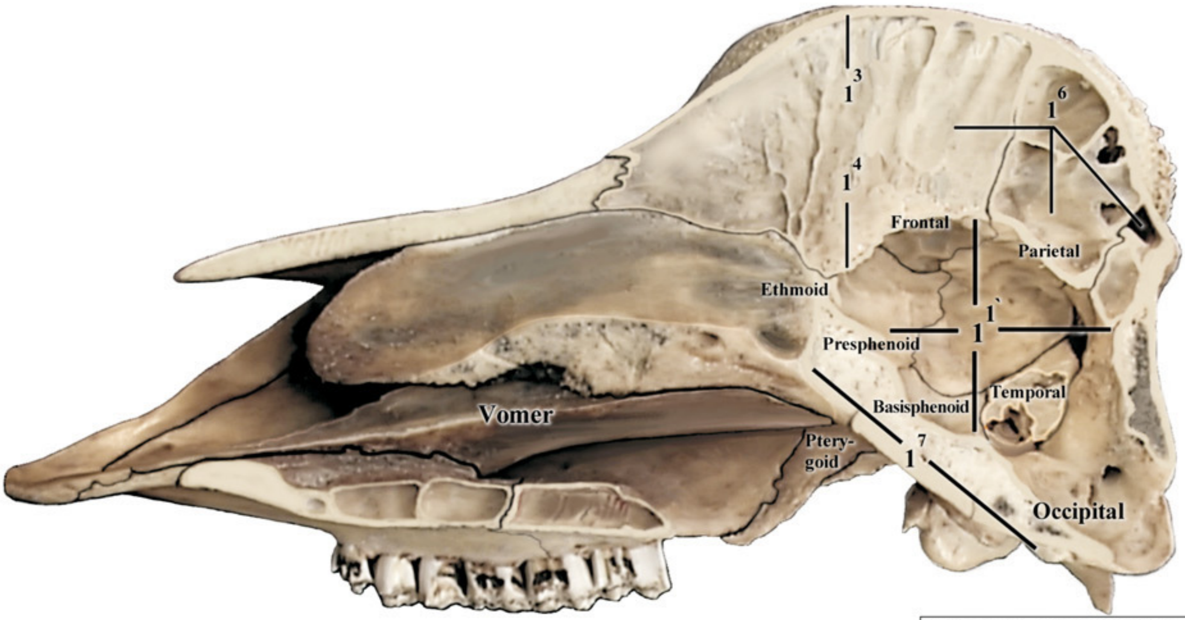
(See figures **3.1 - 3.11**. Also see 3.31.)

The different **bones of the cranium** (*Ossa cranii* **1** [1]), are arranged as paired and unpaired bones around the **cranial cavity** (*Cavum cranii* **1** [1`] ). Only eight of the thirteen participate to form a semi-solid boney [neuro-]**cranium** (*CRANIUM* **1** [2] ) (See also 1 [22] - vide infra.) The cranium, the bones of the face as well as the bones of the **vertebral column** (*COLLUMNA VERTEBRALIS* **1** [2`]) form the **axial skeleton** (*SKELETON AXIALE* **1** [2``]). The bones of the cranium are the occipital, interparietal, basisphenoid, presphenoid, pterygoid, temporal, parietal, frontal and ethmoid bones as well as the vomer. The interparietal bone - or what appears to be a remnant of it - is not always visible in all specimens. The auditory ossicles also belong under the bones of the cranium, but they are not counted in the eight bones that directly contribute to form the cranium. The pterygoid is also not counted (vide infra). Various foramina and canals connect the cranial cavity to the vertebral canal, the face, the nasal cavity and the ventral surface of the skull. (See also subheading 13 for a synopsis of the facial bones.)

Except for the vomer, the interparietal and the pterygoid bones, the other bones of the cranium as listed above, all present both **external** and **internal surfaces** (*Lamina externa / interna* **1** [3 / 4]). The internal and external layers are formed by layers of **compact bone** (*Substantia compacta* **1** [3` / 4`]). These layers are separated from each other by the **diploë** (*Diploë* **1** [5]) which consists of **spongy bone** (*Substantia spongiosa* **1** [5`] ). The spongy bone is usually of a **trabecular type** (Spongiosa trabeculosa* **1** [5`a]), but it can also be of a

FIGURE 3.1 : OSTEOLOGY

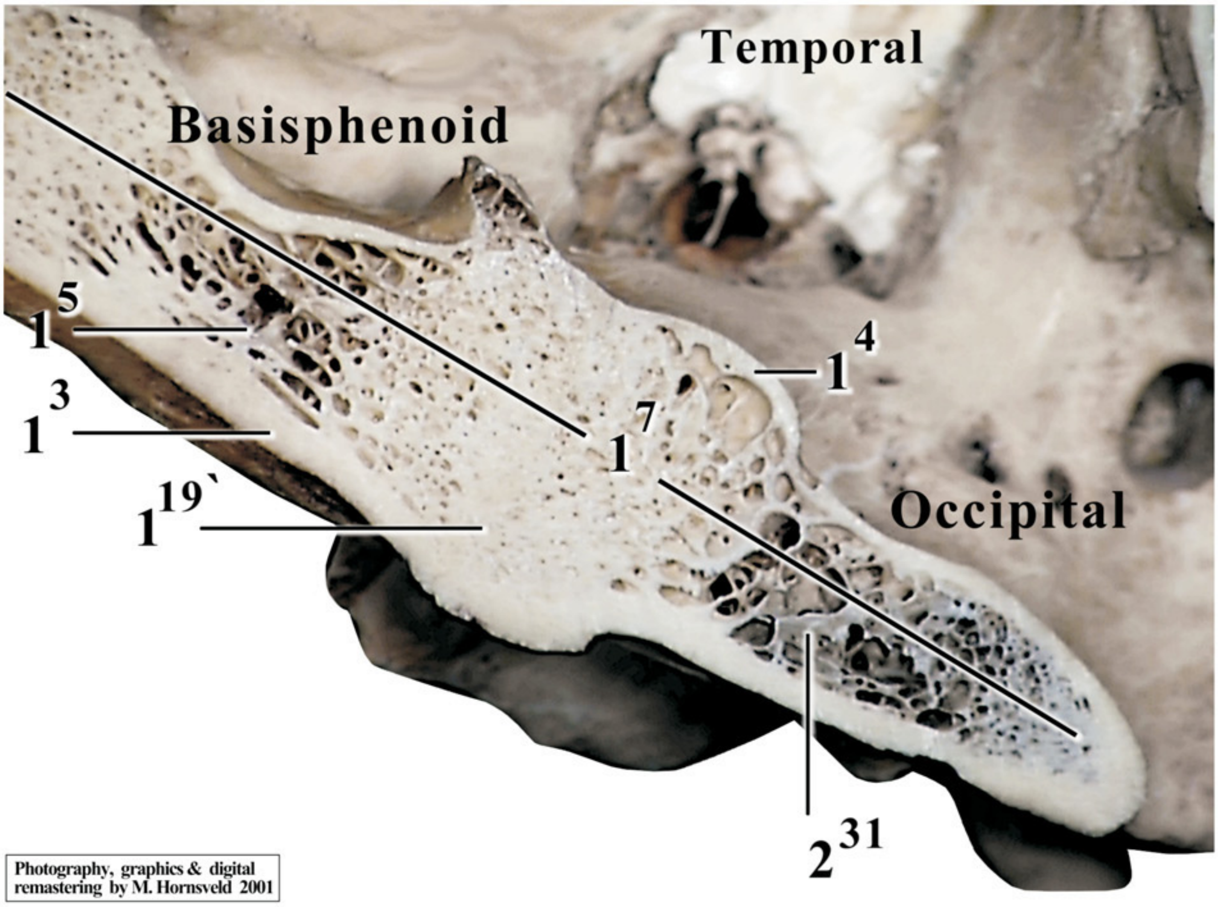
THE BONES OF THE CRANIUM (MEDIAL VIEW)



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.2 : OSTEOLOGY

COMPACT AND SPONGY BONE AT THE BASE OF THE SKULL (MEDIAL VIEW)



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.3 : OSTEOLOGY

VIEW ONE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

FIGURE 3.3 : OSTEOLOGY
VIEW ONE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

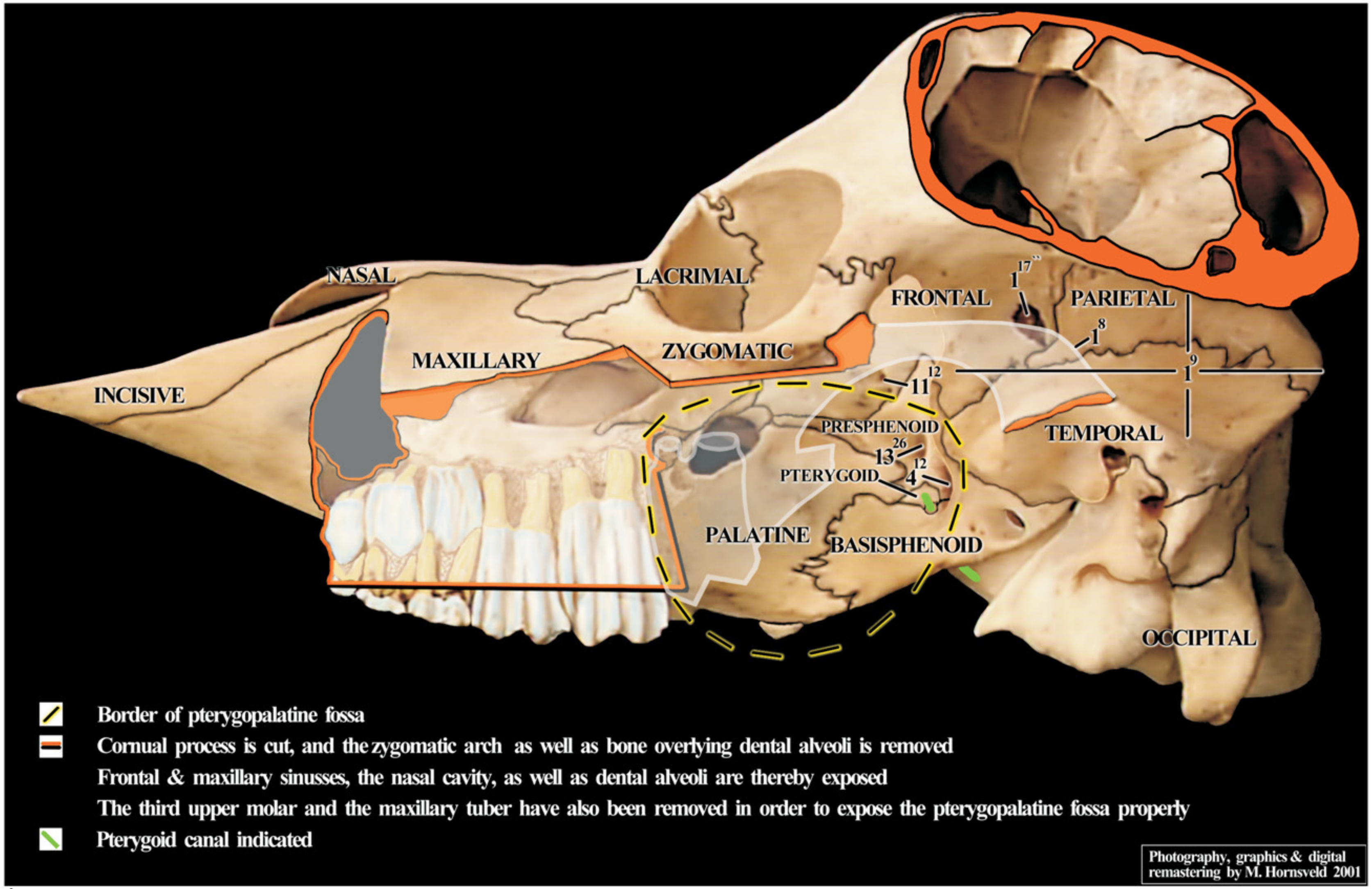


FIGURE 3.4 : OSTEOLOGY

VIEW ONE OF THE *OCCIPUT* OF A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

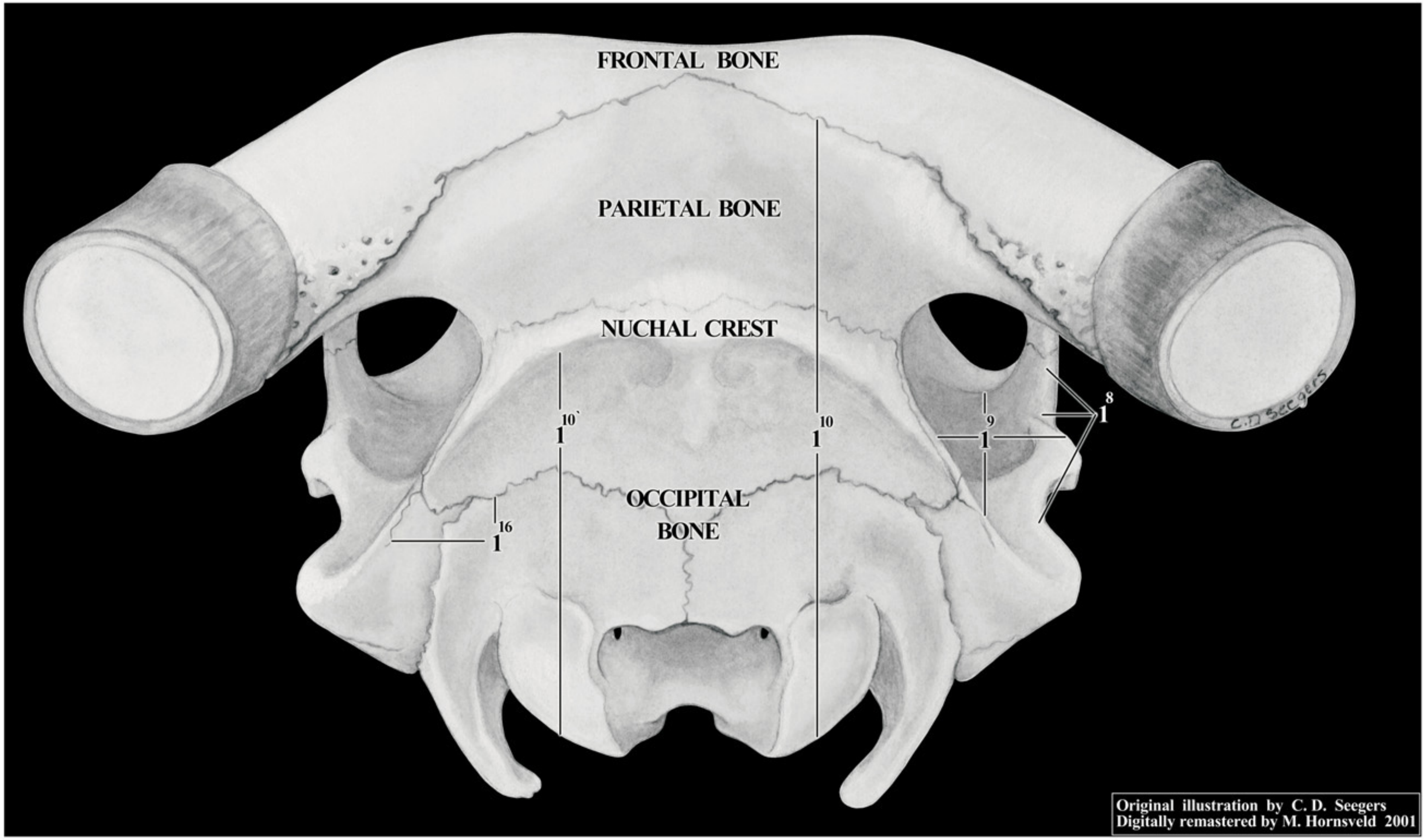


FIGURE 3.4 : OSTEOLOGY
VIEW ONE OF THE *OCCIPUT* OF A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

FIGURE 3.5 : OSTEOLOGY

THE *OCCIPUT* OF A MATURE SAVANNAH BUFFALO COW (CAUDAL VIEW)

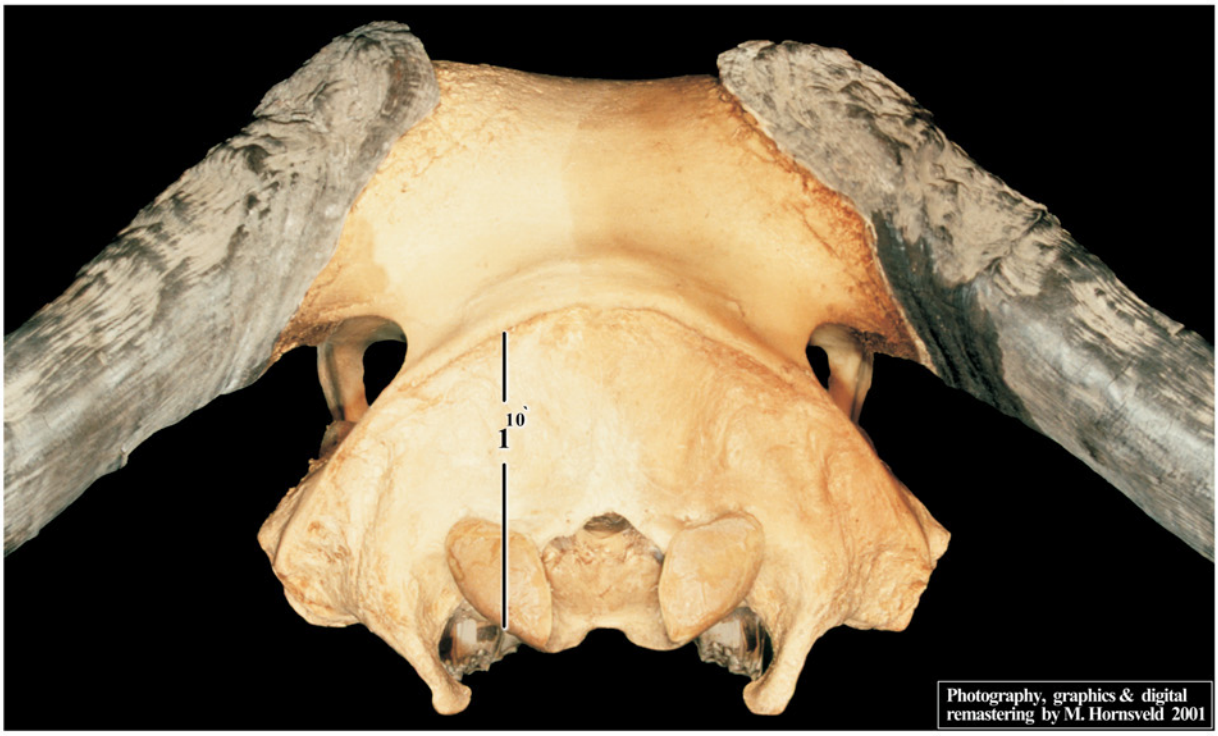


FIGURE 3.6 : OSTEOLOGY

THE ROOF, SUMMIT AND FOREHEAD OF THE SAVANNAH BUFFALO BULL (MEDIAL VIEW)

FIGURE 3.6 : OSTEOLOGY
THE ROOF, SUMMIT AND FOREHEAD OF THE SAVANNAH BUFFALO BULL (MEDIAL VIEW)

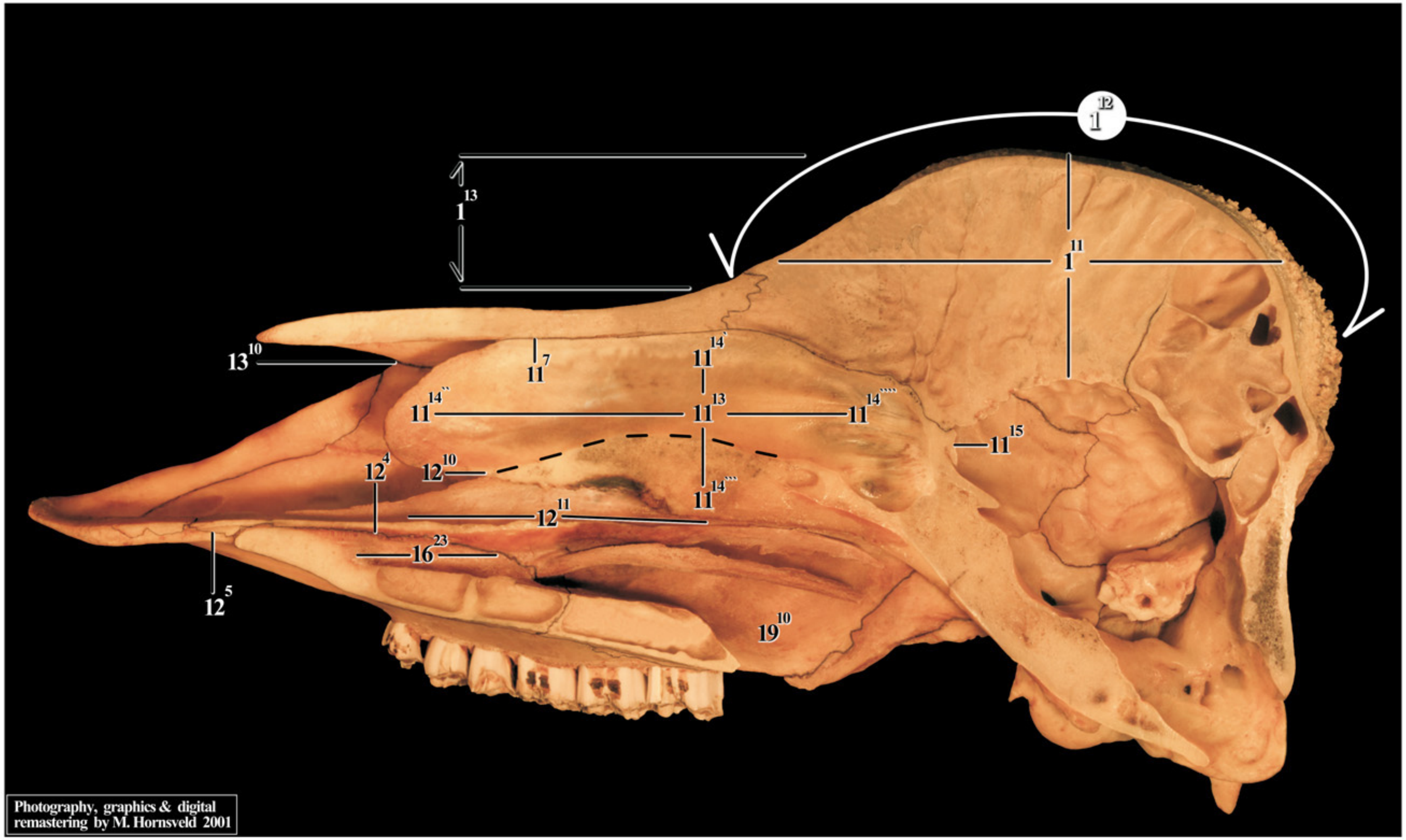


FIGURE 3.7 : OSTEOLOGY

THE FOREHEAD AND THE FRONTAL FOSSA IN AN OLD BULL (OBLIQUE ROSTRAL VIEW)

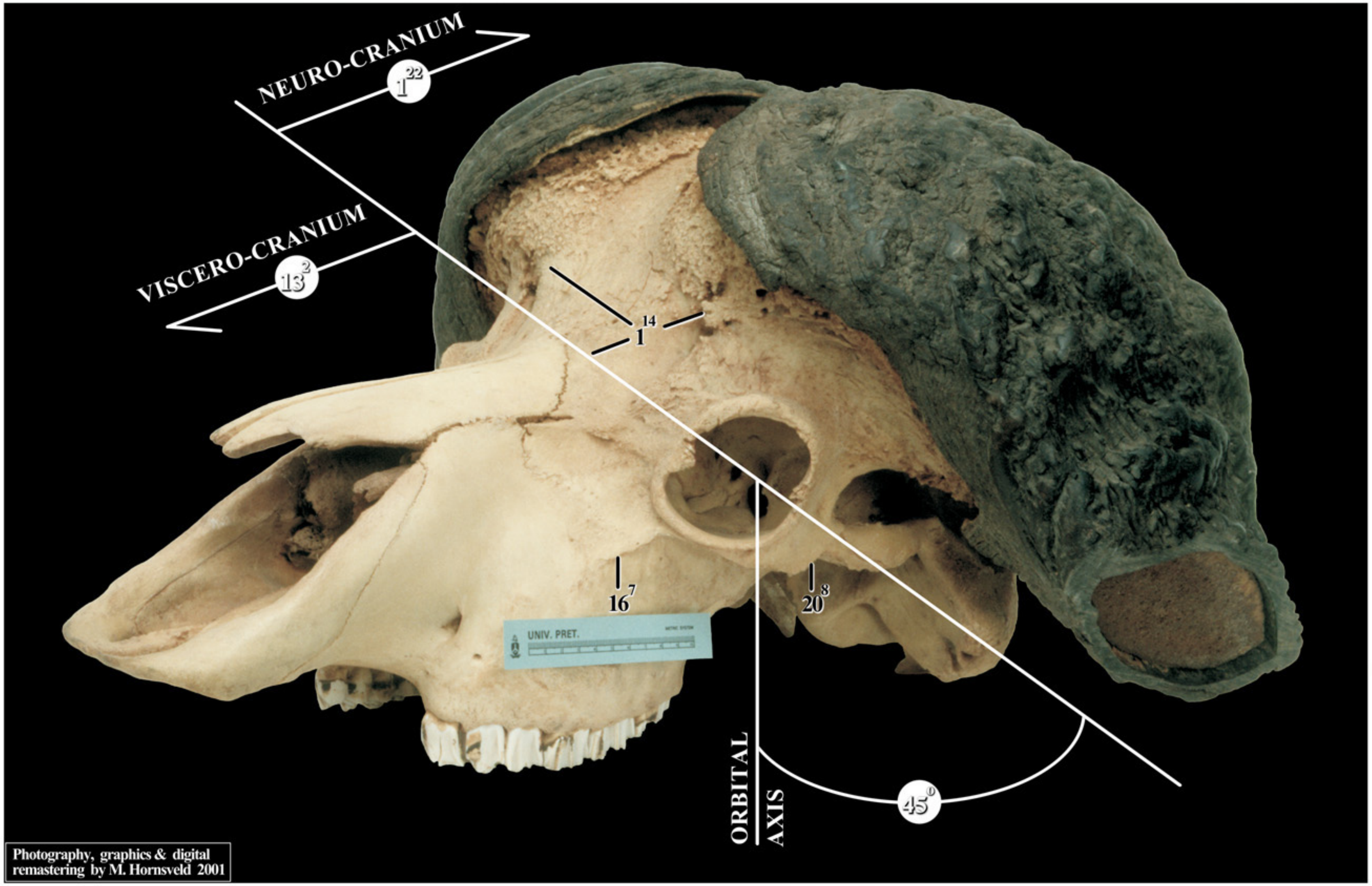


FIGURE 3.7 : OSTEOLOGY
THE FOREHEAD AND THE FRONTAL FOSSA IN AN OLD BULL (OBLIQUE ROSTRAL VIEW)

FIGURE 3.8 : OSTEOLOGY

SUTURES AND FONTANELLES IN THE SKULL OF A YOUNG CALF OF APPROXIMATELY 3 - 4 MONTHS OF AGE (MEDIAL VIEW)

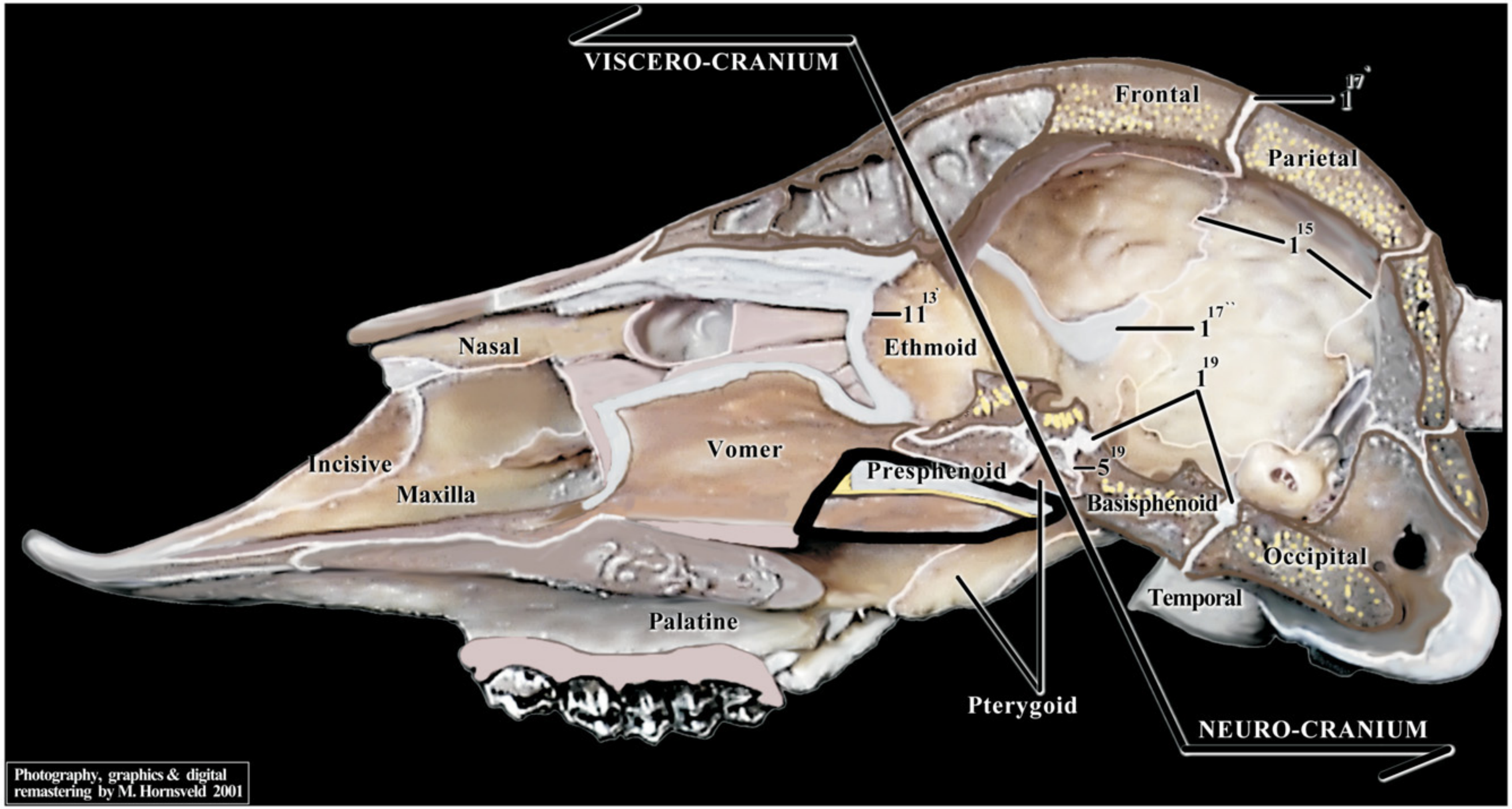
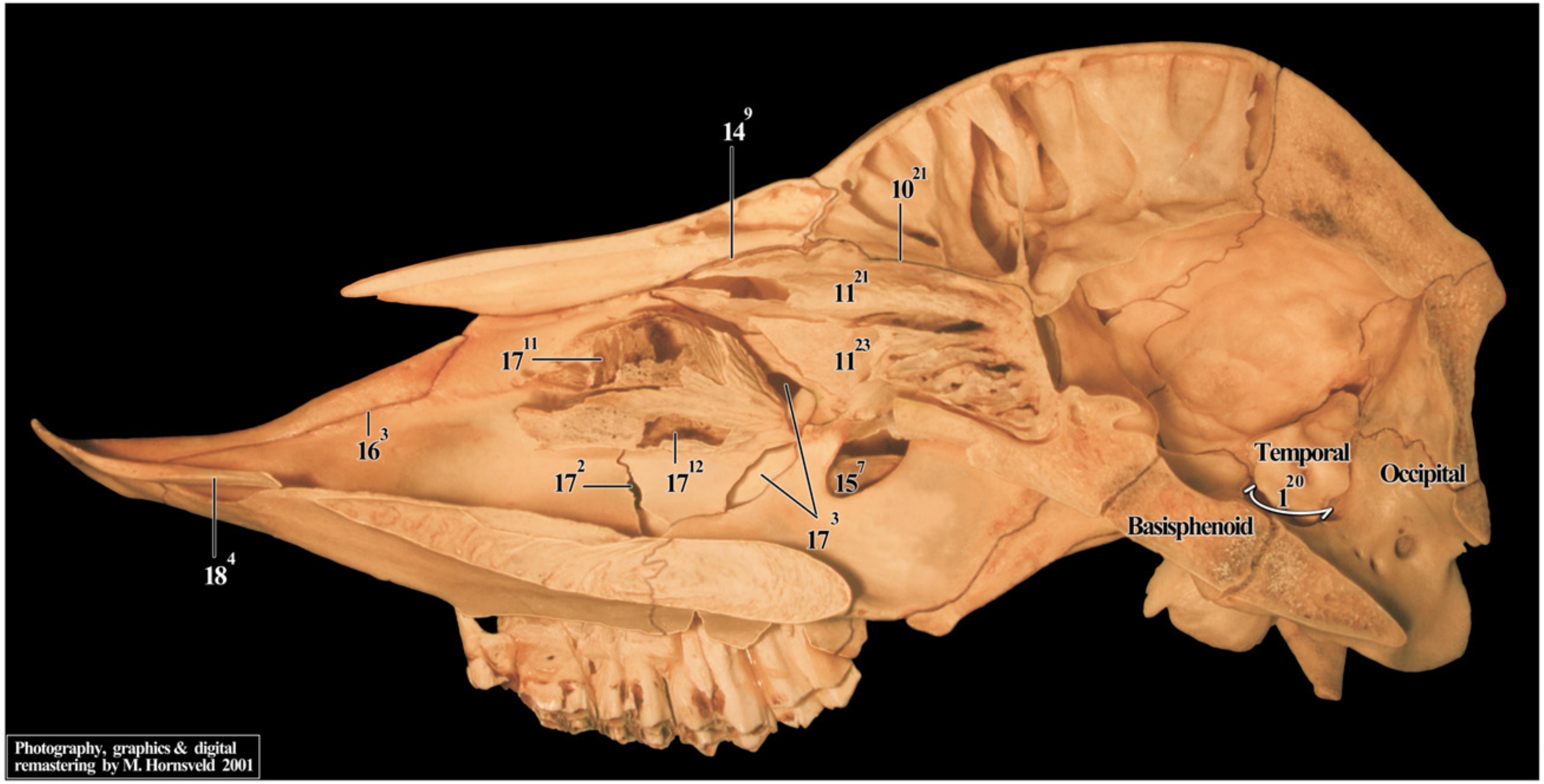


FIGURE 3.8 : OSTEOLOGY
SUTURES AND FONTANELLES IN THE SKULL OF A YOUNG CALF OF APPROXIMATELY 3 - 4 MONTHS OF AGE (MEDIAL VIEW)

FIGURE 3.9 : OSTEOLOGY

THE LACERATED FORAMEN (MEDIAL VIEW)



THE LACERATED FORAMEN (MEDIAL VIEW)

FIGURE 3.9 : OSTEOLOGY

FIGURE 3.10 : OSTEOLOGY

THE TEMPOROMANDIBULAR JOINT AND THE SKULL-HYOID ARTICULATION IN A YOUNG CALF (LATERAL VIEW)

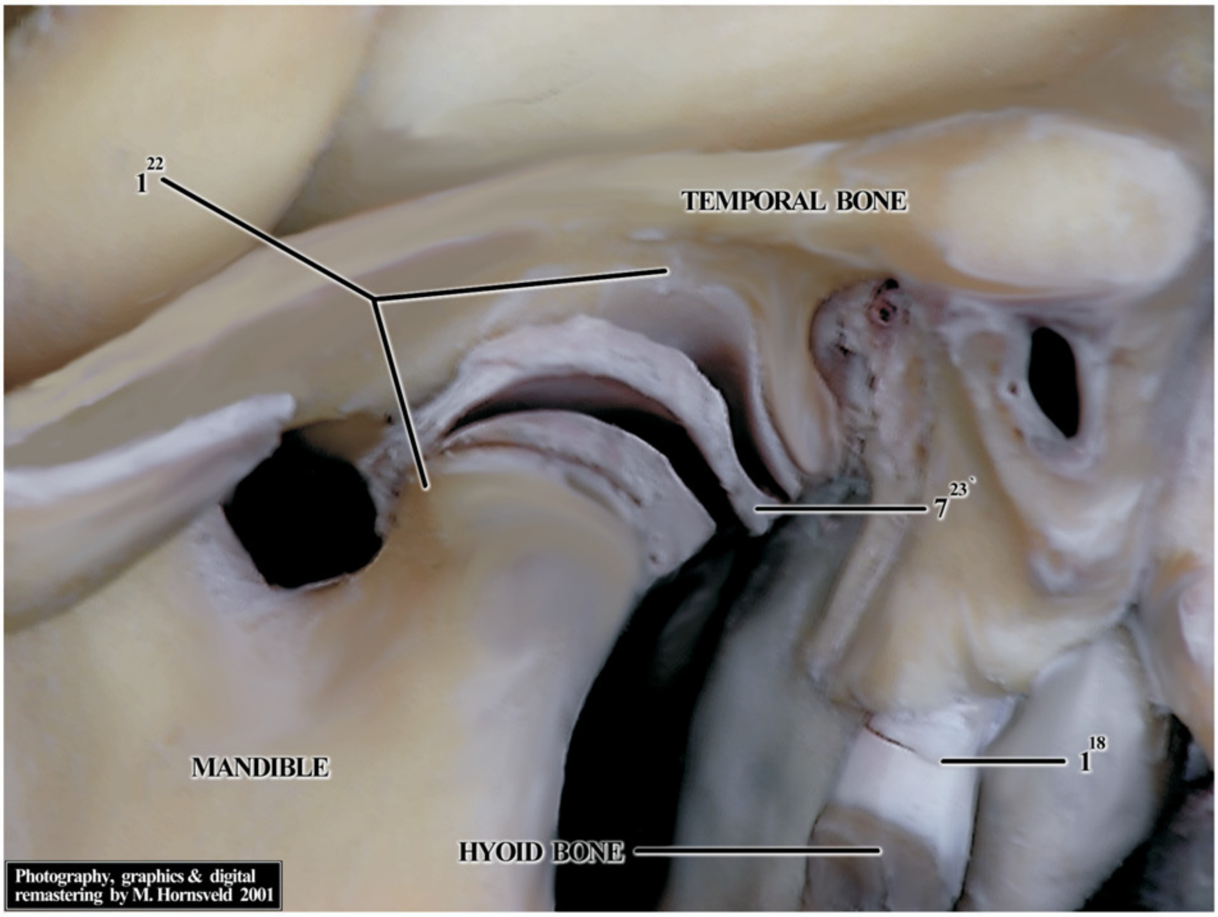
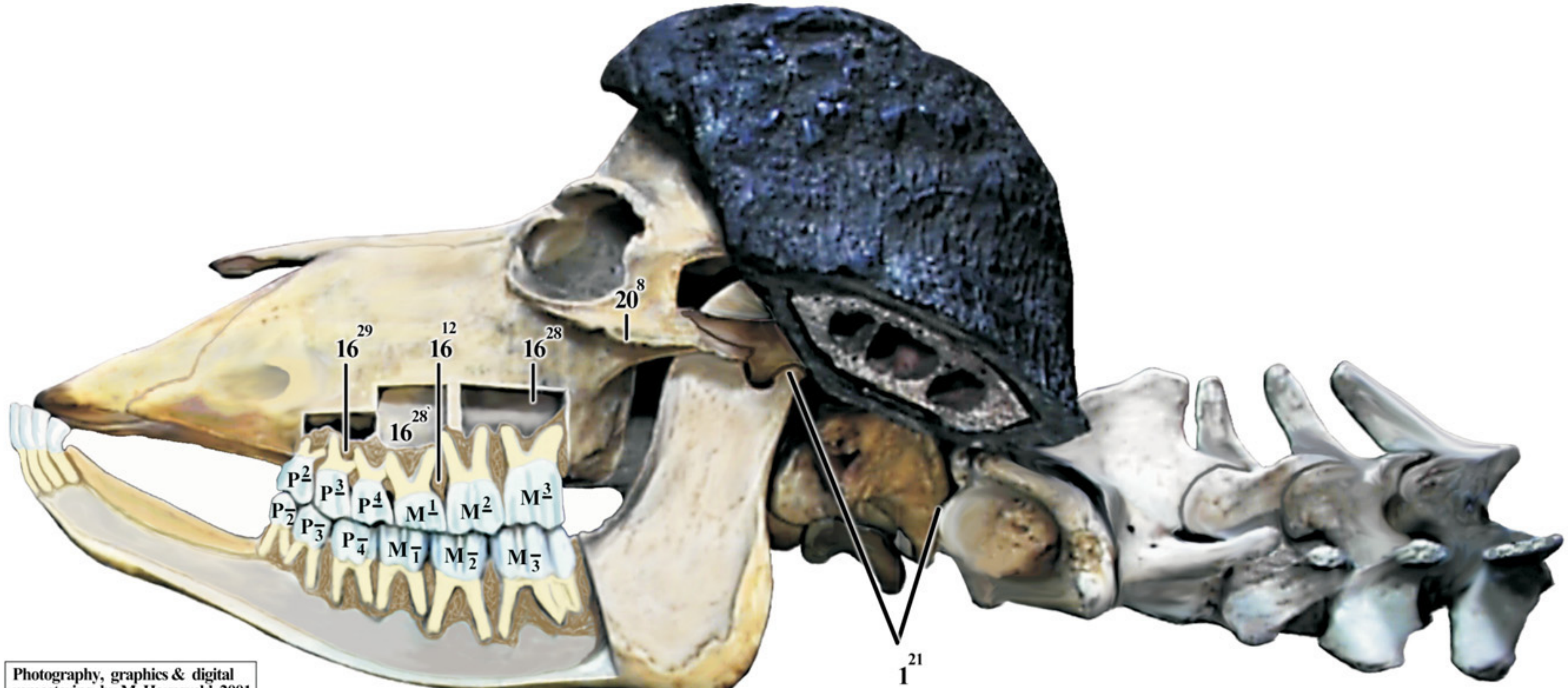


FIGURE 3.11 : OSTEOLOGY

**THE SKULL, MANDIBLE AND CERVICAL VERTEBRAE IN THE DATUM PLANE (LATERAL VIEW) :
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY**

FIGURE 3.11 : OSTEOLOGY
THE SKULL, MANDIBLE AND CERVICAL VERTEBRAE IN THE DATUM PLANE (LATERAL VIEW) :
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY



Photography, graphics & digital remastering by M. Hornsveld 2001

lamellar type (see 2[31]). In the live animal, the diploë can be filled with either **red** or **yellow** **bone marrow**(*Medulla ossium rubra / flava* **1**[5`` / 5```]). The diploë of especially the frontal bone is extremely well developed. Displacement of the diploë and aeration of especially the frontal and parietal bones - and other bones - forms large sinuses. All these sinuses are connected directly or indirectly to the nasal cavity to form **paranasal sinuses** (*Sinus paranasales* **1**[6]). (See also 2[32], 5[10], 9[11 & 12], 10[31 & 32], 14[10], 15[16], 16[16] as well as section C under chapter 3 **: The Skull Cavities**.) The paranasal sinuses contribute to a large extend to the massive size and pyramidal shape of the skull.

The occipital, the interparietal, the basisphenoid and the presphenoid bones are unpaired bones. The bodies of these bones - or in the case of the interparietal bone, only remnants of it - lie on the median plane, and all but the interparietal, are situated at the base of the cranium. Excluding the dorsally situated interparietal bone, they form the **skull base** (Basis cranii* **1**[7]). (See also 5[12` & 12``] and section D **: Craniometric data**, for basal axis*.) The bodies of the pterygoid bone, and the (paired) wings and processes of the basisphenoid and presphenoid bones participate - together with the palatine bones of the face - to form the pterygopalatine fossa (13[30]) on either side of the skull. The fossa on each side is connected to the cranial cavity via the combined round and orbital foramen (4[12]), the optic canal (13[26]), and the ethmoid foramen (11[12] or 13[27]).

The temporal, the parietal and the frontal bones are paired bones that are fused to their counterparts or antimeres across the median plane. The temporal bone forms the latero-ventral part of the skull and a major part of the **zygomatic arch** (*Arcus zygomaticus* **1**[8]). Internally, the parietal bone forms the lateral walls of the cranial cavity and externally it forms a minor part of the **temporal fossa** (*Fossa temporalis* **1**[9]). The occipital bone as major contributor, and the parietal (- and interparietal -) bones as minor contributors, form the **caudal part of the skull** (*Occiput* **1**[10]). The occiput is flat, lies transversely, and is extensive, being formed by the bones dorsal and ventral to the nuchal crest (see 2[24]). That part of the occiput that lies ventral to the crest, forms the **nuchal surface*** (**1**[10`]) of the skull. The frontal bone forms the major part of the **roof** (*Calvaria* **1**[11]) of the skull. The frontal bone also forms the cornual processes. The Calvaria and the bases of the cornual processes are prominent, forming a pronounced **summit** (*Vertex* **1**[12]). The summit is marked by the presence of an intercornual groove (see 10[12]). Rostrally, the summit projects dorsally beyond the level of the [viscero-]cranium* (see 13[2]) to form a **forehead** (*Frons* **1**[13]). At the junction between the frontal bone and the bones of the face, an unpaired concavity forms the **frontal fossa** (*Fossa frontalis* **1**[14]). (See also glabella 10[12``] .) In cows, the forehead and the frontal fossa are less clearly defined. The frontal bone of old bulls extends caudally to the caudal-most end of the skull, and reaches the occiput (1[10]). By that, the frontal bone forms a smaller frontal part of the occipital surface. However, it does not project further caudally than the nuchal surface itself.

The paired bones of the skull articulate with each other - usually and typically, but not always - by means of **fibrous joints** (*Articulationes fibrosae* **1**[15]) of different **suture types** (*Sutura* **1**[16]). Some sutures of the [neuro-]cranium* (see 1[22] below) ossify late in life. Atypical for a mammal, the skull of the savannah buffalo is marked by the presence of a paired **cranial fontanelle** (*Fonticuli cranii* **1**[17]) in sub-adults. The unpaired **frontoparietal fontanelle** (*Fonticulus frontoparietalis* **1**[17`] ) is - as can be expected - small. At the age of three to four months of age, it is still visible, but becomes partially ossified soon afterwards. (See 9[5`] , 10[5] , 10[28] , footnotes 28 & 94, as well as chapter four **: Discussion**, point two.) The paired cranial fontanelle that is of interest is situated laterally in the wall of the cranium and remains dormant. However, in sub-adult animals of approximately 2 years of age, a larger, but temporary, fontanelle becomes reestablished. It is atypical in many respects. In external view, this fontanel is situated in the temporal fossa, and it can therefore be considered as homologous to the **sphenoid fontanelle** (*Fonticulus sphenoidalis* **1**[17``]) of man. It usually becomes ossified in late adulthood again, except sometimes for a smaller internal part. (See footnote 42.)

The unpaired bones at the base of the skull articulate by means of **cartilaginous joints** (*Articulationes cartilagineae* **1**[18]) of the **synchondrosis type** (*Synchondrosis* **1**[19]) to each other. These joints ossify late in life, forming **synostosis** (*Synostosis* **1**[19`]). Incomplete fusions between the unpaired bones at the base of the skull and the temporal bone, form, among others, the **lacerated foramen** (*Foramen lacerum* **1** [20]). (See also 7 [1] and footnote 56.)

The squamous part of the temporal bone articulate by means of a **synovial joint** (*Articulationes synoviales* **1** [21]) with the mandible. The petrous part of the temporal bone articulate by means of a fibro-cartilaginous joint of the symphysis type (22 [10]) with the hyoid bone. (See subheadings 13 and 22.) The occipital bones' articulation with the first cervical vertebra is also by means of a synovial joint.

Although the vomer traditionally belongs to the bones of the cranium, the vomer does not contribute to the formation of the **[neuro-]cranium*** (**1** [22]). (See footnote 120.) The ethmoid bone forms the rostral wall of the cranial cavity. By that, the cranial cavity (1 [1`]) is separated from the nasal cavity (13 [4]). Together, the vomer and the ethmoid bone - with some contribution of the rostrum of the presphenoid bone - form an incomplete boney nasal septum (13 [11] or 11 [14]). This septum lies in the median plane, dividing the nasal cavity into equal halves. (See subheading 13 for a synopsis of the facial bones and the nasal septum.) The frontal bone extends rostrally beyond the borders of the cranium (1 [2]). By that, it also forms part of the boney orbit (13 [21]), and a small part of the external facial surface. Therefore, the frontal bone (as external component), together with the vomer, ethmoid and presphenoid bones (as internal components), contribute partially to the formation of the [viscero-] cranium (13 [2]) - even though they are cranial bones. The boney orbit (13 [21]) and the dorsum of the skull is connected to each other by means of a large supraorbital canal (13 [29] or 10 [22`]).

The pterygoid bone is traditionally also considered to be a cranial bone. However, the wings of the pterygoid only contributes to a small part of the lateral wall of the boney choana (13 [12]). The body of the pterygoid only contributes to a small area of the medial wall of the pterygopalatine fossa (13 [30]). The pterygoid as a whole therefore, contributes only to the formation of the face. (See also **Discussion**, point 7.)

2. THE OCCIPITAL BONE

(*OS OCCIPITALE*)

(See figures **3.12 - 3.14**. Also see 1.4, 3.1 - 3.5, 3.8 & 3.9.)

The occipital bone consists of paired lateral parts interposed between unpaired squamous and basilar parts. The lateral and basilar parts are arranged around the **large occipital foramen** (*Foramen magnum* **2** [1]), the diameter of which varies considerably among old animals (32 - 45 mm). The external surfaces of the lateral and the squamous parts form a major part of the caudal aspect, or nuchal surface, (1 [10`]) of the skull. The lateral parts have paramedian condyles that articulate with the first cervical vertebra, the atlas or C_1. The body or **basilar part** (*Pars basilaris* **2** [2]) forms the caudal third of the base of the cranium. The internal surfaces of all the parts of the occipital bone forms the **floor** (*Fossa cranii caudalis* **2** [2`] ) - as well as the caudal wall - of approximately the **caudal third** of the cranial cavity (Cavum cranii 1 [1`]). (See also 4 [1`] & 5 [12] for middle and rostral thirds.) The occipital bone harbours a very small part of the frontal sinus complex, to form the most caudal end of that sinus.

The basilar part or body (2 [2]) is unpaired and lies in the median plane. The axis of the body is directed at an angle of approximately 140 degrees to the general longitudinal axis of the skull. (See basal axis* under the **Glossary of terms**. Also see FINAL COMMENT 8 and measurement §74 under section D **: Craniometric data**. The bodies of the basisphenoid and presphenoid bones also contribute to the basal axis*.) The rostral half of the body of the occipital bone is cylindrical and its rostral end articulates with the body of the basisphenoid bone at the **spheno-occipital synchondrosis** (*Synchondrosis spheno-occipitalis* **2** [3]). In old animals the joint is ossified, forming a synostosis (1 [19`]).

The ventral or external surface of the body is laterally convex. Rostrally it carries the larger part of the paired **muscular tubercle** (*Tuberculum musculare* **2** [4]) on the fusion line with the basisphenoid bone. (See also basisphenoid bone for smaller rostral part.) The muscular

FIGURE 3.12 : OSTEOLOGY

VIEW TWO OF THE *OCCIPIT* IN A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

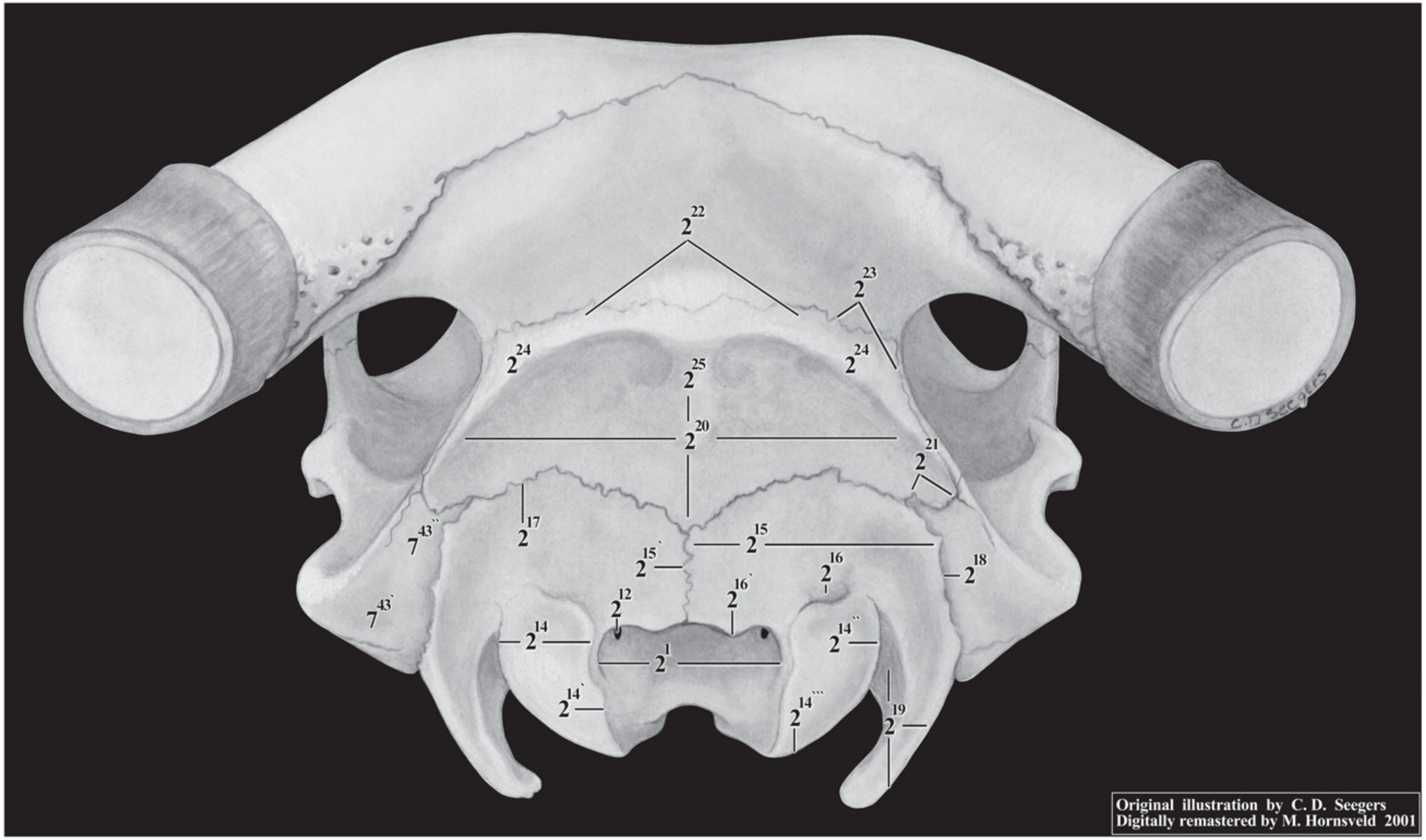


FIGURE 3.12 : OSTEOLOGY
VIEW TWO OF THE *OCCIPIT* IN A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

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FIGURE 3.13 : OSTEOLOGY

VIEW ONE OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)

Note : The skull was cut to the right of the median plane, except for the rostral part of the hard palate where the median septum can still be seen. Part of the rostrum presphenoidale has been cut even more paramedially (to the right) to expose its sinus. Because it is a paramedian section, the vomer is not shown.

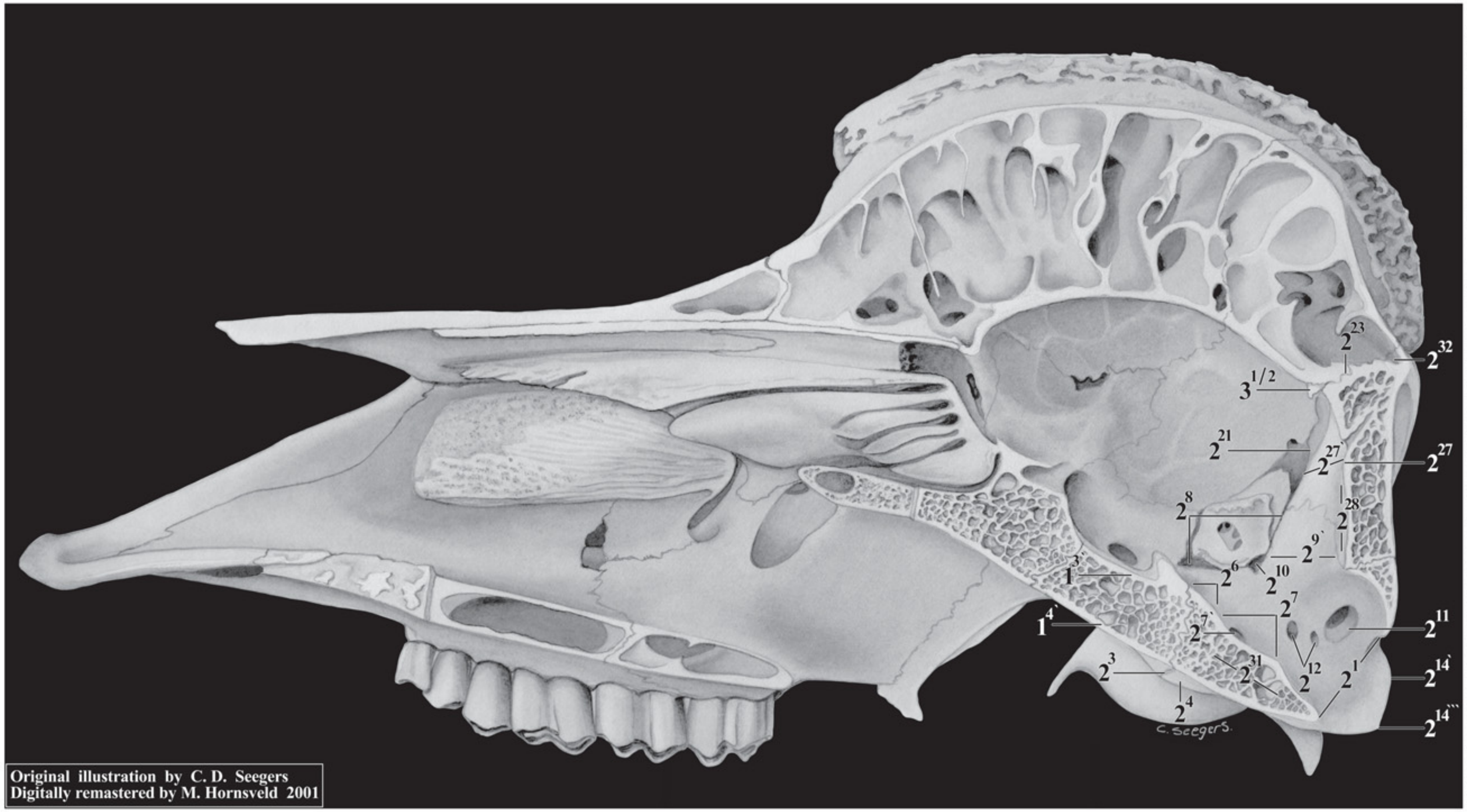

FIGURE 3.13 : OSTEOLOGY
VIEW ONE OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)
Note : The skull was cut to the right of the median plane, except for the rostral part of the hard palate where the median septum can still be seen. Part of the rostrum presphenoidale has been cut even more paramedially (to the right) to expose its sinus. Because it is a paramedian section, the vomer is not shown.

FIGURE 3.14 : OSTEOLOGY

VIEW ONE OF THE SKULL OF A MATURE BULL (VENTRAL VIEW)

tubercle is elongated along the basal axis* of the skull and its roughened surface is raised to varying degrees in different animals. Caudally the external surface of the body bears the paired **pharyngeal tubercle** (*Tuberculum pharyngeum* **2** [5]). The pharyngeal tubercle is wide and elongated in the transverse plane. Its surface is rounded and raised. Differences in how much it can be raised in the skulls of different animals, does not vary as much as that of the muscular tubercle (2 [4]).

The dorsal or internal surface of the body is laterally concave, forming part of the caudal part of the floor of the cranial cavity (vide supra, Fossa cranii caudalis 2 [2`]). It is divided into rostral and caudal parts.

The rostral part lies at a higher dorsal plane and it bears the larger caudal part of the negative **impression of the pons** (*Impressio pontina* **2** [6]). (Note **:** A much smaller rostral part of this impression, lie even further rostrally, on the basisphenoid bone. That basisphenoidal part of the impression, lies just caudal to the ‘Turkish saddle’ - see 4 [7] .) The caudal part of the internal surface is less concave and it bears the **medullary impression** (*Impressio medullaris* **2** [7]). In some old animals, a **foramen** (**2** [7`]) may open onto the impression, just off the median plane, and in both antimeres. The diameter of such a foramen can vary between 1 mm and 5 mm. The paired foramina lead to **diploïc canals** (*Canales diploici* **2** [7``]) which immediately divides into one main and a few side branches. The side branches end in the diploë of the (unpaired) body of the occipital bone. Each opening to a side branch can therefore also be regarded as a **nutrient foramen** (*Foramen nutricium* **2** [7```]) with a **nutrient canal** (*Canalis nutricius* **2** [7````]). (See 2 [19`] and footnote 24, 7 [88] , 10 [22] and 20 [8```] for homologous canals. Also see 2 [29] , 4 [12`] ,4 [19] and 7 [9``/````] .) The main part of each of these diploïc canals, opens into the petro-occipital fissure (2 [8] , vide infra). The lateral surface of the rostral half of the body is free and it borders the rostral part of the spacious **petro-occipital fissure** (*Fissura petrooccipitalis* **2** [8]). (See also 7 [1] , 7 [31, 32 & 33] , the accompanying footnotes 56 & 69, as well as 1 [20] .)

The caudal half of the body expands laterally and is dorso-ventrally flattened. It is continuous with the lateral part of the occipital bone (vide infra under 2 [9]).

At the caudal end of the body, the internal and the external surfaces meet, forming the ventral margin of the occipital foramen (2 [1]). (See Basion*# - the point **B** - and FINAL COMMENT 8 under section D **: Craniometric data :** The ventral margin of the occipital foramen defines the most caudal point of the basal axis* - or **axis I** - by definition, even though the condyles project further caudally.)

The **lateral parts** (*Pars lateralis* **2** [9]) of the occipital bone consist of three paired parts namely
perpendicular parts (2 [9`]) - which are situated rostrally -
articulatory condyles (2 [14]) - which are situated caudally - and
flat parts (2 [15]), which are situated dorsally.

The **perpendicular part** (**2** [9`]) of the **pars lateralis** is placed sagittally on the caudal half of the body and presents internal and external surfaces and a rostral free margin. The rostral free margin borders that caudal part of the petro-occipital fissure which is also the internal opening of the **jugular foramen** (*Foramen jugulare* **2** [10]). The internal surface (of the perpendicular part) is continuous with the internal surface of the body. It is perforated dorsally by a much larger and ventrally by one or two smaller foramina. The dorsal foramen - which is approximately 5 - 10 mm in diameter - is the internal opening of the **condylar canal** (*Canalis condylaris* **2** [11]). (See footnote 24.) The ventral foramen or foramina are the internal openings of the **canals for the hypoglossal nerves** (*Canalis n. hypoglossi* **2** [12]). They are approximately 2 - 5 mm in diameter. The external surface of the perpendicular part is profoundly concave to form the **ventral condylar fossa** (*Fossa condylaris ventralis* **2** [13]), into which both the above canals (both 2 [11] and 2 [12]) open separately. The **external openings of the condylar and hypoglossal canals** are denoted **2** [11`] and **2** [12``] respectively in illustrations. These openings can be single or double. Their diameters are not necessarily related in size (or shape) to the corresponding internal openings. (See also footnote 24.)

Caudally, the perpendicular part of the pars lateralis bears the large **articulatory condyle** (*Condylus occipitalis* **2**[14]). The condyle presents two free margins and an articulatory surface. The **medial margins** (**2**[14`]) of the left and right condyles diverge dorsally, forming the lateral margins of the occipital foramen (2[1]). The **lateral margin** (**2**[14``]) of a condyle borders the ventral condylar fossa (2[13]) ventrally and caudally. A **low ridge** (**2**[14```]) divides the articular surface of the condyle into dorsal and ventral parts. (See FINAL COMMENT 11 in section D **: Craniometric data**, where the caudo-medial end of this ridge is allocated the point **P`**, as opposed to the point **P**, the Prosthion, at the apical end of the skull. The distance between **P** to **P`** gives the maximum skull length which is more accurate than the 'condylobasal length' - compare measurements 2 and §63 in section D.) The ventral and dorsal ends of the condyles blend with the pharyngeal tubercles (2[5]) and with the flat parts of the pars lateralis (vide infra) respectively.

The paired **flat part** (**2**[15]) of the **pars lateralis** lies transversely. Each antimere is semi-lunar in shape, with the convex borders curving dorsally. In young animals, younger than approximately 24 months of age, the antimeres are not fused yet and an **interoccipital suture** (Sutura interoccipitalis **2**[15`])*[23] can therefore be seen. In animals older than 24 months, the flat parts of the pars lateralis are completely fused to each other in the median plane. By then, the flat parts of the lateral part of the occipital bone, are also fused to the unpaired squamous part (2[20]) of the occipital bone (vide infra), and all appear as a single bone from then on.

The external surfaces are flat to form the ventral half of the nuchal surface of the skull, ventral to the nuchal crest. (See 2[20], and what follows, for dorsal half of nuchal surface.) Each flat part (2[15]) of the pars lateralis, is not strictly flat, but is slightly concave especially near the dorsal edge of the adjacent condyle. This concave area on the external surface of the flat part, forms the shallow **dorsal condylar fossa** (*Fossa condylaris dorsalis* **2**[16]).

23 The *N.A.V.* does not list an interoccipital suture (Sutura interoccipitalis 2[15`]).

The internal surfaces of the flat parts form a small part of the caudal wall of the cranial cavity. The external and internal surfaces meet medial to the condyles to form the dorsal margin of the occipital foramen (2 [1]). This dorsal margin is concave and wide. In some individuals the margin can bear **two short ill-defined processes** (**2** [16`]).

Dorsally, the flat parts are fused to the unpaired squamous part (vide infra) of the occipital bone at the **occipitosquamous suture** (*Sutura occipitosquamosa* **2** [17]). In animals of 24 months or older, the suture is completely ossified. Laterally, the flat parts are fused to the medial aspect of the mastoid processes of the temporal bone (7 [43]), at the **occipitomastoid sutures** (*Sutura occipitomastoidea* **2** [18]). This suture can sometimes still be faintly distinguished in older animals.

Lateral to the condyles, each flat part present a large, ventrally directed, **paracondylar process** (*Processus paracondylaris* **2** [19]). The process is sagittally flattened. Apart from its proximal basal attachment, it is free. The process curves medially (parallel to the low ridge of the condyle) and tapers distally. The distal end of the paracondylar process extends beyond the ventral level of the condyle. The base and the medial concave surface of the paracondylar process borders the ventral condylar fossa laterally. Proximally, the rostral surface of the base of the paracondylar process (as seen in ventral views) lies close to the tympanic bulla (7 [30]), and by that subdivides the caudal part of the petro-occipital fissure into medial and lateral parts **:** The medial part is the jugular foramen (2 [10] , vide supra) and the lateral part is the stylomastoid foramen. (See 7 [34] under the temporal bone.)

The condylar canal (Canalis condylaris 2 [11]) has been referred to above. It lies more or less horizontally and extends through the thickness of the perpendicular part of the occipital bone as a short canal. A side branch of the condylar canal - which is also a diploïc canal (2[7``]) - comes off the main canal and extends dorsally for a long distance, traversing the diploë of the flat part of the occipital bone. Having a much larger diameter in old animals, it opens where the internal surfaces of the occipital, the temporal and the parietal bones meet. It therefore opens in the dorsal part of the caudal cranial cavity. The appearance of this opening differs in young and old animals **:** In young animals this **opening of the side branch of the condylar canal** (**2** [19`])* [24] , lies caudo-medial to the internal opening of the temporal meatus. In old animals it forms the medial part of it. (See 7 [88] and footnote 89 under the temporal bone.)

The unpaired **squamous part of the occipital bone** (*Squama occipitalis* **2** [20]) is continuous with - and in the same transverse plane - as the paired flat parts (2 [15]). It presents external and internal surfaces and dorsal and ventral margins.

In caudal view, the ventral margin of the external surface is concave on either side of the median plane where it is fused to the paired semi-lunar flat parts (2 [15]). This ventral margin of each antimere, extends laterally for a short distance beyond the lateral extend of the convex borders of the semi-lunar lateral parts, to form additionally - albeit short - **mastoid margins** (*Margo mastoideus* **2** [21]). Externally, this part of the ventral margin is fused to the apical part of the mastoid process (7 [43``]) of the temporal bone at the occipitomastoid suture (2 [18]). Internally, the mastoid margin borders the internal opening of the (large) temporal meatus (7 [88]) dorsally and caudally in old animals. The dorsal or **parietal margin** (*Margo parietalis* **2** [22]) of the external surface of the unpaired squamous part of the occipital bone, is also semi-lunar in shape. This semi-lunar or convex parietal margin, is fused to the parietal bone at the **occipitoparietal suture** (Sutura occipitoparietalis **2** [23])* [25] . In animals older than approximately 16 - 24 months, the

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24 The condylar canal (2 [11]) should be described as having two ventral openings, one internally (as it opens into the cranial cavity) and one externally (where it opens on the ventral condylar fossa), as well as having an additional dorsal (internal) opening (2 [19`]). The internal surface for the condylar canal itself and that of its diploïc branch, should also be described. Nevertheless, being diploïc canals in essence, neither the condylar canal nor its side-branch, have external surfaces. (See 16 [28] for a canal that with both internal and external surfaces.) The condylar canal and its diploïc side-branch, are homologous to the temporal meatus and its diploïc canals. (See **footnote 89**.) Other examples of branching diploïc canals are found in the supraorbital canal (10 [22]) and the diploïc canals (2 [7`]) in the body of the occipital bone. The nutrient canal of the zygomatic bone (20 [8```]) does not have such side-branches that open on other bones.

25 The *N.A.V.* only lists an occipitointerparietal suture (Sutura occipitointerparietalis), not an occipitoparietal suture (Sutura occipitoparietalis 2 [23]). (See also interparietal and parietal bones.) The central part of the suture may in fact be the remains of the sutura occipitointerparietalis - that is if the interparietal bone / s actually did fuse to the parietal bones. However, this study excludes a study on the ontogenetic fusion of those bones that contribute to the formation of that part of the occiput during pre- and early postnatal development. (See also **footnotes 91 - 93**.) This footnote is **repeated under footnote 96**. In section D **: Craniometric data**, the median point on the occipitoparietal suture (externally) is allocated the term Lambda, showed by the abbreviation **L**. Because the external part of this suture ossifies between 16 and 24 months of age, disappearing totally, a median point on the nuchal crest - indicated as **L`** - is taken as a substitute.

external part of this suture is ossified and cannot be identified in older skulls. (The internal part of the occipitoparietal suture remains visible even in old animals and it lies on a deep groove or recess - see also 3 [1]). Externally, near the dorsal or parietal margin, the squamous part of the occipital bone is marked by the very prominent, dorsally convex, **nuchal crest** (*Crista nuchae* **2** [24])* [26] . The crest extends laterally beyond the level where the mastoid and the parietal margins of the occipital bone meet, to terminate laterally, more or less at the level of the base of the mastoid process (7 [43`] ) of the temporal bone. This termination of the nuchal crest is usually slightly more ventrally situated than the end of the temporal line. (See 7 [9`] under the temporal bone.) The **external occipital protuberance** (*Protuberantia occipitalis externa* **2** [25]) lays ventral to the crest as a triangular and irregular area on the median plane. In some older individuals, an inconspicious **external occipital ridge** (*Crista occipitalis externa* **2** [26]) extends ventrally from the apex of the protuberance to the edge of the occipital foramen (2 [1]).

The external surface of the unpaired squamous part of the occipital bone thus forms part of the nuchal surface (1 [10`] ) of the skull. This surface is outlined dorsally and dorso-laterally by the nuchal crest and accentuated further dorso-laterally by the temporal line. In older animals, the nuchal and parietal parts of the parietal bone are reshaped with age. (See 9 [4] and 9 [7`] as well as footnote 97.) Those parts of the parietal bone, plus the part of the paired flat and unpaired squamous parts of the occipital bone dorsal to the nuchal crest, together forms the dorsal lesser part of the whole occiput (1 [10]).

The internal surface of the unpaired squamous part of the occipital bone is smaller than the external surface. It forms the larger part of the caudal wall of the caudal-most compartment of the cranial cavity (Fossa cranii caudalis 2 [2`]). Dorsally, the internal surface bears a wide **internal occipital protuberance** (*Protuberantia occipitalis interna* **2** [27]). **Two low**

26 It is more typical to describe this structure in the domestic Bovine as the nuchal line (*Linea nuchae*). However, in the savannah buffalo, the structure is so prominent that it necessitates the term '**nuchal crest**'.

ridges (**2**[27`]) extend ventro-laterally, from the single protuberance, in the direction and in line with the petrous crest. (See 7[50] under the temporal bone.) The two low ridges divide the caudal wall of the cranial cavity into two dorso-lateral areas, and a ventro-medial one. The former areas face the cerebral hemispheres. The latter ventro-medial area face the cerebellum, and bears an oval **impression of the vermis** (*Impressio vermialis* **2**[28]), reflecting that part of the cerebellum. Dorsally, in a less prominent part of the impression, this ventro-medial area can be perforated by **8 - 10 foramina** (**2**[29]) in some older individuals. These foramina lead to diploïc canals that end in the diploë of the unpaired squamous part of the occipital bone (see 2[31] , vide infra). (See also 2[7````] & 4[19] for nutrient canals of the occipital and basisphenoid bodies, and 7[9``/````] for similar diploïc canals in the temporal bone.) In some individuals, **osseus structures, resembling partially ossified meninges** (**2**[30]), can be fused to this ventro-medial area, lateral to the central part of the impression. Dorsally, (and less frequently) another osseus structure - but which can be confluent with the above osseus structures - lies on the deeply grooved occipitoparietal suture (2[23]) in the median plane. (See 3[1 & 2] under the interparietal bone as well as the paragraph following 10[30] .)

The diploë (1[5]) between the internal and the external lamina (Lamina interna / externa 1[3 / 4]) of all the parts of the occipital bone consists mainly of a trabecular type (Spongiosa trabeculosa 1[5`a]) of spongy bone. It is filled with red bone marrow (Medulla ossium rubra 1[5``]) in young animals but with yellow marrow (Medulla ossium flava 1[5```]) in old animals. (Evidence of the type of marrow can easily be seen in skulls prepared from formalin fixed heads.) However, the trabecula (1[5`a] ) in the centre of the body and in the dorsal part of the unpaired squamous part are more of a **lamellar type** (Spongiosa lamellosa* **2**[31] ). The internal and the external laminae are of compact bone (Substantia compacta 1[3` / 4`]). The internal laminae are much thinner than the external laminae.

In some old animals, the squamous part of the occipital bone is aerated across the median plane by diploic displacement from the adjacent sinus of the parietal bone. The sinus extends ventrally for a short distance into the unpaired squamous part of the occipital bone. This extension of the sinus forms the small - and usually unpaired - occipital part of the **caudal part of the frontal sinus** (*Sinus frontalis caudalis* **2** [32])* [27] .

[27] See also under the parietal, frontal, lacrimal, ethmoid and nasal bones for the parietal (9 [10`]), frontal (10 [31]), lacrimal (15 [16]), dorsal conchal (11 [22]) and nasal (14 [10]) components of the **frontal sinus complex**. Also see paranasal sinus (1 [6]), maxillary sinus (16 [26]), - and under the palatine and lacrimal bones - for the palatine (19 [6]) and the lacrimal (15 [16]) components of the **maxillary sinus complex**. Note that the lacrimal sinus has two components **;** one (15 [16`]) belongs to the frontal sinus complex only, the other (15 [16``]) to the maxillary sinus complex only. Also note that the sinuses of the presphenoid bone and the lacrimal bone may have a separate compartment each (see 5 [10`] and 15 [16```] respectively) that communicates directly with the ethmoidal meatuses and not with any of the above complexes. (See also 9 [11`] and **footnotes 108 & 147.**)

3. THE INTERPARIETAL BONE
(*OS INTERPARIETALE*)

(See figure **3.13**.)

An osseus structure that appears to be a small **remnant of the interparietal bone** (*Processus interparietalis* **3**[1]) is seen in some individuals. Unlike the parietal bone, it cannot be distinguished as originally having developed from a paired bone. (Also see 9[1] under the parietal bone.) This osseus structure only consists of a short, ventrally directed, free process that is visible on the internal surface only. It is of inconstant length and it lies on the median plane in the well recessed (or deeply grooved) occipitoparietal suture (2[23]). When the process is well developed, it is approximately 5 - 7 mm long, and it forms what can then be regarded as a small **ventral tentorial process** (*Processus tentoricus* **3**[2]). The base of this process fills the groove or recess formed by the occipitoparietal suture. In those cases where it is present and large, it can be regarded as contributing - together with the other osseus structures (2[30]) as described under the occipital bone - to the formation of an **osseus cerebellar tentorium** (*Tentorium cerebelli osseum* **3**[3]). As no proper body can be distinguished, no true occipito<u>inter</u>parietal suture is formed but only an occipitoparietal suture (Sutura occipitoparietalis 2[23])*[28] .

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28 It is assumed for the purpose of this descriptive study (based on circumstantial evidence), that the bodily part of the interparietal bone fuse pre- or early postnatally (at least before 3 months of age) with the parietal bone (or rather bones), to form the single, unpaired, (or combined) parietal bone of sub-adults and mature animals. (That is also the pattern of fusion of these bones in *Bubalus bubalis*.) What appears to be the interparietal process, may however be just an ossification of the membranous cerebellar tentorium of the dura mater. But it could also be an interparietal ossicle on the internal surface of these bones of the skull or the remains of an [präe-interparietal] bone. As no ontogenetic study was undertaken, none of these alternatives can be rejected. It falls outside the scope of this study to determine exactly how the parietal region formed originally. Bones that form on suture lines should just be termed **suture / sutural bones** (*Ossa suturarum*). In literature, they are also referred to as Ossicula Kerkringii, Inca bones, pterion ossicles, epiteric bones, ossa triqueta or - as is more often used in Veterinary Anatomy literature - **Wormian bones**. (See 5[16`] for an example.) In this study, sutural bones and Wormian bones are used synonymously, together with 'osseus scars'. An ossification that does not occur on a suture line is referred to as a **'mark'**. (See 21[31] for an example.) Regarding the sutures involved, the *N.A.V.* only lists an occipitointerparietal suture (Sutura occipitointerparietalis), and not an occipitoparietal suture (Sutura occipitoparietalis 2[23]). (See also **footnotes 25 & 91 - 93**.) The 'frontoparietal fontanelle' (1[17`] ) on the other end (the rostral end) of the parietal bone, should also be mentioned at this point. It is mentioned here only because it involves the parietal bone as a whole. This 'fontanelle' lies in the median plane on the frontoparietal suture (9[5`]). Externally - even in animals as young as 3 to 4 months of age - it is small, and hardly larger than the rest of the cartilaginous frontoparietal suture.

4. THE BASISPHENOID BONE
(*OS BASISPHENOIDALE*)

(See figures **3.15 - 3.19**. Also see 1.4, 3.1 - 3.3, 3.8, 3.9 & 3.34.)

The basisphenoid bone consists of a **body** (*Corpus* **4**[1]) and paired wings (4[8] , vide infra). The internal surface of the body and its wings form the **floor of the middle third** (*Fossa cranii media* **4**[1`] ) of the cranial cavity (Cavum cranii 1[1`]). The body forms the middle third of the base of the cranium. (See also 9[8] for the dorsal and lateral walls of this part of the cranial cavity, and 5[12`] for a wider concept of floor of the internal surface of the base of the cranium.)

Note **:** If skulls of young animals are compared with skulls of older animals, and considered in lateral and medial views, then the registration of the internal and external surfaces of the wings of the basisphenoid bone in particular, becomes ever more distorted with age. Similarly, the surfaces of the wing of the presphenoid bone, as well as the internal and external surfaces of the parietal bone, also de-register with age. Such de-registration of surfaces - surfaces that one would rather expect to match each other - makes an understanding of the appearance of sutures relevant to these surfaces, difficult three-dimensionally. Figures 3.16 and 3.17 should be consulted when dealing with this.

The unpaired body is cylindrical and lies in the median plane. The axis of the body is directed rostro-dorsally along the same axis as the body of the occipital bone, at approximately 140 degrees to the general longitudinal axis of the skull. (See basal axis* under the **Glossary of terms**. Also see FINAL COMMENT 8 and measurement §74 under section D **: Craniometric data**. The bodies of the occipital and presphenoid bones also contribute to the basal axis*.) The body of the basisphenoid bone articulates rostrally with the body of the presphenoid bone at the **intersphenoidal synchondrosis** (*Synchondrosis intersphenoidalis* **4**[2]). Caudally, the body of the basisphenoid bone articulates with the occipital bone at the spheno-occipital synchondrosis (Synchondrosis spheno-occipitalis 2[3]). In old animals these joints ossify,

FIGURE 3.15 : OSTEOLOGY

VIEW TWO OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

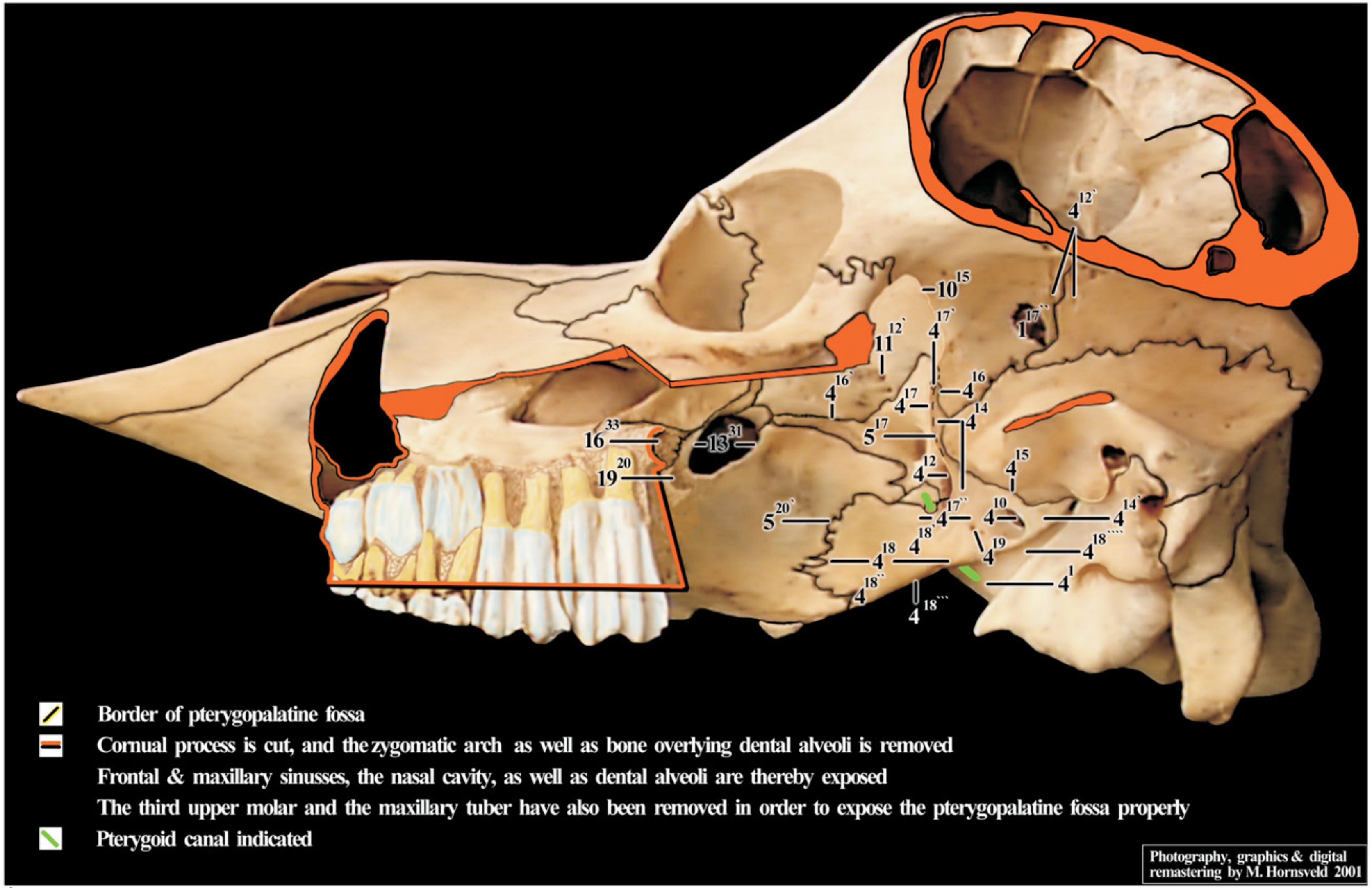
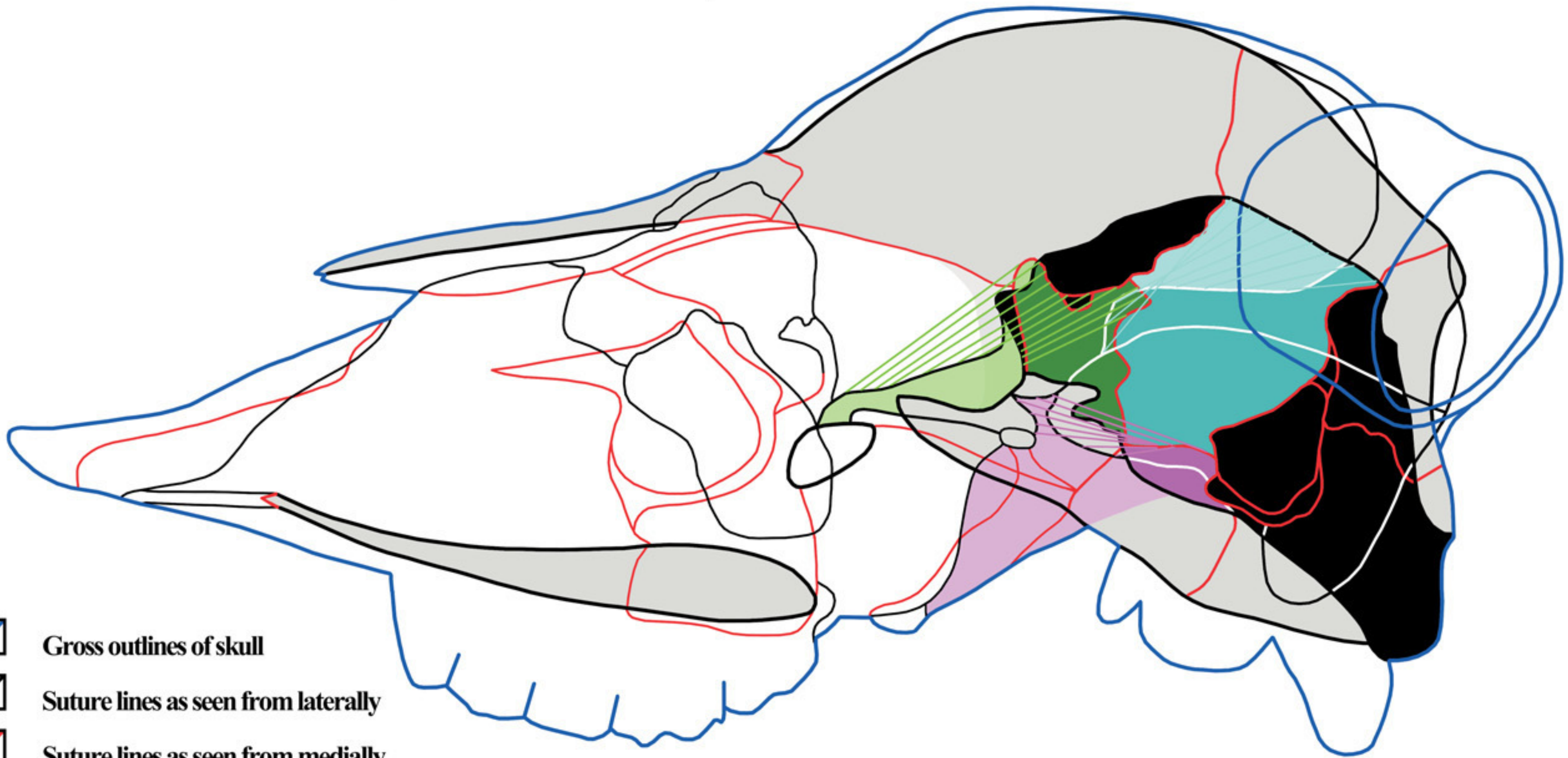


FIGURE 3.15 : OSTEOLOGY
VIEW TWO OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

FIGURE 3.16 : OSTEOLOGY

SUPERIMPOSED VIEWS OF SKULL SUTURES ON THE INTERNAL AND THE EXTERNAL SURFACES OF YOUNG ANIMALS (LATERAL VIEW, SEMI-SCHEMATIC)



Gross outlines of skull

Suture lines as seen from laterally

Suture lines as seen from medially

Cut surface of skull as seen in median plane

Outlines of cranial cavity (black suture lines as seen from laterally, revert to white when crossing this area)

Lines connecting dorsal border of wing of presphenoid bone internally and externally

Lines connecting dorsal border of wing of basisphenoid bone internally and externally

Lines connecting dorsal border of parietal bone internally and externally

390 mm (83 % shorter than skull of bull in figure 3.17)

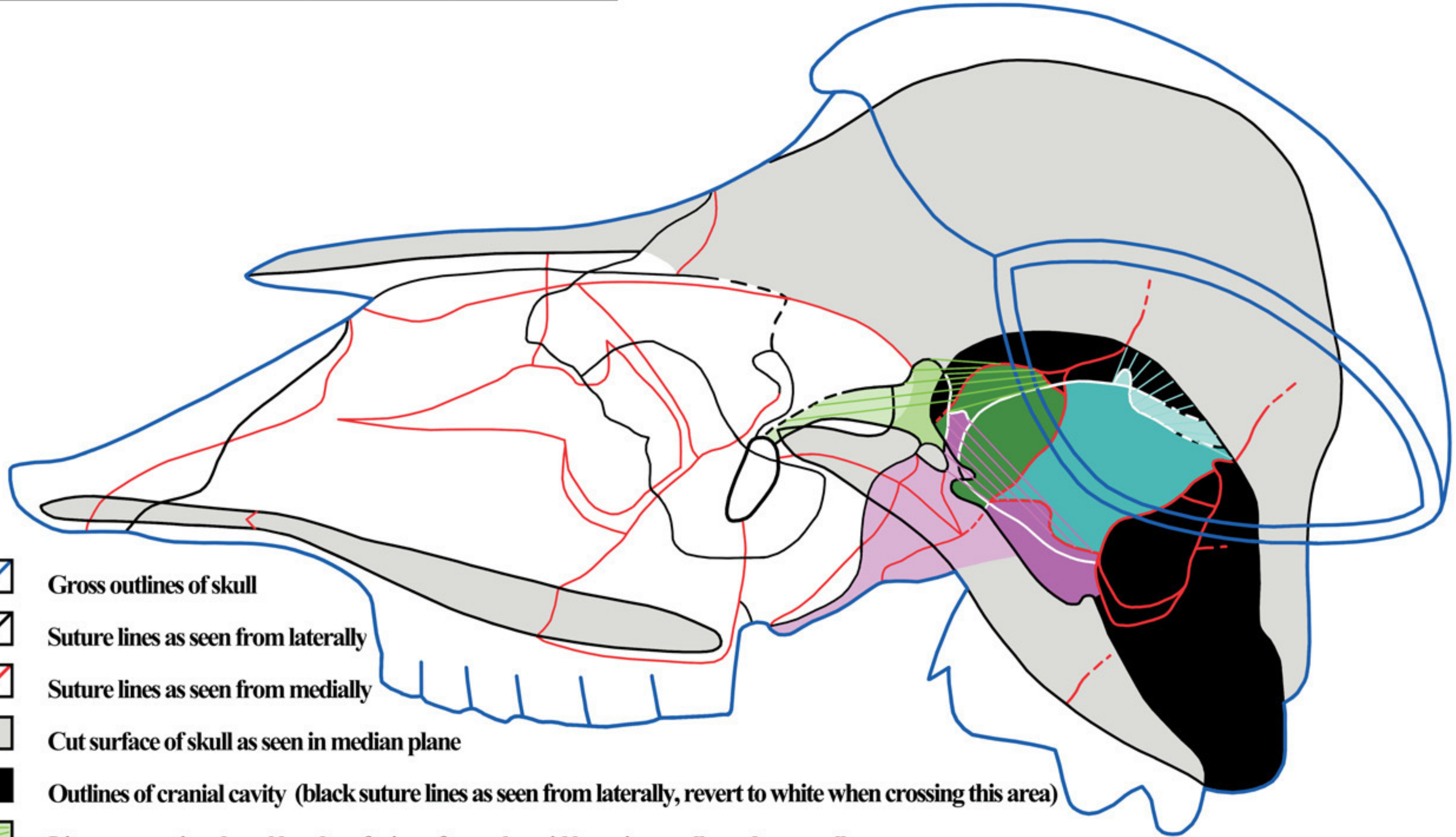
Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.16 : OSTEOLOGY
SUPERIMPOSED VIEWS OF SKULL SUTURES ON THE INTERNAL AND THE EXTERNAL SURFACES OF YOUNG ANIMALS (LATERAL VIEW, SEMI-SCHEMATIC)

FIGURE 3.17 : OSTEOLOGY

SUPERIMPOSED VIEWS OF SKULL SUTURES ON THE INTERNAL AND THE EXTERNAL SURFACES OF OLD BULLS (LATERAL VIEW, SEMI-SCHEMATIC)

FIGURE 3.17 : OSTEOLOGY
SUPERIMPOSED VIEWS OF SKULL SUTURES ON THE INTERNAL AND THE EXTERNAL SURFACES OF OLD BULLS (LATERAL VIEW, SEMI-SCHEMATIC)



- Gross outlines of skull
- Suture lines as seen from laterally
- Suture lines as seen from medially
- Cut surface of skull as seen in median plane
- Outlines of cranial cavity (black suture lines as seen from laterally, revert to white when crossing this area)
- Lines connecting dorsal border of wing of presphenoid bone internally and externally
- Lines connecting dorsal border of wing of basisphenoid bone internally and externally
- Lines connecting dorsal border of parietal bone internally and externally

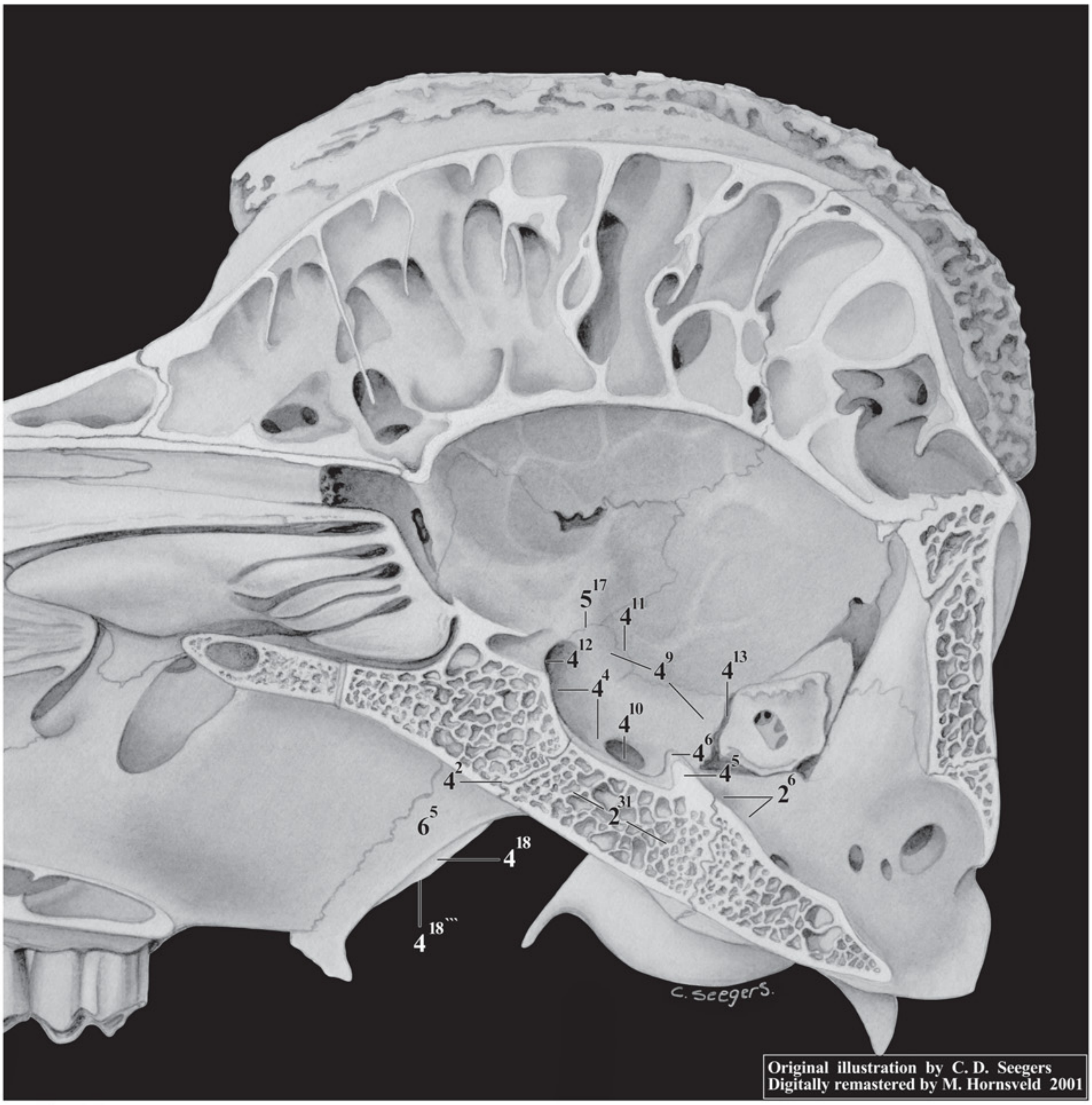
← 470 mm (120 % longer than skull of heifer in figure 3.16) →

Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.18 : OSTEOLOGY

VIEW TWO OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)

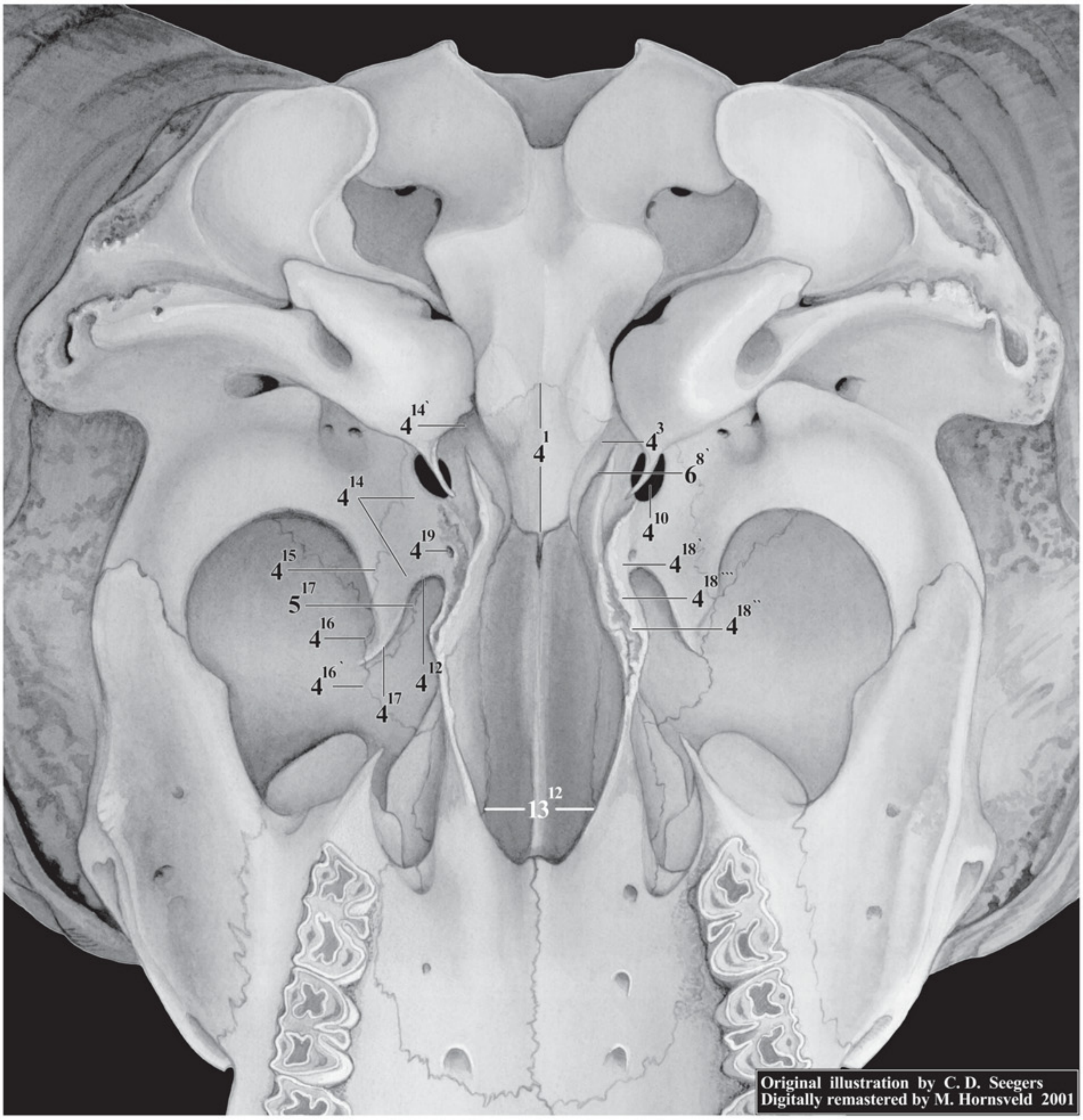
Note : The skull was cut to the right of the median plane, except for the rostral part of the hard palate where the median septum can still be seen. Part of the rostrum presphenoidale has been cut even more paramedially (to the right) to expose its sinus. Because it is a paramedian section, the vomer is not shown.



Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.19 : OSTEOLOGY

VIEW TWO OF THE SKULL OF A MATURE BULL (VENTRAL VIEW)



forming synostoses (1[19`]).

The ventral or external surface of the body is laterally convex. Ventrally - near the spheno-occipital synchondrosis (2[3]) - the body of the basisphenoid bone bears the smaller rostral part of the muscular tubercle (2[4]). (See also under occipital bone for larger caudal part.) Rostro-ventrally, at the junction between the body and the base of the wing (4[8] , vide infra), a groove can be seen. The groove can be either indistinct, or well defined. It is the **groove for the pterygoid canal** (*Sulcus n. canalis pterygoidei* **4**[3]). Further rostrally, the groove terminates under the smaller caudal process (6[7]) of the pterygoid bone. The rostral end of the groove, forms the caudal end of the roof of the pterygoid canal (Canalis pterygoideus 6[3`] ). The canal is approximately 1 - 2 mm in diameter in adult bulls. (See also 6[8 and 8`] under the pterygoid bone.)

The rostral part of the dorsal or internal surface of the basisphenoid bone, is concave in all directions. Centrally, the concavity is more pronounced to form the **hypophysial fossa** (*Fossa hypophysialis* **4**[4]) which is oval. In old bulls, the hypophysial fossa is better circumscribed and can measure 14 mm wide by 20 mm long. At the caudal border of the hypophysial fossa, a short **stubby process** *(Dorsum sellae* **4**[5]) projects dorsally. It is nearly as wide as the body itself. Laterally the dorsum bears a left and a right **clinoidal processes** (*Processus clinoideus caudalis* **4**[6]). These processes as well as a transverse groove on the dorsum can be seen better in some old animals. (See figure 3.54.). The processes are short and they project rostrally. The fossa, the dorsum and its processes have a shape described in mammalian osteology as resembling a **'Turkish (horse) saddle'** (*Sella turcica* **4**[7]). Caudal to the Dorsum sellae, the dorsal surface of the body bears the rostral smaller part of the impression of the pons. (Impressio pontina - see 2[6] under the occipital bone for caudal part.) The position of the Dorsum sellae - and its processes - demarcates the border between the caudal and middle parts of the cranial cavity floor (Fossa cranii caudalis / media). (See also 2[2`] & 4[1`] , as well as 5[12`]).

The **wings** (*Alae* **4**[8]) of the basisphenoid bone are flattened in a near dorso-ventral plane, presenting internal and external surfaces. The external surface of the wing additionally has another wing-like process (vide infra under 4 [18]) **:**

The dorsal or internal surface of the wing forms the **cerebral surface** (*Facies cerebralis* **4** [9]), facing more dorso-medially than just dorsally. This surface of the wing is as wide and as long as the body itself, having lateral, rostral and caudal borders. In caudal view, the profile of the wing is laterally concave. In the centre, it bears the internal opening of the **oval foramen** (*Foramen ovale* **4** [10]). (Vide infra under 4 [14] for the external opening of the oval foramen.) The dorsal surfaces of the wings forms part of the middle third of the floor (Fossa cranii media 4 [1`] ) of the cranial cavity. (See also Cavum cranii 1 [1`] and 5 [12`] .)

The lateral border of the wing articulates but never completely fuses to the internal surface (9 [9]) of the parietal bone at the basisphenoidal part of the **sphenoparietal suture** (*Sutura sphenoparietalis* **4** [11])* **[29]**.

The rostral border of the internal surface is subdivided into a medial free part and a fused lateral part. The medial free part forms the ventral and lateral margins of the internal opening of the **combined round and orbital foramen** (*Foramen orbitorotundum* **4** [12])* **[30]** . The lateral part of the rostral border is fused to the wing of the presphenoid bone, lateral to the combined foramen, at the spheno-sphenoidal suture (Sutura spheno-sphenoidalis 5 [17])* **[31]** . This region of the spheno-sphenoidal suture is marked by the internal openings of two diploïc canals (2 [7``] ). These canals open on the external surface of the skull, specifically in the temporal fossa, just dorsal to the region - and in old animals the remains of - the sphenoidal fontanelle. (See 1 [17``] & 10 [14] and footnote 42.) The internal as well as the external openings of these diploïc canals are marked by **deep grooves** (**4** [12`]) that lead towards the respective openings. Rarely, only

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29 A distinction should be made between the pre- and basisphenoidal parts of the sphenoparietal suture (Sutura sphenoparietalis 4 [11]). **Footnote 39** under the presphenoid bone has this same comment.

30 The *Sulcus nn. opthalmici et maxillaris* & *Fossa piriformis* are unclear.

31 The (pre-)spheno-(basis-)sphenoidal suture (Sutura spheno-sphenoidalis 5 [17]) - which is an intersphenoidal suture - is not listed in the *N.A.V.* (See also **footnotes 34 & 44** and the intersphenoidal synchondrosis 4 [2] .)

a single opening is found. Whatever the case may be, the pattern of this part of the spheno-sphenoidal suture, shows great variation due to these diploïc openings and the deep grooves associated with them.

The caudal border of the internal surface of the basisphenoid wing, is completely free. It forms the rostral border of the **sphenopetrous fissure** (*Fissura sphenopetrosa* **4**[13]). This fissure is continuous caudally with the petro-occipital fissure. (See 2[8] under the occipital bone as well as 7[31 / 32 / 33] under the temporal bone.)

The external or **temporal surface** (*Facies temporalis* **4**[14]) of the wing of the basisphenoid bone is triangular, and faces ventro-laterally. The external opening of the oval foramen (4[10]) opens more caudally, near the caudally positioned **apex** (**4**[14`]) **of the wing**. The triangular surface of the basisphenoid wing, have a fused dorsal border, a rostral base, and a ventral margin. The latter margin is difficult to define (vide infra under 4[18```]).

The dorsal border is fused to the squamous part of the temporal bone - mainly the infratemporal part (7[10]) - at the **sphenosquamous suture** (*Sutura sphenosquamosa* **4**[15]). The rostral end of the dorsal border, is also fused for a short distance to the frontal bone at the basisphenoidal part of the **sphenofrontal suture** (*Sutura sphenofrontalis* **4**[16])*[32] .

In a lateral view of older skulls, the wings of the basis- and presphenoid bones cannot easily be distinguished from one another. Therefore the sphenosquamous suture (4[15]) may seem to be continuous with the sphenofrontal suture (4[16]). Strictly speaking, that part of the presphenoid bone should be discussed in the next subsection, but for the sake of understanding paragraphs to follow in this section, the suture has to be mentioned here **:** This **presphenoidal part of the sphenofrontal suture** (**4**[16`]) - see footnote 32 - between the wing of the

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[32] The *N.A.V.* does not distinguish between the basisphenoidal (4[16]) and presphenoidal (4[16`]) parts of the sphenofrontal suture (Sutura sphenofrontalis 4[16]). A distinction should be made as the presphenoidal part (internally) is of particular interest in the savannah buffalo. (See also **footnotes 40 & 45**.)

presphenoid bone and the frontal bone, will be discussed in more detail under the presphenoid and frontal bones. (See orbital surface of frontal bone under 10 [16], as well as the description of the dorsal border of the external surface of the wing of the presphenoid bone under 5 [17]. The presphenoidal part of the sphenofrontal suture (4 [16`]) is annotated in figures 3.15 & 3.20 (for external views) and figures 3.21 & 3.35 (for internal views). See also the lateral margin of the internal surface of the wing of the presphenoid under 5 [14 & 15] and footnote 46.)

To continue with the temporal surface (4 [14]) of the basisphenoid wing **:**
The rostral base of the triangular wing is free, or rather appears to be free, as seen in lateral view. It is concave from dorsal to ventral (except a small section dorsally which is convex) and it forms the **pterygoid crest** (*Crista pterygoidea* **4** [17])***** [33]. The crest borders the pterygopalatine fossa (13 [30]) caudally and it demarcates the caudal extreme of the boney orbit (13 [21]). The pterygoid crest extends from the **intersection** (**4** [17`]) of the pre- and basisphenoidal parts of the sphenofrontal suture (dorsally), to end ventrally, in a **broad base** (**4** [17``]) on the lateral surface of the pterygoid process (4 [18]) of the basisphenoid bone (vide infra). Medial to the pterygoid crest, along approximately the dorsal half of the triangular base, the wing of the basisphenoid bone is however not free - as it appears in lateral view - but is fused to the base of the wing of the presphenoid bone at the spheno-sphenoidal suture ***** [34]. The ventral half of the base of the wing - which is totally free - forms the ventral and lateral parts of the external opening of the combined round and orbital opening (4 [12]). This large combined opening connects the middle part of the cranial cavity to the pterygopalatine fossa (13 [30]). A faint line can be made out that joins the dorsal end of the pterygoid crest to the orbitotemporal crest (10 [15]). Although the two crests are not clearly continuous with each other, they demarcate the boney orbit (13 [21]) from the temporal fossa (1 [9]).

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33 The pterygoid crest (Crista pterygoidea 4 [17]) does not involve the pterygoid bone at all.

34 The (pre-)spheno-(basis-)sphenoidal suture (Sutura spheno-sphenoidalis 5 [17]) - which is an intersphenoidal suture - is not listed in the *N.A.V.* (See also **footnotes 31 & 44**, and the intersphenoidal synchondrosis 4 [2].)

The ventral margin of the basisphenoid wing is difficult to define. It is taken up in the ventral margin (vide infra under 4[18```]) of the pterygoid process (4[18]). The pterygoid process has to be described first **:**

Ventrally, the wing of the basisphenoid bone carries another wing-like process. It is flattened and triangular, forming the **pterygoid process** (*Processus pterygoideus* **4**[18]). It can only be appreciated on the external surface of the skull and is best seen in lateral view (although a small part may be visible in some individual skulls in medial view). It projects rostrally beyond the pterygoid crest in a near sagittal plane. The triangular pterygoid process (4[18]) has a base rostrally, an apex caudally, with fused dorsal and rostral margins, but a free ventral border. The ventral border merges with the ventral margin of the basisphenoid wing, which makes it difficult to define (vide supra). The lateral surface of the pterygoid process is exposed, but the medial surface is only partially visible **:**

Caudally, the **apical part** (**4**[18`]) is continuous with the lateral surfaces of both the body and the wing of the basisphenoid bone.

The base of the pterygoid process (that lies rostrally), is fused to the lamina perpendicularis (19[10`] ) of the palatine bone at the basisphenoidal part of the sphenopalatine suture. (See 5[20`] under the presphenoid bone) *[35] .

Although the basisphenoidal part of the sphenopalatine suture (5[20 and 20`] ) could also be mentioned here, it is more conveniently described under the presphenoid bone where it belongs best. It is annotated 5[20`] and 5[20] in figures 3.15 and 3.20 respectively.

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35 The *N.A.V.* does not distinguish between presphenoidal (5[20]) and basisphenoidal (5[20`]) parts of the sphenopalatine suture.

The **ventral angle of the base** (**4** $^{18``}$), may be fused in some animals to the larger process of the pterygoid bone at the pterygosphenoidal suture. (See 5 ^{19} under the presphenoid bone and compare figure 3.15 with figure 3.20 in this regard.)

The dorsal border of the pterygoid process is shorter than the other borders and is fused to the body of the pterygoid bone (6 ^{1}) and the wing of the presphenoid bone. (See 5 ^{19} and 5 ^{17} for the sutures involved.)

The **ventral margin** (**4** $^{18```}$) is free to form the caudal free margin of the lateral wall of the boney choana (13 ^{12}). Caudally, this ventral margin merges with the ventral margin of the basisphenoid wing (vide supra).

The lateral surface of the process forms a part of the medial wall of the pterygopalatine fossa (13 ^{30}).

The medial surface of the pterygoid process of the basisphenoid wing (4^{8}), is not exposed except for a narrow strip near the ventral margin in some individual skulls as stated above. As the width of the exposed strip may vary, smaller variations therefore do occur in the pattern of the suture lines, as seen from medially. The rest of the medial surface of the pterygoid process of the basisphenoid bone (or all of it) is not exposed to view, as it is fused to the wing of the pterygoid bone (see 6 ^{5}).

Caudally, the ventral margin of the process (4 $^{18```}$) terminates at the apical part of the wing (4 $^{14`}$), caudo-ventral to which a **shallow groove** (**4** $^{18````}$) is formed on the basisphenoid body (4 ^{1}). This groove forms the dorso-rostral wall of the osseus part of the auditory tube. (See also 7 $^{37-40}$ and footnote 70 under the temporal bone.) The groove lies more dorso-lateral than the much smaller groove for the pterygoid canal. (Vide supra under 4 ^{3} and see 6 $^{3 \text{ and } 8}$.)

Rostrally and caudally, the diploë of the body of the basisphenoid is of a trabecular type

(Spongiosa trabeculosa 1[5`a]). In young animals, it contains red bone marrow (Medulla ossium rubra 1[5``]) which is displaced by yellow marrow (Medulla ossium flava 1[5```]) in old animals. In the centre of the body, the diploë is of a lamellar type (Spongiosa lamellosa 2[31]).

In some old animals, the temporal surface of the wing presents one or more **foramina** (**4**[19]) with diameters of between 1 - 3 mm. When present, these foramina are usually found rostral to the oval foramen. Each leads via a short canal (Canales diploici 2[7``]) to the spongy trabecula of the body. They can be regarded as nutrient foramina and canals (2[7````]). The internal and the external laminae (Lamina interna / externa 1[3/4]) of the body are of compact bone (Substantia compacta 1[3`/4`]). The internal lamina is much thinner than the external lamina.

5. THE PRESPHENOID BONE
(*OS PRESPHENOIDALE*)

(See figures **3.20 - 3.22**. Also see 1.4, 3.1, 3.3, 3.6, 3.8, 3.16, 3.17 & 3.37.)

The presphenoid bone consists of a body and paired wings. Part of the body contributes to the formation of the rostral third of the base of the skull. Further rostrally, an extension of the body - referred to as the rostrum (5^{8}) - also contributes to the formation of the osseus nasal septum. The body and the wings form the floor of the rostral third of the cranial cavity (vide infra under $5^{12`}$). Various parts of the presphenoid bone are obscured from view, and describing them demands a different approach.

Note **:** As also stated under the basisphenoid bone, if skulls of young animals are compared with skulls of older animals, and considered in lateral and medial views, then the registration of the internal and external surfaces of the wings of the basis- and presphenoid bones, become ever more distorted with age. That also holds true for the internal and external surfaces of the parietal bone. This de-registration with age, makes an understanding of the appearance of sutures relevant to these surfaces difficult to comprehend three-dimensionally. Figures 3.16 and 3.17 should be consulted when dealing with this.

The unpaired caudal part of the cylindrical **body** (*Corpus* **5** ^{1}) lies on the median plane, approximately along the same axis as the bodies of the basisphenoid and occipital bones. The rostral extension of the presphenoid body (vide infra under 5^{8}), however lies at a different angle, and redirects the axis of the combined body and rostrum of the presphenoid bone. The rostral end of the rostrum and the caudal end of the occipital body, are the two points that determine the basal axis* **axis I**, as per definition. (See paragraph following 5^{8} below for further discussion.) Therefore, the axes of the bodies of the occipital, basisphenoid and caudal presphenoid bones, do not lie exactly on the basal axis*. The basal axis* makes an angle of approximately 140 degrees with the general longitudinal axis of the skull.

FIGURE 3.20 : OSTEOLOGY

VIEW THREE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

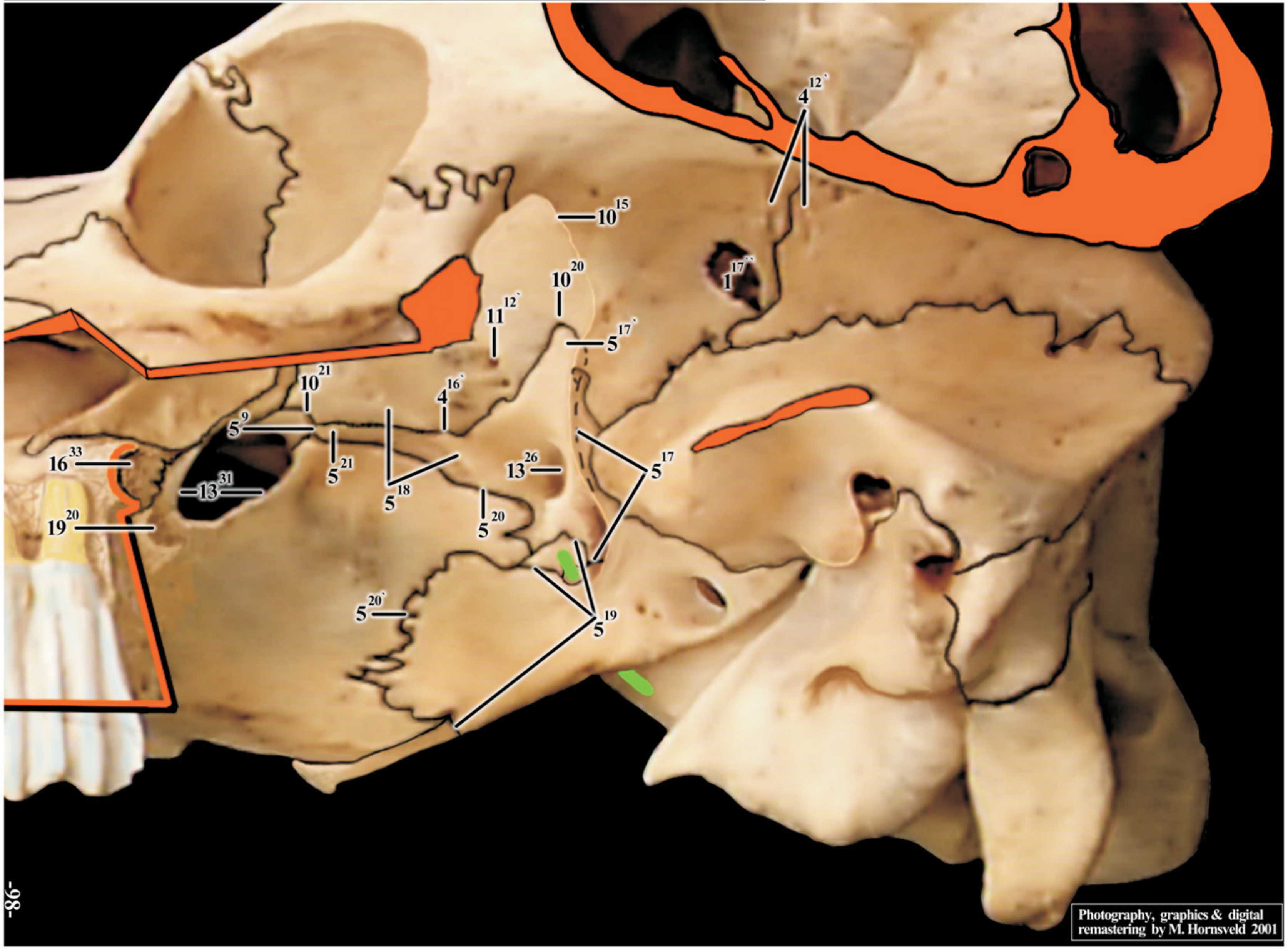


FIGURE 3.20 : OSTEOLOGY

VIEW THREE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

FIGURE 3.21 : OSTEOLOGY

VIEW THREE OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)

Note : The skull was cut to the right of the median plane, except for the rostral part of the hard palate where the median septum can still be seen. Part of the rostrum presphenoidale has been cut even more paramedially (to the right) to expose its sinus. Because it is a paramedian section, the vomer is not shown.

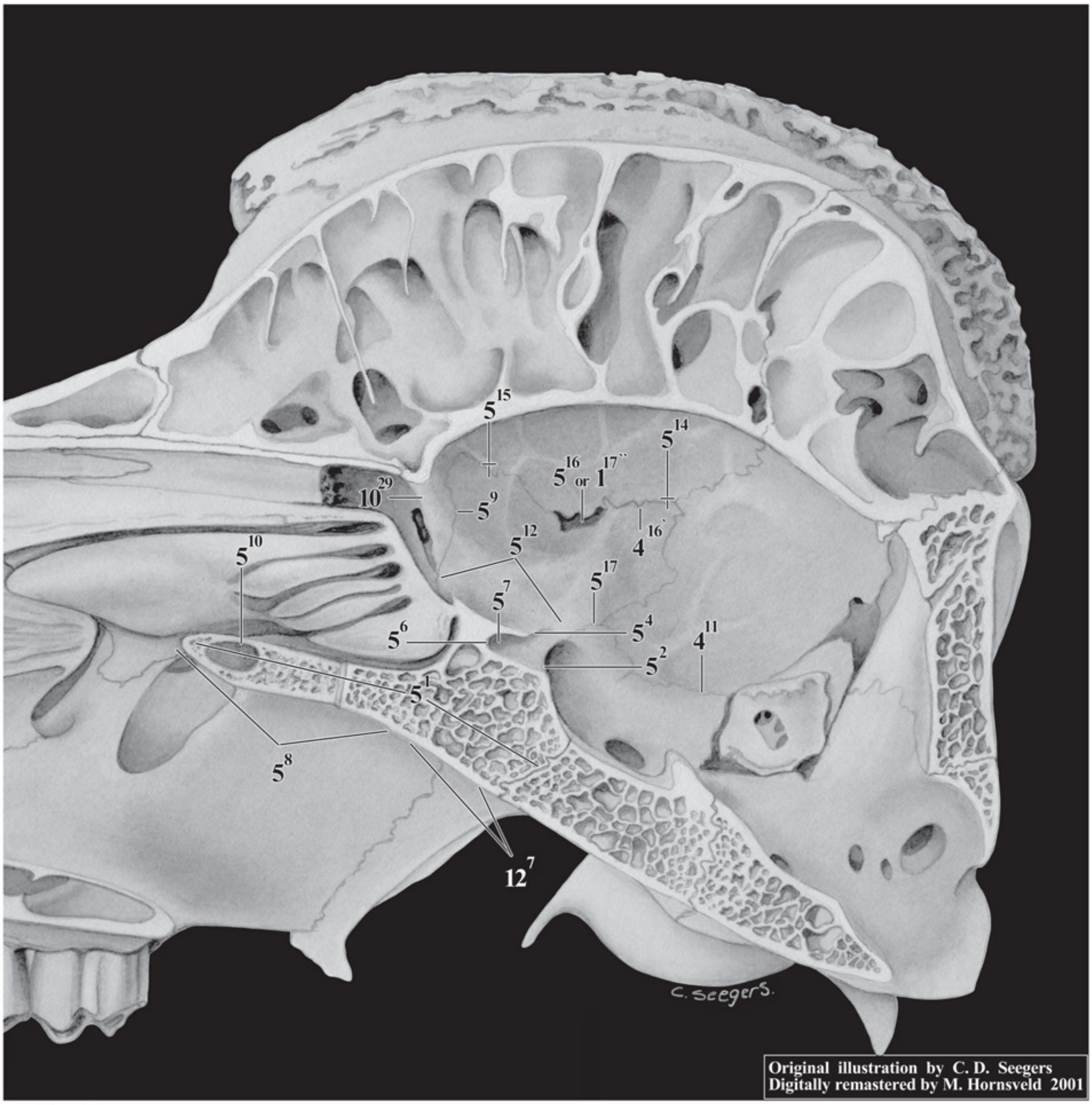
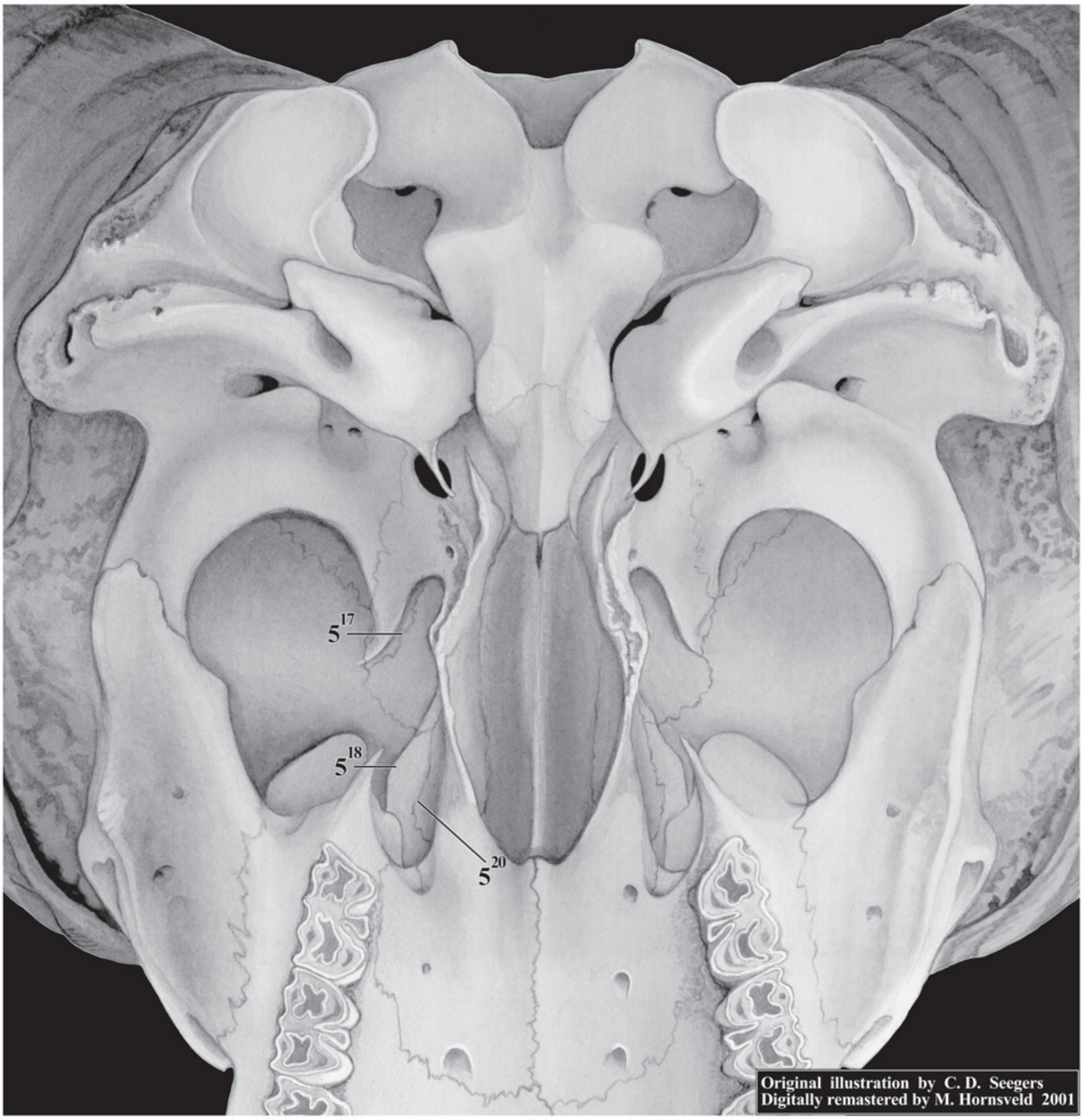


FIGURE 3.22 : OSTEOLOGY

VIEW THREE OF THE SKULL OF A MATURE BULL (VENTRAL VIEW)



The similarities and the differences between rostral extension and the caudal body of the presphenoid bone, will be highlighted in the paragraphs to follow. The ventral surfaces of both parts are fused at the vomerosphenoidal suture (Sutura vomerosphenoidalis 12[7]) to the wings of the middle and caudal sections of the vomer respectively. However, the absolute ventral margin of both parts of the presphenoid body remains unfused to any bone on, and just next to, the median plane. This unfused ventral margin of the presphenoid body forms the caudal part of the roof of a longitudinal canal, the floor and the sides of which are formed by the vomer. (See the vomeral canal *****[36] and see the description of the ventral part of the perpendicular plate of the ethmoid bone under 11[14```] for the rostral part of the roof of the canal.)

The dorsal surfaces of the two parts of the body are separated from each other at the level where the presphenoid bone is fused to the cribiform and base plates of the ethmoid bone. (See 11[8] and 11[9] under the ethmoid bone.) Rostral to the cribiform plate, various parts of the ethmoid bone are totally fused to the rostral part of the presphenoid body (vide infra under 5[8]) except the ventral margin as already said. At that same level, the ventral surfaces of the two parts of the presphenoid body meet at an obtuse angle. That is because the axis of the rostral part lies more horizontally than the axis of the caudal body (vide infra). The diameter of the rostral part of the presphenoid bone is about half that of the caudal body, but its length is nearly twice that of the body. The caudal part of the presphenoid body forms the rostral third of the base of the skull. The caudal end of the body articulates with the basisphenoid bone at the intersphenoidal synchondrosis. (See 4[2] under the basisphenoid bone). In old animals this synchondrosis is ossified to form a synostosis (1[19`]). In ventral view, the caudo-lateral margin of the body is fused to the body and the process of the pterygoid bone. (See 5[19] below, as well as footnotes 48, 51, 52, 54 & 55, and also see 6[1 & 5].) Rostro-laterally, the caudal body of the presphenoid bone is fused for a short distance to the caudal end of the perpendicular part of the palatine bone. (See 5[20] below, and see 19[13] under the palatine bone.)

The dorsal or internal surface of the caudal part of the body is therefore the only part of the

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36 The vomeral canal (Canalis vomeris 12[11]) is not listed in the *N.A.V.* (See also **footnote 119**.)

body of the presphenoidal bone exposed to view in the otherwise uncut skull. The vomer - which covers most of the presphenoid body ventrally - can however be sculptured away easily. However, in some individuals, the vomer is so delicate and loose, that it can be broken away without much difficulty.

Caudally, the internal surface of the body forms mainly the **yoke of the presphenoid bone** (*Jugum sphenoidale* **5** [2]). Without any clear demarcation, the wings of the presphenoid bone continue laterally to the yoke. In the median plane, the internal surface is marked by a low **sphenoidal ridge or crest** (*Crista sphenoidalis* **5** [3]) which is less prominent in young animals. Rostro-dorsally, the ridge is more pronounced and is continuous with the gallic crest. (See Crista galli 11 [15] under the ethmoid bone.) At the caudal end of the sphenoidal ridge, dorsal to the yoke, the sphenoidal crest ends in a horizontal free border, the **orbitosphenoidal crest** (*Crista orbitosphenoidalis* **5** [4]). This crest is usually smooth (see 5 [13] below). The crest is separated from the body by the unpaired **chiasmatic groove** (*Sulcus chiasmatis* **5** [5]). The crest and the groove are as wide as the body is. Being undivided and dorso-ventrally flattened, the groove lies across the median plane. The rostral end of the groove is demarcated by a **particular part of the body of the presphenoid bone** (**5** [6])* [37] **that serves to divide the chiasmatic groove** (the rostral part of it) into a left and a right optic canal (Canalis opticus 13 [26]). This point of division also **marks the position of the caudal openings** (**5** [7]) **of the individual optic canals**, where they join to form the single optic chiasma. From this point, each antimeric canal diverges rostrally, to end at the **rostral opening** (**5** [7`]) **of the optic canal**, in either the left or the and right boney orbit (13 [21]). (See footnote 37.) Osteologically speaking therefore, these canals connect the rostral part of the cranial cavity to the pterygopalatine fossa. (See 13 [30] under the bones of the face.)

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37 This division point of the chiasmatic groove - which marks the caudal openings of the individual optic canals - is not listed in the *N.A.V.* as a definite point. Each optic canal is approximately 14mm to 19 mm long, whereas the unpaired chiasmatic sulcus is only 3 - 5mm long. It would be convenient for descriptive purposes if the caudal openings of the optic canals (5 [7]) could be termed separately by allocating terms for them, as well as a term for the rostral end of the chiasmatic sulcus (5 [6] , at the division point). The rostral ends (5 [7`]) of the optic canals should also be termed. Having terms for both the unpaired caudal as well as the paired rostral ends of the optic canals, would also be more logic and less confusing when describing the components of this "Y-shaped" canal in the savannah buffalo. (See also **footnote 126**.)

The diameter of the rostral extension of the body of the presphenoid bone is approximately half that of the caudal part, but nearly twice as long. The rostral extension projects into the nasal cavity as the rostrum of the presphenoid bone, the **rostrum [prae-]sphenoidale** (*Rostrum sphenoidale* **5** [8]). The rostrum lies at an obtuse angle to the body of the presphenoid bone, and by that effectively changes the general angle of the axes formed by the bodies of the occipital, basisphenoid and caudal presphenoid bones, from approximately 140 degrees to about 150 degrees. That is because the rostral end of the rostrum - allocated the point **B`** - and the caudal end of the occipital body (see Basion*# and the point **B**), are the two points that determine the basal axis* or **axis I**, according to the definition. The distance between the rostral end of the rostrum - **B`** - and the rostral end of the incisive bone - at the Prosthion*# or point **P** - gives the facial axis, **axis II**. (See **Glossary of terms** and FINAL COMMENT 8 under section D **: Craniometric data**, as well as measurements §64 & §75.) Except for the ventral margin of the rostrum - which also forms part of the roof of the vomeral canal (12 [11] and vide supra) - the rostrum is totally fused to surrounding bones as follows **:**

Dorsally, in the median plane, it is "fused" intimately to the perpendicular plate (11 [13]) of the ethmoid bone. This most probably occurs at an early age, as no sutures remain of this fusion, or, both structures develop from a shared or single coalesced cartilaginous anlage. Laterally, the caudal part of the rostrum is fused to the perpendicular part of the palatine bone. (Vide infra under 5 [20] for the sphenopalatine suture.) The rostral part of the rostrum is also "fused" laterally to the basal plate of the ethmoid bone at a part (vide infra) of the **sphenoethmoidal suture** *(Sutura sphenoethmoidalis* **5** [9]) that could not be visualized in the specimens studied. Circumstantial evidence - provided by the presence of remoter parts of the same suture - suggests that this part of the suture should or could have been present at some stage of development. For descriptive purposes, it will be tagged as the "invisible" part of the sphenoethmoidal suture, as it cannot be seen in postnatal stages. The reason why this part of the suture is invisible, is either due to very early (prenatal and complete) ossification, or because both parts also develop from a single cartilaginous anlage that also ossifies from a single ossification centre. Thereby, the dorso-lateral surface of the rostrum-cum-base plate is continuous with the internal surface of the ethmoid parts that forms the floor of the nasal fundus (as well as the floor of the most ventral nasal meatus) without the intervention of any suture. (See below for a visible internal part of the sphenoethmoidal suture - between the wing of the presphenoid bone and the ethmoid bone as seen in the cranial cavity. Also see 5 [21] for an external part of the suture as seen in the pterygopalatine fossa. These visible parts of the suture supply the circumstantial evidence that two bones or ossification centres could originally be involved.) The fact that the rostrum is fused so intimately to both the perpendicular and basal plates of the ethmoid bone (dorsally) - and to a lesser extend to the vomer (ventrally) - functionally incorporates it totally into the osseus nasal septum (13 [11] and 11 [14]) as a uniform structure *** [38]** . (See also the vomer, ethmoid and palatine bones.)

The internal and the external layers (Lamina interna / externa 1 [3 / 4]) of the body of the presphenoid bone are of compact bone (Substantia compacta 1[3` / 4`]). The external lamina is thinner on the caudal part of the body than anywhere else on those bones that contribute to the formation of the skull base. Compact bone is also weakly developed over the dorso-lateral and ventral aspects of the rostrum despite the fact that this part of the presphenoid bone is fused to other bones (viz. the ethmoid and the vomer). The diploë between the internal and the external laminae of both parts of the presphenoid bone consists mainly of a trabecular type

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38 The fact that the vomerosphenoidal suture (12 [7]) between the wings (of the caudal section of the vomer) and the body of the presphenoid bone remains visible till late in life, does not disprove that the rostrum - inclusive of the more caudal body of the presphenoid bone - develops as a single unit, together with the basal and perpendicular plates of the ethmoid bone. Because the presphenoid bone develops less intimately fused to all the parts of the vomer, the components of the osseus nasal septum appear to develop as two structures (at the most) and not from three bones. (If a study on the sutures involving the other parts of the ethmoid bone has to be done, it should be done on animals of various ages, varying from all prenatal stages to postnatal ages less than 4 months. It was not the purpose of this study to elucidate these details although it might be important for zoological classifications of animals based on osteological detail of the skull. See under 5 [21] for a visible external part of the sphenoethmoidal suture.) Thus, what is significant in the savannah buffalo, is that the rostrum presphenoidale and the caudal body of the presphenoid bone, including the perpendicular and basal plates of the ethmoid bone, all appear to develop from one continuous and single cartilaginous anlage, or from cartilaginous centres that coalesced into one. Without any signs of totally separate ossification centres, and in the absence of any sutures (medially and paramedially) or synchondrosis (medially) - which might indicate clearly towards totally separate origins for these sub-components of the osseus nasal septum - the adult presphenoid-cum perpendicular plate, appear as a single bone in the median plane. Depending on how far the perpendicular plate has ossified, this part of the nasal septum (not the combined septum 11 [14]) extends from the basisphenoid bone nearly to the apex of the skull. The presence of the vomeral canal and the clear separation between the different parts of the vomer and the presphenoid bone during all postnatal stages, seems to confirm that the vomer develops separately, despite the indistinct vomerosphenoidal and vomeroethmoidal sutures (12 [7] and 12 [10]) respectively. (See **footnotes 43 & 116**, the base plate (11 [8]) of the ethmoid bone, and chapter 4 **: Discussion**, point 8.)

of spongy bone (Spongiosa trabeculosa 1 [5`a]). It is filled with yellow marrow (Medulla ossium flava 1 [5``]) even in young animals. The trabecula in the caudal part of the body can be of a lamellar type (Spongiosa lamellosa 2 [31]). The diploë of both parts are continuous with each other as well as with the spongy bone of the perpendicular lamina (11 [13]) of the ethmoid bone without the intervention even of a sphenoethmoidal suture or a synchondrosis of any type at any age. (See also footnotes 38 & 116.) The diploë in the rostrum can be aerated in some individuals to form a small paired **presphenoidal sinus** (*Sinus sphenoidalis* **5** [10]). The **septum that divides the presphenoidal sinus** (*Septum sinuum sphenoidalium* **5** [10`]) is not situated in the median plane and is not paired like the median septa of the other components of the frontal and maxillary sinus complexes. It divides the presphenoid sinus into asymmetric antimeres. Each presphenoidal sinus, communicate dorsally with a ventral ethmoidal meatus or laterally with an ethmoidal cell (11 [4]) via an **opening** (*Apertura sinus sphenoidalis* **5** [10``]). On either side of the nasal septum, the dorsal aspect of the presphenoid bone can be ventrally displaced in some individuals by an enlarged caudal recess (not illustrated) of the most ventral ethmoidal meatus. (See also under ethmoid bone, second paragraph following 11 [8].) This recess can extend caudally up to the level of the caudal end of the optic canal. Rostrally, the recess is always continuous with the nasal fundus (13 [13]). Both the sinus and the recess can be present in one and the same animal. The sinus of the rostrum of the presphenoid bone can in some animals be extensive. (See endocast of paranasal sinuses, figures 3.55 & 3.56.)

The dorsal or internal surface of each **wing of the presphenoid bone** (*Ala* **5** [11]) is continuous with the joke and the dorsal surface of the caudal part of the body. The left and right wings project laterally and dorso-laterally so that their dorsal surfaces are concave in all directions to form the **floor of approximately the rostral third** (*Fossa cranii rostralis* **5** [12]) of the cranial cavity (Cavum cranii 1 [1`]). In the region of the wings, the internal surface is marked by the negative impressions of the opposing parts of the cerebral hemispheres and the blood vessels in the meninges that covers them. These impressions are not as clear as those on the internal surfaces of the parietal and frontal bones. (See Impressiones digitatae 9 [8`], Sulci arteriosi 9 [8``] and Sulci venosi 9 [8```].)

The rostral, middle and caudal parts of the floor of the cranial cavity (Fossa cranii rostralis 5[12] / media 4[1`] / caudalis 2[2`]) as well as the ethmoidal fossae (11[10] , and see 10[29] for the partial constriction separating the ethmoidal fossae from the rostral cranial cavity), together form the **floor of the internal surface of the base of the cranium** (*Basis cranii interna* **5**[12`]). The external surfaces of the bodies of the occipital and basisphenoid bones (but the vomer in the region of the presphenoid bone) form the **external surface of the base of the cranium** (*Basis cranii externa* **5**[12``]). (See also 1[7].) The internal surfaces of the occipital, parietal and frontal bones form the caudal, lateral and dorsal walls of the cranial cavity. (See 2[27 - 30] , 9[8] and 10[28] .)

The dorsal or internal surface of each wing of the presphenoid bone (5[11]), is almost rectangular in shape with caudal, lateral and rostral margins. The wings are wider laterally than medially and the margins of their internal surfaces are related to the surrounding cranial bones as follows **:**

The caudal margin has a free part medially and a fused border laterally. That part of the caudal margin ventro-lateral to the yoke is the free part, the ventral aspect of which forms the roof of the combined round and orbital foramen. (See 4[12] under basisphenoid bone.) Laterally, in some old animals, the free margin has an inconspicious, caudally projecting, process. When present, this process forms the **rostral clinoidal process** (*Processus clinoideus rostralis* **5**[13]). Lateral to the combined round and orbital foramen, the caudal margin of the wing articulates but never completely fuses to the lamina interna of the parietal bone at the presphenoidal part of the sphenoparietal suture (Sutura sphenoparietalis 4[11])* [39] .

The lateral margin of the wing is **concave caudally** (**5**[14]) and **convex rostrally** (**5**[15]). (See also footnote 46.) These parts of the lateral margin “articulate” with the lamina interna of the frontal bone at the presphenoidal part of the sphenofrontal suture (Sutura

[39] A distinction should be made between the pre- and basisphenoidal parts of the sphenoparietal suture (Sutura sphenoparietalis 4[11]) as also said in **footnote 29** under the basisphenoid bone.

sphenofrontalis 4 [16])* [40] . **This presphenoid part of the sphenofrontal suture is of specific interest in the savannah buffalo** because of the following **:**

In young animals, the lateral part of the wing of the presphenoid bone is cartilaginous. Macroscopically, it appears to consist out of hyaline cartilage. This cartilaginous part may be either due to a "defect" in ossification or due to delayed ossification. It must be noted that this cartilaginous part of the wing of the presphenoid bone is only on the internal side of the wall of the cranium in young animals. In animals of approximately three to four months of age, the size of this cartilaginous part is approximately 49 mm long from rostral to caudal. Its width (from medial to lateral) varies **:** Rostrally (5 [15]) it is approximately 10 mm wide, centrally approximately 7 mm wide and widest caudally (5 [14]), measuring up to 17 mm. With age, this lateral part of the wing of the presphenoid bone ossifies gradually in a rostro-caudal direction. However, the caudal-most part does not get ossified, even in old animals. Thus, being only partly cartilaginous in old animals, and articulating with the frontal bone, the "defect" could be considered (in a prepared skull) as a **sphenofrontal fissure** (Fissura sphenofrontalis **5** [16])* [41] .That is, if what fills the fissure in the live animal, consists out of a fibrous component and not cartilage. However, if one considers this defect as a fissure, it renders the following conceptual problems **:**

Contrary to what can be expected, the size of the "fissure" actually increases drastically after the age of approximately 16 months. Also, as was seen in dissections of the young animals, it apparently consists mainly of secondarily developed cartilage or fibro-cartilage, or at least tissue that appears very similar to hyaline cartilage. It attains it largest size (at least in some animals) at approximately 2 to 2½ years of age. It then measures approximately 15 x 10 x 10 mm, actively expanding caudally and peripherally. Eventually, at that age, it not only involves the

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40 The *N.A.V.* does not distinguish between the pre- and basisphenoidal parts of the sphenofrontal suture (Sutura sphenofrontalis 4 [16]). A distinction should be made. (See also **footnotes 32 & 45**.)

41 A sphenofrontal fissure (Fissura sphenofrontalis 5 [16]) is not listed in the *N.A.V.*

internal surface of the presphenoid and frontal bones, but also the external surface of the parietal bone. This external part of the "fissure" (or defect of ossification) can then also be seen in the temporal fossa near the suture where the external laminae of the frontal and the parietal bones meet. Considering this aberrant ossification as a "fontanel" from this point on, helps to describe it further. But, even though the external part of this structure may lie on the frontoparietal suture (9 [5`] ) (externally), it cannot be described as a frontoparietal fontanelle (Fonticulus frontoparietalis 1 [17`]) as such a structure typically lies in the median plane, nuchally, and is unpaired. (See **Discussion**, point 2, chapter four, and footnote 28.) The part of the "fontanel" that lies in the temporal fossa, causes a defect in the external lamina of the cranium (1 [2]), reaching a diameter of approximately 10 mm. Externally it may then even appear as if this fontanel involves the frontal bone only and not the frontoparietal suture (9 [5`]).

From the above reasoning, such a structure in that position could therefore at best be described as a sphenoidal fonticulus (Fonticulus sphenoidalis 1 [17``]) although it is not purely homologous to that fontanelle of man * [42] . Both the internal and the external dimensions of this cartilaginous structure decrease in size after this age. Externally, the "fontanel" ossifies completely, but evidence in the form of an **osseus "scar"** (**5** [16`]) may be seen in the temporal fossa even in old animals. (See **Discussion**, chapter four.) Internally, a part of this structure usually remains un-ossified, giving the impression of a sphenofrontal fissure (5 [16]) as seen in prepared skulls. In some cases, a circumscribed **osseus "scar"** (**5** [16``]) might also develop internally. The internal scar can usually be seen much easier than the external one, and may then represent a typical Wormian bone. (See footnote 28.)

The rostral margin of the dorsal surface of the wing of the presphenoid bone is

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42 In the absence of a better term, this cartilaginous structure that first increases in size before it becomes smaller and ossifies - as seen in the temporal fossa - can only be considered as an **atypical and temporary sphenoidal fontanelle** (Fonticulus sphenoidalis 1 [17``]) for the purpose of this description on the osteology of the skull of the savannah buffalo. (See chapter 4 **: Discussion**, point 2.)

concave and it is fused to the ethmoid bone to form the visible internal part of the sphenoethmoidal suture (5^{9}) that is just about always possible to identify. (Vide supra for an "invisible" part and vide infra under 5^{21} for an external part. Also see the orbital lamina - 11^{3} - under the ethmoid bone.) In some animals it appears as if this suture lies on or just behind the partial constriction (10^{29} and $10^{29`}$) formed by the frontal bone (dorsally) and by the ethmoid bone (laterally and ventrally). In some other animals, the sphenoethmoidal suture appears to lie much more caudally whereas in other older animals, the suture may become vague due to partial ossification. Yet in some other much older individuals, the suture has also been seen to be very clear, but then it usually lies much further rostrally in the ethmoid fossae *[43] .

Topographically, the shape and size of the external surface of the wing, do not nearly match or register with the dorsal or internal surface. (See introductory paragraphs and figures 3.16 & 3.17.) In lateral view, the external surface is smaller and almost triangular with caudal, dorsal and ventral borders. These three borders as well as the relation of the apex (5^{21}) to surrounding bones are as follows **:**

The caudal border forms the base of this triangular surface of the wing of the presphenoid bone. The apex (5^{21}, vide infra) is directed rostrally. (Note that the apex of the wing of the basisphenoid bone - $4^{14`}$ - is directed in the opposite direction, caudally.) The caudal border of the external surface of the wing - forming the base - lies almost vertically and is situated medial to the pterygoid crest (4^{17}). It is fused along most of its length - except at the combined round and orbital foramen - to the basal border of the wing of the basisphenoid bone - i.e. nearly base to base - at the **(pre-)spheno-(basis-)sphenoidal suture** (Sutura spheno-sphenoidalis **5** ^{17})*[44] . (See also lateral part of the rostral border of the internal

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43 The ossification and therefore the visibility - as well as the position - of this internal "visible" part of the sphenoethmoidal suture (5^{9}) is inconstant. Variations are apparently due to individual variation. "Drifting" of the suture, usually in a caudal direction, could be due to remodelling in the shape of the cranial bones, but a mechanism by which it can occur, has not been studied. (See also **footnote 38**.) However, "drifting" of the suture and remodelling may also explain variations in the position of the partial constriction ($10^{29`}$) which may either lie on, or rostral to, the sphenoethmoidal suture. (See **footnote 46**.)

44 The (pre-)spheno-(basis-)sphenoidal suture (Sutura spheno-sphenoidalis 5^{17}) - which is an intersphenoidal suture - is not listed in the *N.A.V.* (See also **footnotes 31, 34 & 47**, and the intersphenoidal synchondrosis 4^{2}.)

surface of the wing of the basisphenoid bone as well as the rostral margin of the external surface of the wing of the basisphenoid bone, as referred to under footnotes 31 & 34.) This suture lies medial and parallel to the pterygoid crest, at the caudal extreme of the boney orbit (13[21]). The remaining ventral part of the basal border of the wing of the presphenoid bone is free and it forms the dorso-medial wall of the combined round and orbital foramen (4[12]).

The dorsal border of the external surface is concave and is fused at the presphenoidal part of the sphenofrontal suture (Sutura sphenofrontalis 4[16`]) to the frontal bone. (See 4[16] for the basisphenoidal part of the suture *** [45]** and also see the orbital surface 10[17] of the frontal bone.)

The ventral border of the external surface lies essentially horizontally and is fused to three different bones (see also description following 4[18]). To ease the description of the fusions of this ventral border, a few aspects regarding the wing of the presphenoid bone have to be noted first **:**

- The ventral border intersects the dorsal border at the (true) apex (5[21], vide infra) of the wing of the presphenoid bone. Another acute angle, between the caudal and the dorsal borders of the wing, is **process-like** (**5**[17`])*** [46]** and is fused to the frontal bone at the sphenoidal incision. (See Incisura sphenoidalis 10[20] under the frontal bone. This process-like part must not be confused with the true apex of the wing - vide infra.)
- The external opening of the optic canal (13[26]) opens near the centre of the external surface of the wing.
- The external surface of the wing of the presphenoid bone is marked by the **ventral orbital ridge** (*Crista orbitalis ventralis* **5**[18]). The ridge lies rostral to the optic canal,

45 The *N.A.V.* does not distinguish between the pre- and basisphenoidal parts of the sphenofrontal suture (Sutura sphenofrontalis 4[16]). A distinction should be made. (See also **footnotes 32 & 40**.)

46 Although the external surface of the wing of the presphenoid bone does not match or register the internal surface exactly (lateral versus medial views), this process-like part of the external surface corresponds best to the rostral end of the lateral border of the internal surface. The caudal end of the lateral margin (5[14]) does not have an external equivalent. (See figures 3.16 & 3.17 for a schematic presentation of the disproportionate growth of especially certain parts of the sphenoid and parietal bones.)

mostly parallel to the ventral border of the wing. It divides the external surface of the wing into a larger dorsal and a smaller ventral part. The former part face laterally and forms part of the medial wall of the caudal part of the boney orbit (13 [21]). The latter part face ventrally and it forms part of the dorso-medial wall of the pterygopalatine fossa (13 [30]). Rostrally, the ridge extends onto the orbital part of the frontal bone. (See 10 [16 and 17] under the frontal bone.) The ridge demarcates the ventral limit of the boney orbit (13 [21]) (Also see 10 [15] and 4 [17] for the caudal demarcation.)

Thus, the ventral border is fused to the three different bones as follows **:**

Caudal to the optic canal, the ventral border is fused to the bodies of the basisphenoid and pterygoid bones. (The body of the pterygoid bone is usually only discernable in animals younger than 2 years of age, but sometimes also clearly discernable in old bulls.) Rostral to the optic canal, the ventral border is fused to the perpendicular lamina of the palatine bone (19 [10`]). (See also palatine bone.) From caudal to rostral, the ventral border of the wing is therefore fused at the spheno-sphenoidal * **[47]** and **pterygosphenoidal** (*Sutura pterygosphenoidalis* **5** [19])* **[48]** sutures as well as to the **presphenoidal part of the sphenopalatine suture** (*Sutura sphenopalatina* **5** [20])* **[49]** to the said three bones. The **basisphenoidal part of the sphenopalatine suture** (**5** [20`]) has been referred to under the pterygoid process of the basisphenoid bone and requires no further discussion than what has been said here.

The apex (**5** [21]) of the triangular wing of the presphenoid bone is positioned differently (that is topographically) in the pterygopalatine fossa of young versus old animals. This is seen best in close-up lateral views of this fossa where the sphenopalatine foramen (13 [31]) is

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47 See **footnotes 31, 34 & 44**.

48 In lateral view of the pterygopalatine fossa, the pterygosphenoidal suture (Sutura pterygosphenoidalis 5 [19]) has three different positions around the pterygoid bone. (See figure 3.20 and note how it differs from figure 3.15.) A fourth part of this suture lies between the body of the pterygoid bone and the body of the presphenoid bone. This fourth part of the suture cannot be seen without removing the body of the pterygoid bone. (See **footnote 51**.) A fifth part of the suture can only be seen after the vomer is sculptured away. (See **footnote 52**.) A sixth part of the suture always remains visible between the caudal border of the larger process of the pterygoid bone and the ventral angle of the base (4 [18``]) of the pterygoid process of the basisphenoid bone. (See **footnotes 54 & 55**.)

49 The *N.A.V.* does not distinguish between presphenoidal (5 [20]) and a basisphenoidal (5 [20`]) parts of the sphenopalatine suture. (See also the paragraph where 4 [18] is discussed.)

properly exposed **:**

Even though it is not so typical for the ethmoid bone to contribute much to the external surface of the face, the apex of the wing of the presphenoid bone is fused to a minor part of the ethmoid bone that contributes to a particularly small external part of the ethmoid bone in later life. Fusion is therefore at an external part of the sphenoethmoidal suture (5^{9}), and this suture is fairly easy to see in most skulls and even in some skulls of old animals. This particular part of the ethmoid bone (11^{5}) which is involved here, appears to be in the region where the original orbital and basal plates could have united prenatally. In young animals it only forms a small part of the edge of the dorsal quadrant of the sphenopalatine foramen (13^{31}). (See 10^{21} for a contribution of the frontal bone and see the paragraph on the orbital plate of the ethmoid bone under 11^{3} .) With age, this part of the ethmoid bone enlarges slightly (in a caudal direction), following a regression of the apical part (5^{21}) of the wing of the presphenoid bone, with compensatory enlargement of the orbital part of the frontal bone. Therefore, in animals older than approximately 2 - 2½ years of age, the apex of the external surface of the wing of the presphenoid bone usually does not extend as far rostrally - to end right into the sphenopalatine foramen (13^{31}) - but ends some distance away from it. Although individual variation also occurs, the tendency for the particular part of the ethmoid bone to contribute to the formation of the medial osseus wall of the pterygopalatine fossa as described above, is constant and of interest. That interest is possibly wider than just this academic study **:** This part of the sphenoethmoidal suture is part of the complex sphenoethmoidal suture. Of all the parts of the sphenoethmoidal suture, only this external part can be seen well in all skulls. All other (internal) parts of the sphenoethmoidal suture, are hard to find in skulls of just about any age. This may be of importance in the zoological classification of skulls.

6. THE PTERYGOID BONE

(*OS PTERYGOIDEUM*)

(See figures **3.23 - 3.25**. Also see 3.1, 3.3, 3.8 & 3.15 - 3.17.)

The pterygoid bone is laterally flattened, consisting of a small body (6[1], vide infra) and two processes ventrally * [50] . One of these is larger (6[5], vide infra) and it projects ventrally. The other process is small (6[7], vide infra) and it projects caudally - that is - from the caudal border of the larger process. Both processes are almost triangular in shape, delicate and thin. Although the exposed surface of the body faces laterally, and the exposed surface of the processes medially, they are in the same sagittal plane. The body contributes to a small part of the pterygopalatine fossa, and the processes contribute to the lateral wall of the boney choana (13[12]). Despite this, the pterygoid bone is considered a bone of the cranium.

The **body of the pterygoid bone** (**6**[1]) is fused medially to the lateral aspect of the body of the presphenoid bone at the pterygosphenoidal suture (5[19])* [51] . The body is seen as a small round to oval bone of approximately 9 mm in diameter, forming part of the medial wall of the pterygopalatine fossa (13[30]). In lateral view of the skull, the body lies roughly between the wing of the presphenoid bone and the pterygoid process of the basisphenoid bone.

The body is surrounded and fused to the palatine, presphenoid and basisphenoid bones as follows **:** Rostrally it is fused to the caudo-dorsal extremity of the lamina perpendicularis of the palatine bone at the **pterygopalatine suture** (*Sutura pterygopalatina* **6**[2]).

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50 The *N.A.V.* does not distinguish between a body and processes for the pterygoid bone. It is however convenient to make a distinction between the body and two processes for descriptive purposes. Without doing so, it would be impossible to describe the pterygoid canal (6[3``]).

51 The pterygosphenoidal suture (5[19]) has various parts or components that must be distinguished from each other. Three of these can be seen in lateral views of the pterygopalatine fossa. (See figure 3.20 and note how it differs from figure 3.15.) The fourth part of this suture is not found around the circumference of the body of the pterygoid bone, but between the body itself and the **body of the presphenoid bone** - the suture that this footnote refers to. (See figure 3.8). It can only be visualized when the body of the pterygoid bone is removed or in sagittal sections of young skulls when viewed from medially. A fifth part of this suture (5[19]) can be seen between the pterygoid bone and the **basisphenoid body**, but only if the vomer is sculptured away. It lies more towards the caudal end of the theoretical line (6[4]). (See **footnote 52**.) A sixth part of the suture - involving the larger pterygoid process and not the body - is visible in un-sculptured skulls, between the caudal border of the larger process of the pterygoid bone and the ventral angle of the base (4[18``]) of the basisphenoid bone. (See **footnotes 54 & 55**.)

FIGURE 3.23 : OSTEOLOGY

VIEW FOUR OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

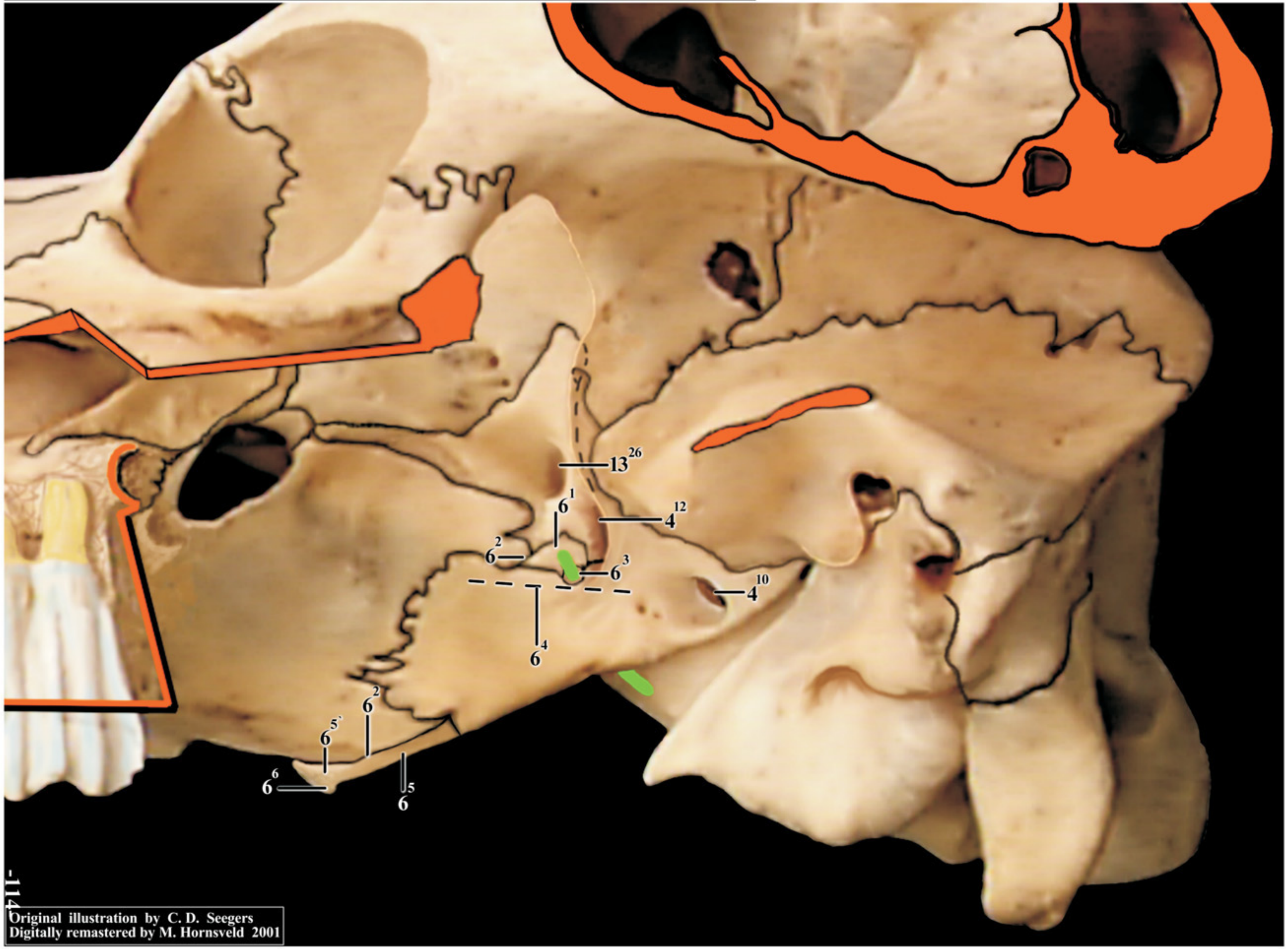


FIGURE 3.23 : OSTEOLOGY
VIEW FOUR OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

FIGURE 3.24 : OSTEOLOGY

VIEW FOUR OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)

Note : The skull was cut to the right of the median plane, except for the rostral part of the hard palate where the median septum can still be seen. Part of the rostrum presphenoidale has been cut even more paramedially (to the right) to expose its sinus. Because it is a paramedian section, the vomer is not shown.

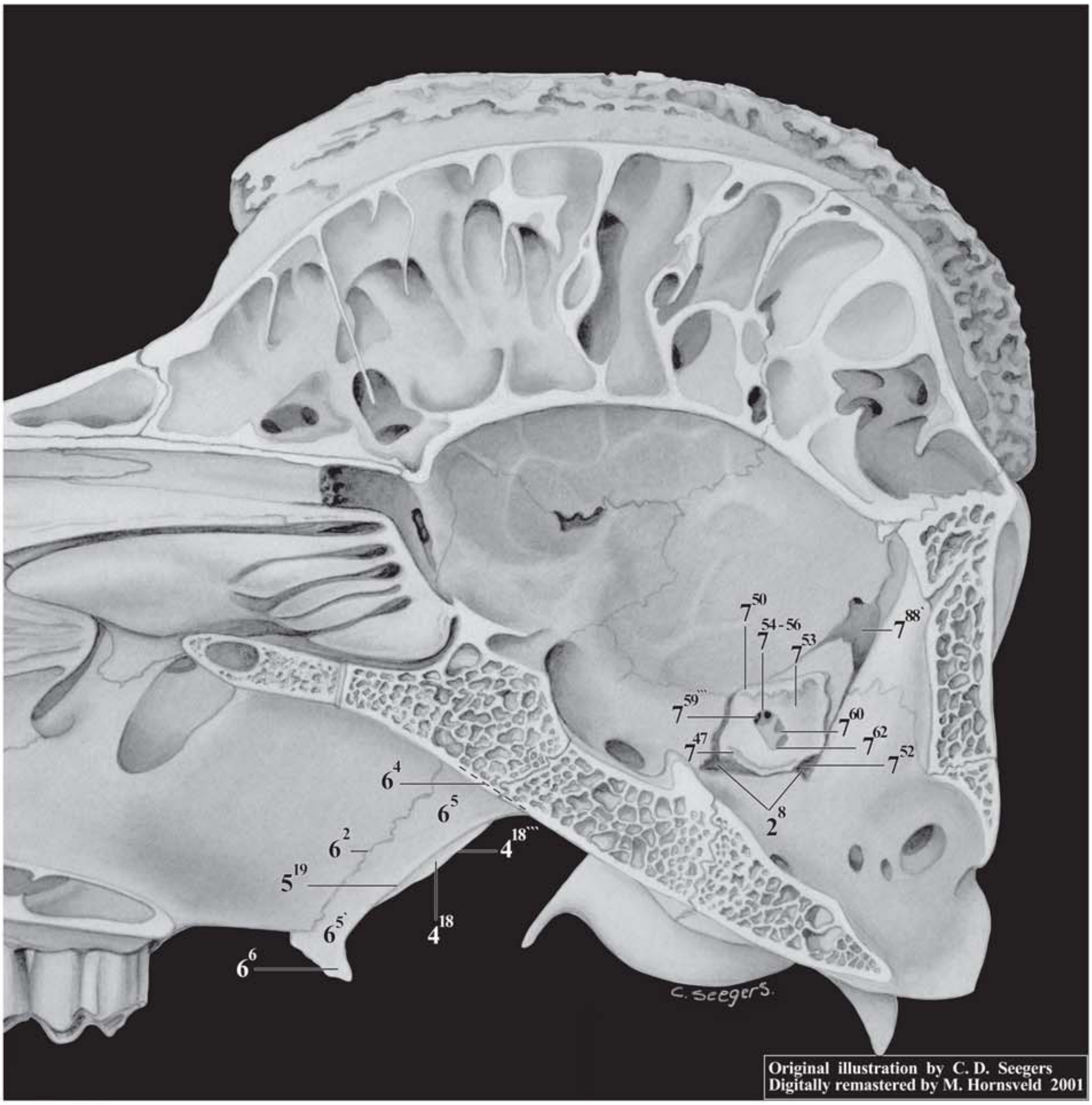
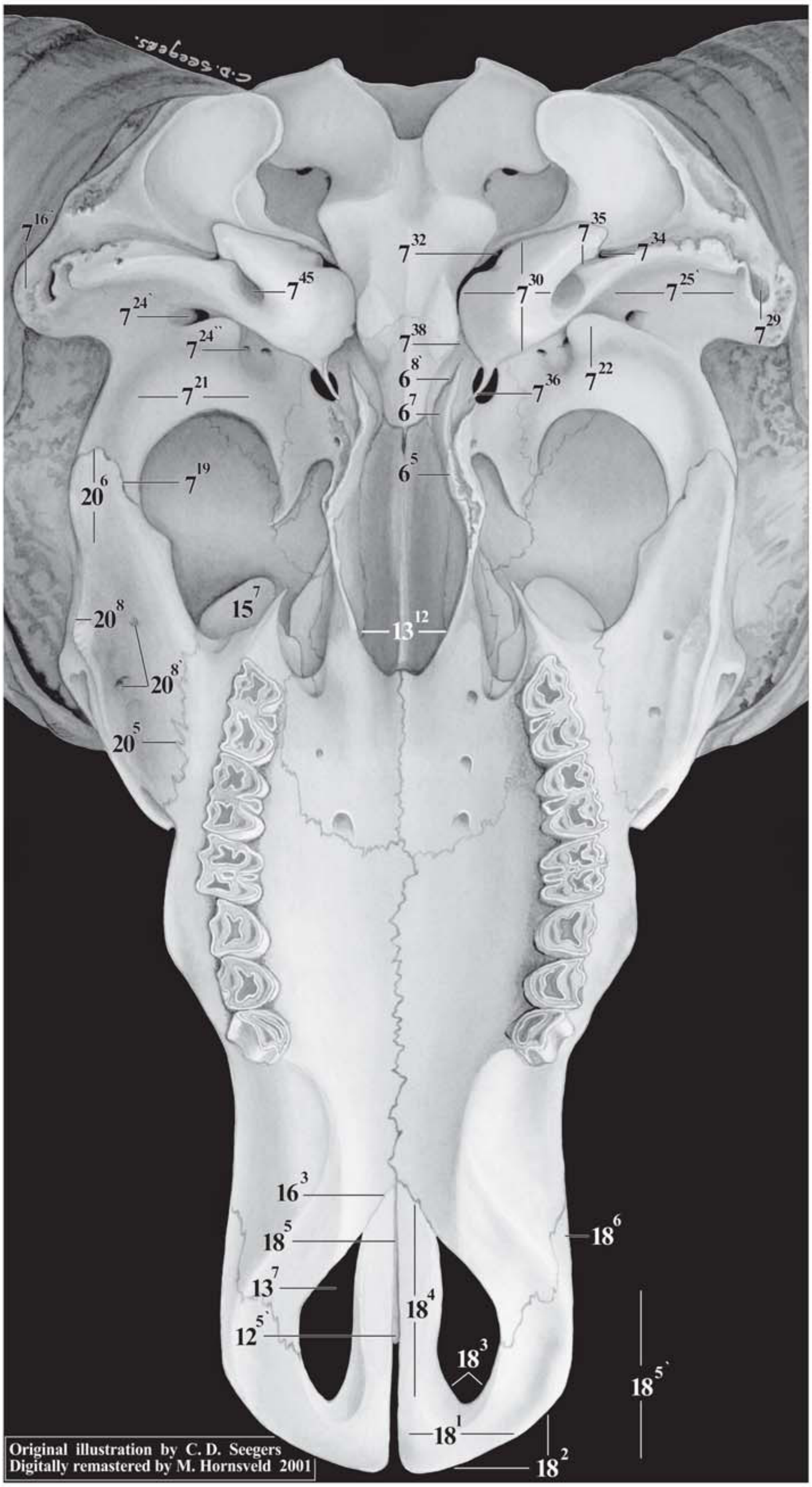


FIGURE 3.25 : OSTEOLOGY

VIEW FOUR OF THE SKULL OF A MATURE BULL (VENTRAL VIEW)



Dorsally, the body is fused at the presphenoidal part of the pterygosphenoidal suture (5[19]) to the wing of the presphenoid bone.

Ventrally, the body is fused at the basisphenoidal part of the pterygosphenoidal suture (5[19]) to the pterygoid process of the basisphenoid bone. This suture is marked by the **rostral opening** (**6**[3]) **of the pterygoid canal** (*Canalis pterygoideus* **6**[3\`]). (See also 4[3] under the basisphenoid bone for the formation of the pterygoid canal and vide infra under 6[8\`] for the caudal opening.) The opening is approximately 1 - 2 mm in diameter and it lies rostral to the combined round and orbital foramen (4[12]), ventral to the rostral (external) opening of the optic canal (Canalis opticus 13[26]).

Note : The transition or changeover point from the body of the pterygoid bone to the wings cannot be seen without sculpturing the surrounding bones away. The exposed parts of the processes can however be seen in ventral or in median views as stated above, and they form part of the boney choana (13[12]). Based on what is seen in sculptured skulls, a line can be defined, that makes the description of the un-exposed parts of the pterygoid bone in the un-sculptured skull much easier **:**

The body gives rise, along a **theoretical line** (**6**[4]) that lies just ventral to the basisphenoidal part of the pterygosphenoidal suture (5[19])***[52]**, to the large process of the pterygoid bone (vide infra under 6[5]). Ventro-medially, at the base of this larger process, a small medial unexposed part of the body is fused - just above the level of the theoretical line - to the dorso-lateral edge of the wing of the vomer at the vomero-pterygoidal suture. (See Sutura vomero-pterygoidalis 12[8])***[53]**. In ventral view - of un-sculptured skulls - another part of this vomero-pterygoidal suture is nevertheless visible, but it is between the vomer wing (lateral aspect) and the pterygoid process (and not the body). This suture can be seen even better if the wing of the vomer is sculptured away. Furthermore, a median view of a sagittally cut skull of a young animal, exposes a fourth part of the pterygosphenoidal suture (5[19]). The position of the fourth part of the

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52 It is the fifth part of the pterygosphenoidal suture (5[19]). (See also **footnotes 48, 51, 54 & 55**.)

53 The vomero-pterygoidal suture (Sutura vomero-pterygoidalis 12[8]) is not listed in the *N.A.V.* (See also **footnote 118.**)

pterygosphenoidal suture, helps one to form a mental picture of where the theoretical line lies. (See footnotes 48 & 51 and figure 3.8.)

Apart from defining the theoretical line, the following also helps to understand the pterygoid bone **:** Except for a small part in some individuals (vide infra), the lateral surfaces of both the processes of the pterygoid bone are fused flush to the medial surfaces of especially the rostral part of the pterygoid process of the basisphenoid bone and to a lesser extend to the caudal part of the perpendicular lamina of the palatine bone ($19^{10`}$). In spite of that, a pterygopalatine suture (6^{2}) can be seen in medial and in lateral views. The medial surfaces of the processes of the pterygoid bone that face the caudal end of the nasal cavity, therefore forms part of the lateral wall of the boney choana (13^{12}).

The **larger process** (**6**^{5}) **of the pterygoid bone** is much longer than it is wide, and it ends distally in an apical part (**6**$^{5`}$). Medially, the base of this process takes origin from the theoretical line as defined. Just distal to the line, the medial surface of the larger process is fused to the edge of the wing of the vomer at the vomero-pterygoidal suture. (See 12^{8} under the vomer.) This suture can always be seen in ventral views of un-sculptured skulls. The rostral border of the process is fused flush with the caudal aspect of the perpendicular part of the palatine bone at the pterygopalatine suture (6^{2} , vide supra). The distal apical part projects ventrally beyond the level of the nasal surface of the hard palate to form a **free hook** (*Hamulus pterygoideus* **6**^{6}) which is usually poorly defined. In young animals, it consists mostly of cartilage and is therefore lost in the process of skull preparation. The lateral surface of the hook (6^{6}) and sometimes the apical part of the process ($6^{5`}$) is exposed to a lateral view of the skull as these part project distally beyond the level of the pterygoid process of the basisphenoid bone. The caudal border of the large process is fused at a basisphenoidal part of the pterygosphenoidal suture (5^{19})* **[54]** . In some individuals however, the caudal border of the large process may extend caudally beyond the ventral margin of the pterygoid process of the basisphenoid bone ($4^{18```}$). In those cases the large

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[54] It is the sixth part of this suture. (See also **footnotes 48, 51, 52 & 55.**)

process of the pterygoid bone then forms the ventral part of the caudal free border of the lateral wall of the boney choana (13 [12])* [55] .

The proximal part of the caudal border of the large process carries the triangular **small process** (**6** [7]) **of the pterygoid bone**. The apex of the small process projects caudally. The dorsal border of this process is concave, the ventral curvature of which faces the groove of the pterygoid canal. (See Sulcus n. canalis pterygoidei 4 [3] under the basisphenoid bone.) The dorsal border of the small process is related to the groove in three different positions **:** Apically it borders the groove laterally, in the middle it forms the floor of the pterygoid canal, whilst at the base, it borders the canal rostro-medially. The dorsal border of the small process of the pterygoid bone therefore completes the **caudal part** (**6** [8]) **of the pterygoid canal** (6 [3]). The precise position of the **caudal opening** (**6** [8`]) **of the pterygoid canal** cannot be defined accurately as the apex of the smaller process can vary in length and also because the canal has incomplete boney borders caudally. (See above under 6 [3] for the rostral opening.)

In some individuals the two processes of the pterygoid bone are so weakly developed that they are less than 1 mm thick, and may even be shrivelled up in prepared skulls. In some mature animals it is difficult to identify the body of the pterygoid bone due to ossification of its sutures to the surrounding bones. (See footnotes 48, 51 & 52.) The processes however can always be discerned.

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55 In those cases the sixth part of the pterygosphenoidal suture (5 [19]) is usually much reduced.

7. THE TEMPORAL BONE

(*OS TEMPORALE*)

(See figures **3.24 - 3.30**. Also see 1.4, 3.1 - 3.3, 3.8 - 3.11.)

The temporal bone consists of **squamous**, **tympanic** and **petrous** parts. (See under 7[2], 7[25] and 7[42] respectively.). Together they form a small part of the latero-ventral wall of the skull.

Externally the temporal bone is bordered by the occipital, parietal, frontal, basisphenoid and zygomatic bones. Internally it is bordered by the occipital, parietal and basisphenoid bones. Ventro-medially and ventro-caudally, the petrous part is separated from the occipital bone by the petro-occipital fissure (Fissura petrooccipitalis 2[8]) and from the basisphenoid bone by the sphenopetrous fissure (Fissura sphenopetrosa 4[13]) in medial and rostral positions respectively. These two fissures are continuous with each other and also with the sphenotympanic (7[33]) and the tympanooccipital (7[32]) fissures (vide infra). Together, these fissures separate the petrous part from the basisphenoid and the occipital from the temporal bones, to form a complex **compounded fissure** (**7**[1]). This compounded fissure constitutes a lacerated foramen (Foramen lacerum 1[20])* [56].

Of the three parts of the temporal bone, the **squamous part** is positioned most laterally in the skull. It presents a divided external surface only. This external surface contributes to the formation of the temporal surface (7[3]), part of the zygomatic arch (20[1]) - including an articulation facet for articulation with the mandibular ramus (21[1]) - and occipital (7[14]) and retrotympanic processes (7[16]). Visible on the external surface of the skull only, the **tympanic part** of the temporal bone is positioned ventral to the squamous part. It is divided into a lateral semi-tubular (7[25`]) and a medial thin-walled bulbous part (7[30]). The latter harbours a major

56 Although it is not typical to classify the opening between the temporal, the basisphenoid and the occipital bones of large ruminants such as the domestic Bovine as a lacerated foramen (1[20]), such a term is called for in the savannah buffalo for this large compound fissure. It includes the petrotympanic (7[31]), tympanooccipital (7[32]) sphenotympanic (7[33]), sphenopetrous (4[13]) and petro-occipital (2[8]) fissures.

FIGURE 3.26 : OSTEOLOGY

VIEW FIVE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

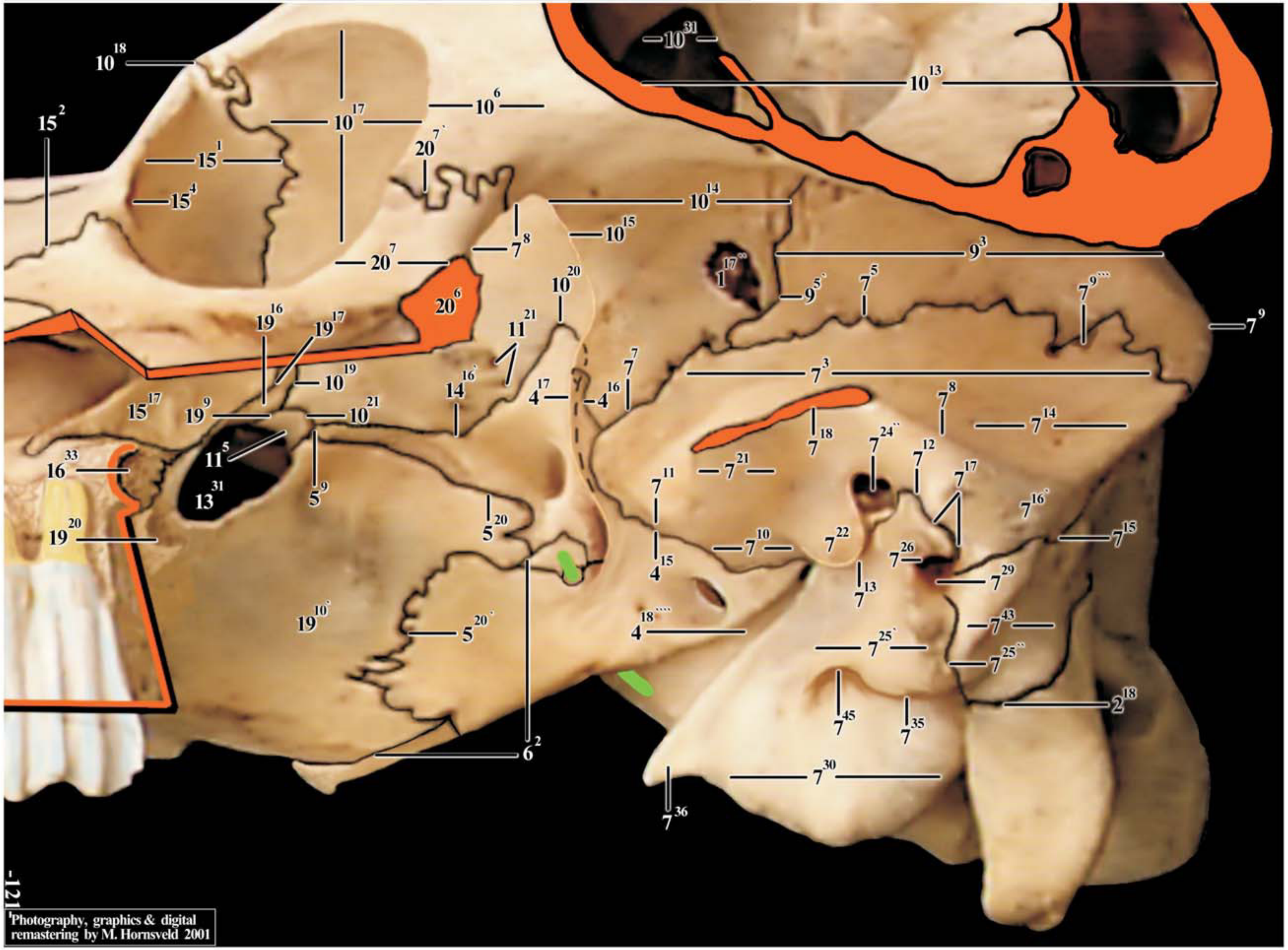


FIGURE 3.26 : OSTEOLOGY

VIEW FIVE OF THE PTERYGOPALATINE FOSSA AT APPROXIMATELY 2½ YEARS OF AGE (LATERAL VIEW)

[1]Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.27 : OSTEOLOGY

VIEW THREE OF THE *OCCIPIT* IN A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

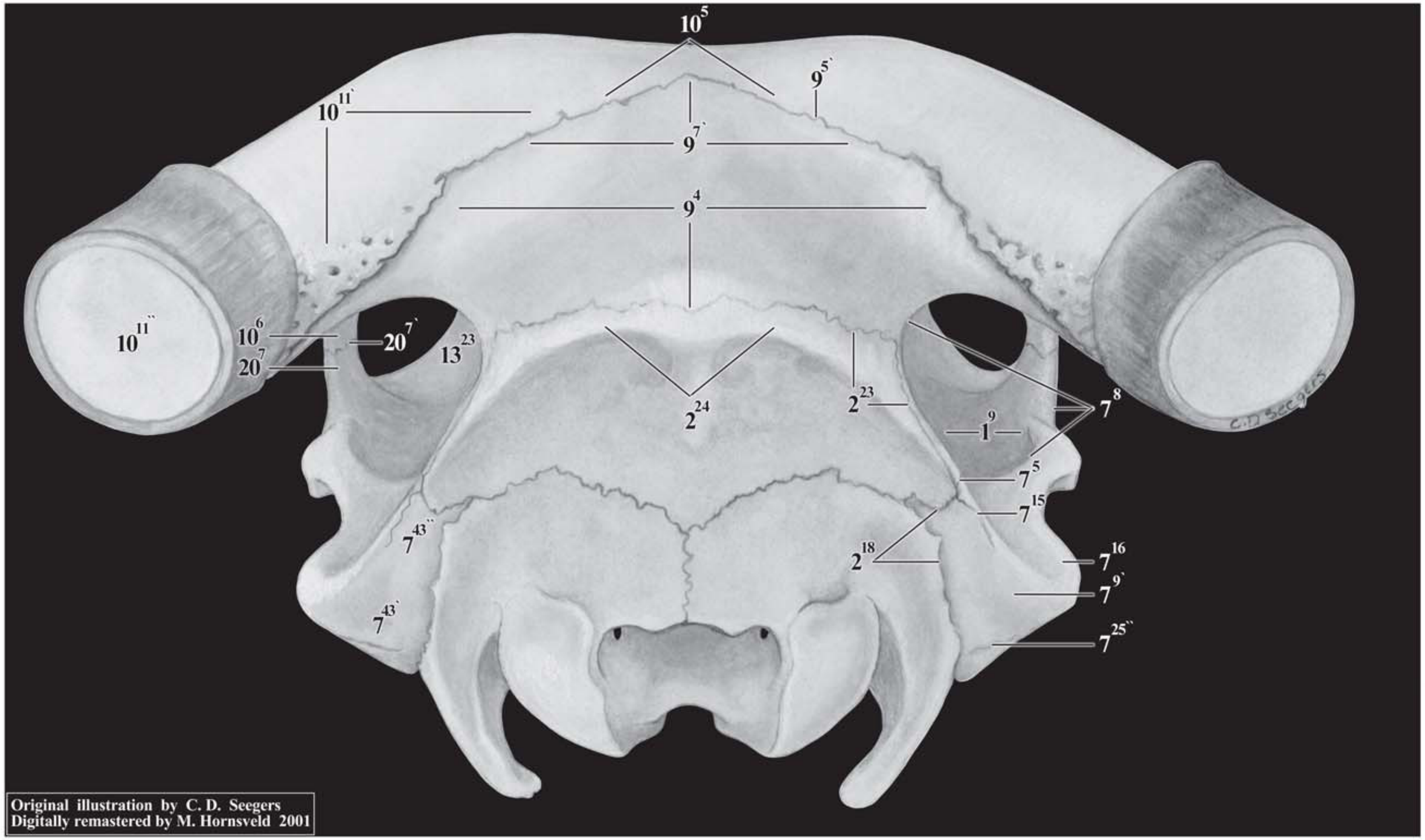
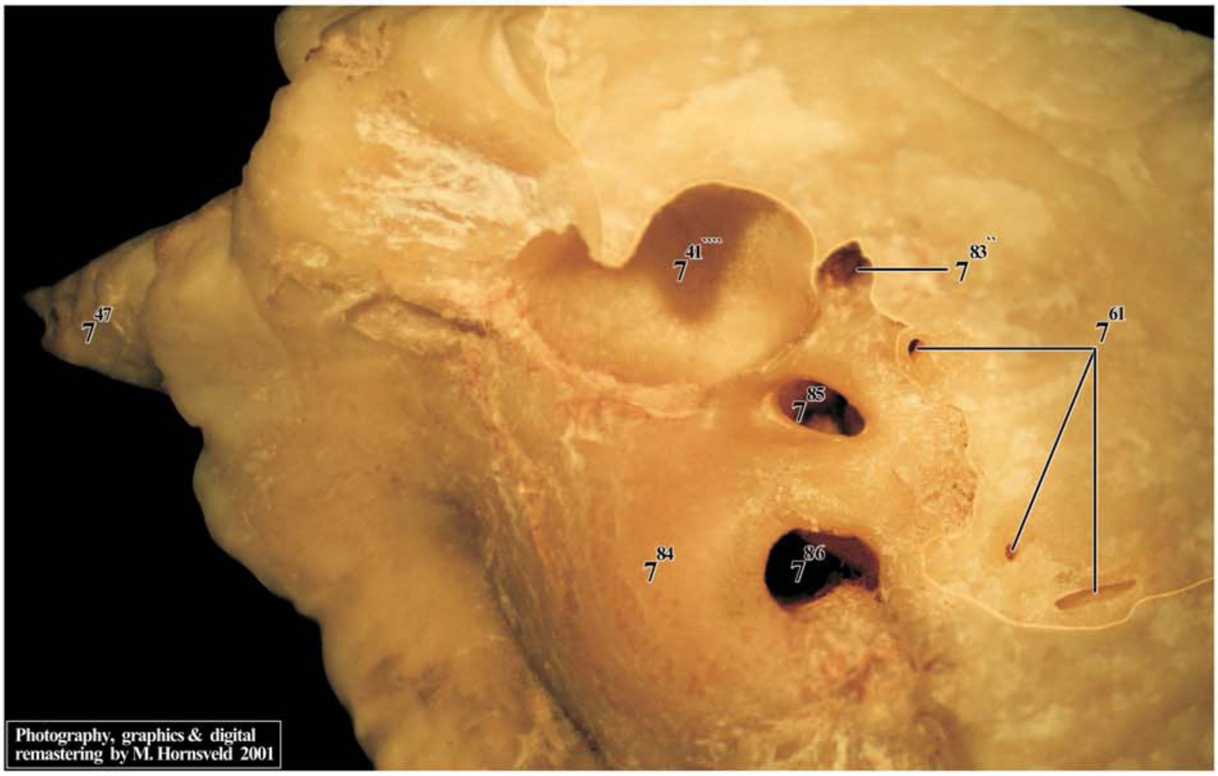


FIGURE 3.27 : OSTEOLOGY
VIEW THREE OF THE *OCCIPIT* IN A HEIFER OF APPROXIMATELY 16 MONTHS (CAUDAL VIEW)

FIGURE 3.28 : OSTEOLOGY

THE VENTRAL SURFACE OF THE PETROUS PART OF THE TEMPORAL BONE (LATERAL VIEW)

LEFT PETROUS BONE : PROMONTORIUM INTACT



RIGHT PETROUS BONE : PROMONTORIUM SCULPTURED AWAY TO EXPOSE MODIOLUS

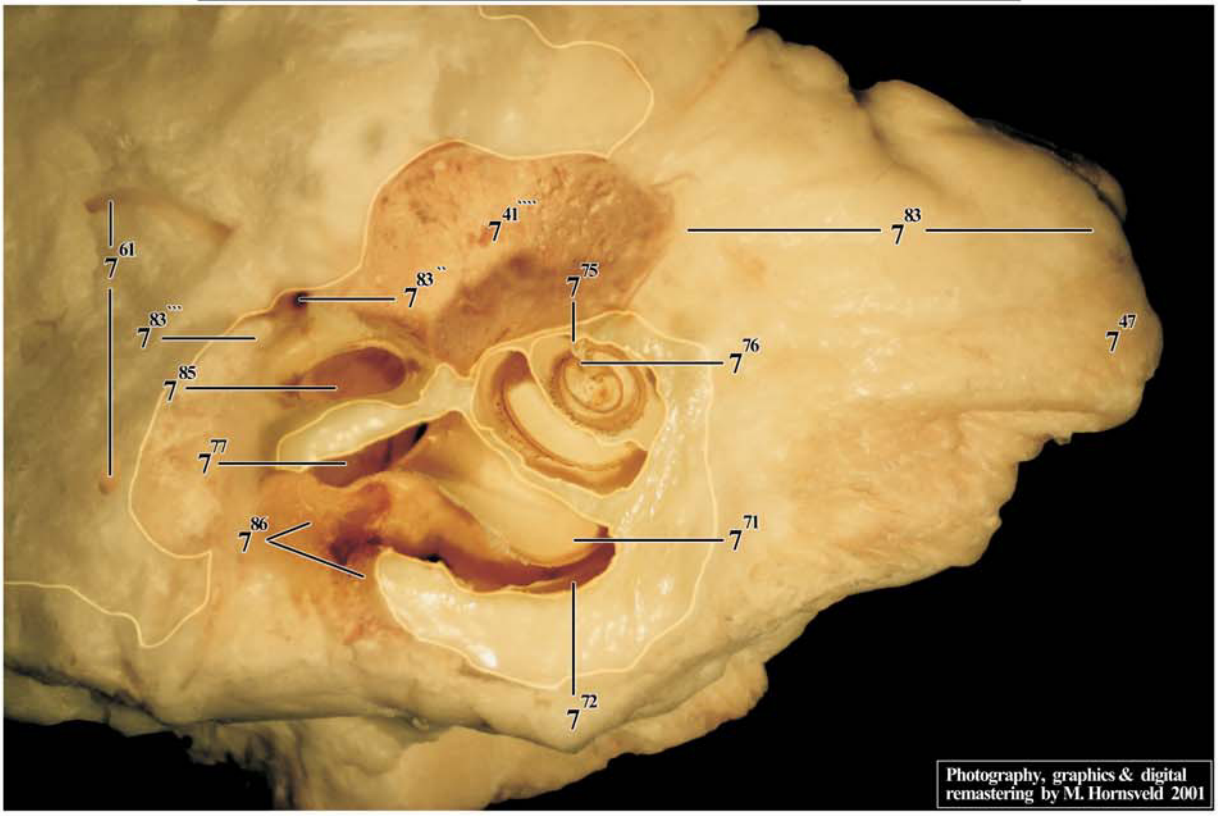
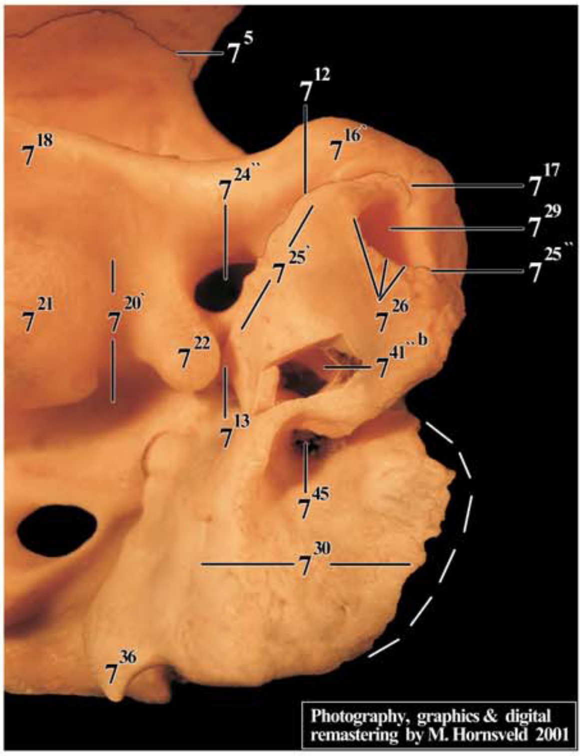


FIGURE 3.29 : OSTEOLOGY

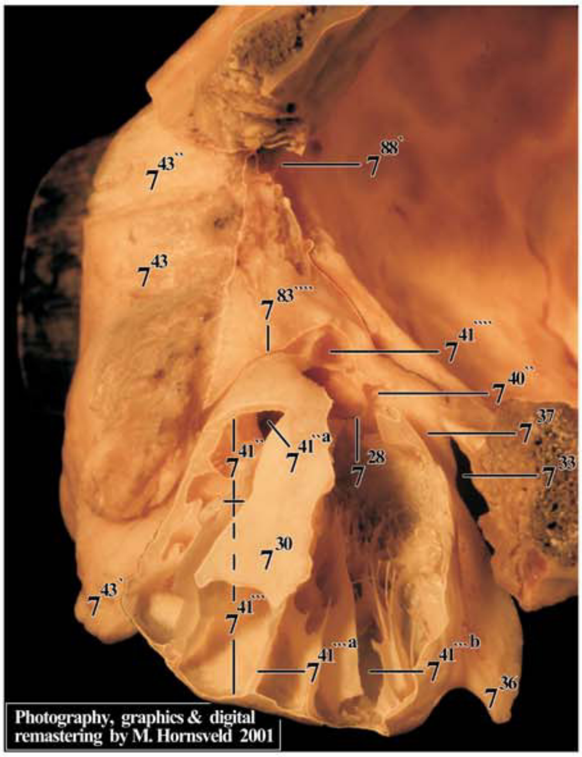
TYMPANIC AND PETROUS PARTS OF THE TEMPORAL BONE EXPOSED BY CUTTING SECTIONS OF BONE AWAY (MEDIAL AND LATERAL VIEWS)

IMMATURE FEMALE : PETROUS PART OF TEMPORAL AND COMPLETE OCCIPITAL BONE REMOVED

OBLIQUE VENTRO-LATERAL VIEW

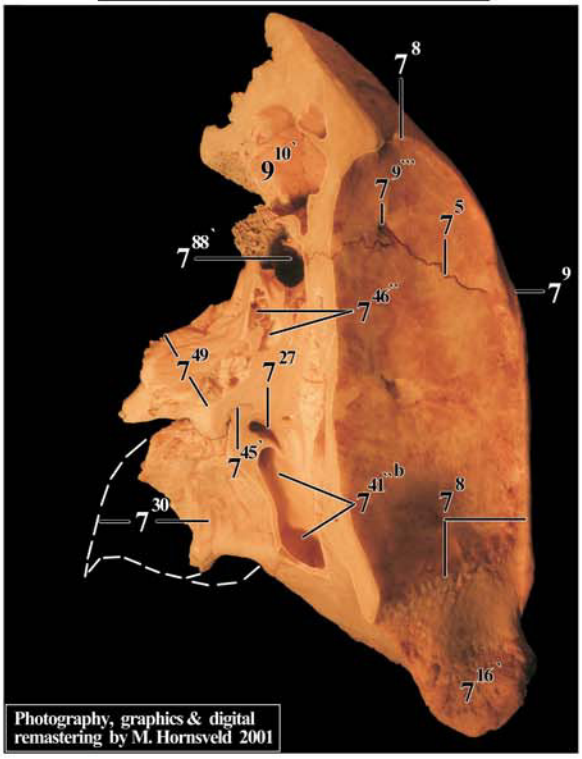


MEDIAL VIEW

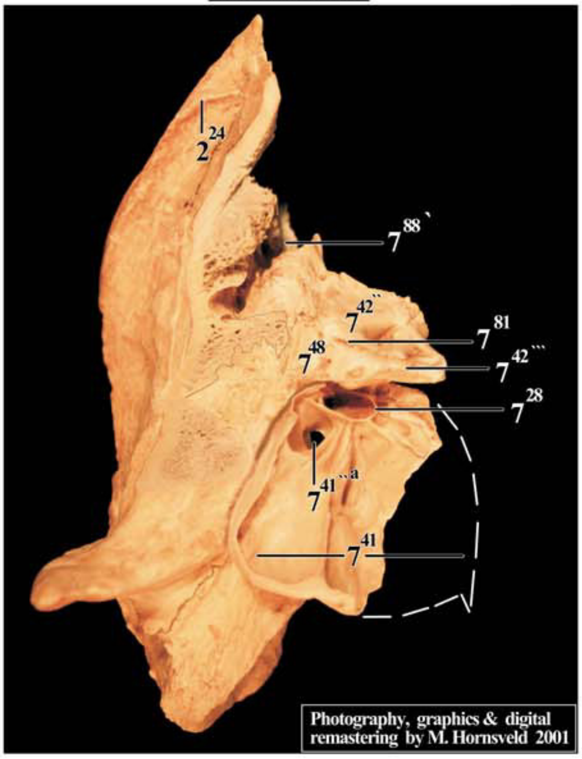


OLD BULL : WEDGE-SHAPED SECTIONS OF OCCIPITAL BONE REMOVED BUT PETROUS PART INTACT

OBLIQUE ROSTRO-LATERAL VIEW



MEDIAL VIEW



part of the middle ear cavity, whereas the former contains the external ear canal. The **petrous part** of the temporal bone consists of a body (7[42`]) and two processes. The body is situated medially and it forms part of the lateral wall of the caudal compartment of the cranial cavity, also enclosing the vestibulocochlear organ (7[46`]). The body of the petrous part is visible on the internal surface only. The processes of the petrous part of the temporal bone are the styloid and mastoid processes (7[43/45]), and only parts of them are visible on the external surface. The mastoid process contributes to a small but significant part of the nuchal surface (1[10`]) of the skull. (See also 2[24] under occipital bone.)

The squamous part of the temporal bone **:**

In lateral view, the **squamous part** (*Pars squamosa* **7**[2]) of the temporal bone is marked by a prominent rostral zygomatic process (7[18]) and a caudal occipital process (7[14], vide infra). The occipital process also has a lateral retrotympanic process (7[16]). The former process - the zygomatic process - divides the external or **temporal surface** (*Facies temporalis* **7**[3]) of the squamous part of the temporal bone into a large dorsal and a small ventral or infratemporal part (7[10], vide infra).

The dorsal part of the temporal surface faces laterally and it forms the major ventral half of the temporal fossa (1[9], and see also parietal bone for dorsal half). It has parietal, frontal and sphenoidal margins dorsally, dorso-rostrally and ventrally respectively **:**

The **dorsal margin** (*Margo parietalis* **7**[4]) of the temporal surface is convex and is fused to the temporal part of the parietal bone at the **temporoparietal suture** (Sutura temporoparietalis **7**[5])* [57]. (See also parietal bone.)

The dorso-rostral border or **frontal margin** (*Margo frontalis* **7**[6]) is also convex and it is fused dorsally at the **squamosofrontal suture** (*Sutura squamosofrontalis* **7**[7]), to the frontal bone, and rostro-ventrally at the sphenosquamous suture (Sutura

57 The temporoparietal suture (Sutura temporoparietalis 7[5]) is not listed in the *N.A.V.* It remains visible externally and internally. This footnote is **repeated under footnote 95.**

sphenosquamosa 4 [15]), to the wing of the basisphenoid bone. (See also frontal and basisphenoid bones.) The temporal surface (7 [3]) is continuous with the dorsal surfaces of the zygomatic, occipital and retrotympanic processes of the squamous part of the temporal bone (vide infra).

The periphery of the temporal surface is marked by a low, ridge-like line, the **temporal line** (*Linea temporalis* **7** [8]). The line is more prominent caudally and ventrally but less prominent on the dorsal aspect of the retrotympanic process. The ventral and caudal parts of the line also extend onto other bones of the skull **:**

The ventral part of the temporal line extends from the retrotympanic process (7 [16], vide infra), over the length of the dorsal free edge of the zygomatic arch and further rostrally to the frontal process of the zygomatic bone. (See 20 [7] under the zygomatic bone.)

The caudal part of the temporal line lies parallel and near to the caudal border of the temporal surface, forming a **supramastoid ridge** (*Crista supramastoidea* **7** [9]) ventrally. Ventro-laterally, the **crest terminates at an ill-define point** (**7** [9`]) on the mastoid process (7 [43] , vide infra). This supramastoid ridge emphasizes the lateral border of the nuchal crest, as can best be appreciated in a caudal view of the skull. (See also 2 [24] under the unpaired squamous part of the occipital bone.)

Caudo-dorsally, the temporal line separates from the nuchal crest and continues dorsally onto the parietal and frontal bones, as well as further rostrally onto the base of the zygomatic process of the frontal bone, to form the parietal and frontal parts of the temporal line. (See also parietal and frontal bones.) Due to the development of the cornual process (see 10 [11] under frontal bone) and an increase in the thickness of the lateral edge of the zygomatic arch with age, the temporal and the frontal parts of the temporal line eventually approach each other in some very old bulls. (See the end of the paragraph under 7 [19] , the paragraph that precedes 10 [11] under the frontal bone, as well as dimension 39 under the section on **Craniometric data**.) The temporal line delineates the temporal fossa (Fossa temporalis 1 [9]) peripherally, except rostrally. Rostrally, the pterygoid and orbitotemporal crests (4 [17] & 10 [15]) demarcate the boundaries of the temporal fossa from the osseus limits of the boney orbit (13 [21]). In old animals, the temporal line is more prominent.

Foramina ***[58]** of various sizes open at two localized areas on the temporal fossa, the one group rostrally (7 [9``]), the other area caudo-dorsally (7 [9```], vide infra). The largest foramen is usually found in the rostral area, and can measure up to 7 mm in diameter. However, at that site, the largest foramen can also be as small as 0,5 mm.

The **rostral grouping of foramina** (**7** [9``]) is situated near the base of the zygomatic process (7 [18], vide infra). The foramina of this area lead to diploïc canals which open into the ventral part of the temporal meatus (7 [88]) near its external opening at the retro-articular foramen. (Vide infra under 7 [24].)

The **caudo-dorsal grouping of foramina** (**7** [9```]) in the temporal fossa, usually consists of foramina that are smaller than those of the rostral grouping. They open on or near the temporoparietal suture (7 [5]), or can even overlap onto the adjacent lesser parietal part of the temporal fossa. These foramina connect the temporal fossa - via diploïc canals - to the dorsal part of the temporal meatus (7 [88]), close to its internal opening. (Vide infra under 7 [88`], and also see 2 [7```] under the occipital bone.)

The ventral part of the temporal surface - ventral to the zygomatic process - forms a small, concave and triangular **infratemporal part or fossa** (*Fossa infratemporalis* **7** [10]) which faces ventrally. The lateral border of this area is continuous with the ventral surface of the zygomatic process. The medial border - the **sphenoidal margin** (*Margo sphenoidalis* **7** [11]) of this part of the temporal surface - is fused to the dorsal border of the wing of the basisphenoid bone at the sphenosquamous suture (Sutura sphenosquamosa 4 [15]). The caudal border is fused to the medial bulbous part (7 [30]) of the tympanic temporal bone at a medial part of the **squamosotympanic suture** (Sutura squamosotympanica **7** [12])***[59]**. The central part of this suture is situated in a **wide**

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58 These foramina are not listed in the *N.A.V.* (See also **footnote 89**.)

59 A squamosotympanic suture (Sutura squamosotympanica 7 [12]) is not listed in the *N.A.V.* although a tympanosquamosal fissure (*Fissura tympanosquamosa*) is listed. (See also paragraph following 7 [22] for a variation of this suture, when the retro-articular process itself fuses directly to the tympanic part of the temporal bone. Such an incorporation of the retro-articular process into this suture and its ossification to another part of the temporal bone, renders another dimension to the ossification of sutures in the savannah buffalo.)

and deep groove (**7**[13]) immediately caudal to the retrotympanic process (vide infra under 7[22]). The lateral and the medial ends of the groove are marked by groups of foramina (7 [24], vide infra). In general, the suture is ill-defined due to progressive ossification, and much distorted by the foramina. (Vide infra in the part following 7[25``] for the lateral part of this squamosotympanic suture.)

The occipital, retrotympanic and zygomatic processes of the squamous part of the temporal bone **:**

The dorsal surface of the **occipital process** (*Processus occipitalis* **7**[14]) of the squamous part of the temporal bone, forms the caudal part of the temporal fossa (1[9] , and vide supra under 7[3]). It has no exact defined rostral boundary, which separates it from the rest of the squamous part of the temporal bone. Caudally, the occipital process is fused at the **squamosomastoid suture** (*Sutura squamosomastoidea* **7**[15]) to the lateral aspect of the mastoid process (7[43]) of the petrous temporal bone *****[60] .

The **retrotympanic process** (*Processus retrotympanicus* **7** [16]) projects ventro-laterally - without exact boundary between itself and the occipital process - to end distally (laterally) in a blunt and rough **tuberous enlargement** (**7**[16`] )**\***[61] . Ventrally, the retrotympanic process is concave to form the **tympanic incision** (*Incisura tympanica* **7**[17] ). The tympanic incision of the retrotympanic process is fused to the semi-tubular part (7[25`]) of the tympanic part of the temporal bone (vide infra) at a lateral part of the squamosotympanic suture (7 [12]). The retrotympanic process increases in length with age. In older animals, it can project for more than 30 mm beyond the lateral level of the zygomatic arch. (See also zygomatic bone, 7[25`] and FINAL COMMENT 10 under section D **: Craniometric data**). It is especially prominent and massive in old bulls where the distal tuberous end (7 [16`]) can be very rough and uneven. In young animals it is smooth and it does not project beyond the zygomatic arch.

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60 It should be noted that the occipital process (7[14]) is not fused to the occipital bone as the term would imply, but to the mastoid process of the temporal bone at the squamosomastoid suture (Sutura squamosomastoidea 7[15]).

61 The *N.A.V.* does not list a term for this blunt and rough tuberous enlargement (7 [16`] ) of the retrotympanic process. It can measure up to 30 x 20 mm in old bulls. For Craniometric purposes the tuberous enlargement is allocated the point **Ot`**. (See section D **: Craniometric Data**, and also see **footnote 67**.)

The **zygomatic process** (*Processus zygomaticus* **7** [18]) projects laterally from the rostral half of the squamous part of the temporal bone. The zygomatic process forms the temporal part of the zygomatic arch. (See 20 [1] or 1 [8] .) This temporal part of the arch is dorso-ventrally flattened and lies in a horizontal plane **:**

The dorsal surface of the zygomatic process is concave from medial to lateral and it forms a horizontal part - the floor - of the temporal fossa rostrally. It is wider rostrally than caudally. The rostral and the lateral margins are free. The rostral margin is concave from medial to lateral. The lateral margin curves dorsally and is thickened, especially rostrally. The zygomatic process ends in a rostral extension that projects for some distance beyond the rostral margin. The ventral aspect of this extension is fused at the **temporozygomatic suture** (*Sutura temporozygomatica* **7** [19]) to the dorsal aspect of the temporal process (20 [6]) of the zygomatic bone. The zygomatic process of the temporal bone and the temporal process of the zygomatic bone form the caudal part of the zygomatic arch. (See 20 [1`] under the zygomatic bone for rostral part, and see footnote 151.) The temporozygomatic suture remains un-ossified even in old bulls. The thickness of the lateral margin of the zygomatic process increases with age and becomes more prominent. (See also temporal line 7 [8] , vide supra.)

The **ventral (articular) surface** *(Facies articularis* **7** [20]) on the ventral side of the zygomatic process bears the **mandibular "fossa"** *(Fossa mandibularis* **7** [20`]). The "fossa" has two parts, namely a rostral articular surface (7 [21]) and a caudal process (7 [22]) **:**

The articular surface is raised and convex to form an **articular tubercle** *(Tuberculum articulare* **7** [21]). The outline of the articular tubercle is bean-shaped, lying transversely. Its rostral border is concave and lies on the rostral margin of the zygomatic process itself (vide supra). The tubercle articulates with the larger rostral facet of the condyle - or "head" - of the mandible. (See also 21 [10`] under the mandible.) In old animals the articular tubercle can be very prominent.

Caudal to the tuberculum, the **retro-articular process** (*Processus retroarticularis* **7** [22]) is directed either caudo-ventrally, or in some animals, ventrally. A shallow transverse groove - the only part of the mandibular "fossa" that is concave to justify the term 'fossa' - separates the tubercle from the process. The process is short and stubby and placed medially, obliquely behind the tubercle. It is convex from medial to lateral with a sharp edge and its width is less than half the width of the articular tubercle. It is well developed and its rostral surface articulates with the caudal lesser facet of the condyle - or "head" - of the mandible (21 [10```]). In young animals, the caudal surface of the retro-articular process is separated from the semi-tubular part of the tympanic temporal bone (vide infra) by a wide and deep groove (7 [13]). The groove narrows down with age. In some old bulls the caudal surface of the whole retro-articular process may fuse directly to the semi-tubular part of the tympanic bone, obliterating that part of the squamosotympanic suture and the wide groove. (Vide infra in the part following 7 [25``] for a lateral part of this squamosotympanic suture, and see 7 [12 & 13] .)

The articulation between the retro-articular process (7 [22]), the articular tubercle (7 [21]) and the condyles of the mandible, form the synovial **temporomandibular joint** *(Articulatio temporomandibularis* **7** [23]). In the living animal, a single biconcave fibro-cartilaginous **articular disc** (*Discus articularis* **7** [23`]), separates both the tubercle and the retro-articular process from the condyle of the mandible. (See also footnotes 59 and 191.)

The retro-articular process is bordered caudo-medially and caudo-laterally by the external opening of the temporal meatus (7 [88], vide infra), represented by two groups of openings. These groups of openings are in fact just a duplication of the **retro-articular foramen** (*Foramen retroarticulare* **7** [24])* [62] . The **caudo-medial group of openings** (**7** [24`]) lies in the triangular infratemporal fossa (Fossa infratemporalis 7 [10], vide supra), consisting of smaller foramina. The **caudo-lateral opening** (**7** [24``]) is a single (but sometimes partially divided) foramen, measuring approximately 8 mm in diameter. All these foramina decrease in diameter with age, especially those of the caudo-medial group. In some old bulls the foramina may be very small.

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62 The *N.A.V.* does not distinguish between the caudo-lateral and caudo-medial groups of the retro-articular foramen. It would be convenient to have the terms **Foramina retro-articularis medialis** / **lateralis** available.

The tympanic part of the temporal bone **:**

The **tympanic part** (*Pars tympanica* **7** [25]) of the temporal bone consists of two parts, one lateral (7 [25`]) and the other medio-ventral (7 [30]) to the styloid process (7 [45], vide infra) **:**

The **lateral part** (**7** [25`]) is **semi-tubular** and it has a **primary sound conducting** function * [63] . It is caudo-rostrally flattened and projects - by virtue of its width - slightly in a latero-ventral direction (when considering the skull in the datum plane). It increases in length (or rather the width) with age at a rate that is in par with the increase in length of that of the retrotympanic process (7 [16], vide supra). It presents a single flat or somewhat concave external surface that faces rostrally. The surface is rectangular and smooth and it can be extensive, having a dorsal attached border and free lateral and ventral margins. Medially it is continuous with the medio-ventral tympanic part (7 [30]). The caudal aspect of the semi-tubular part is fused to the base of the mastoid process (7 [43`]) at the **tympanomastoid suture** (Sutura tympanomastoidea **7** [25``])* [64] . The dorsal border is fused to the retrotympanic process (7 [16]) at the lateral part of the squamosotympanic suture (7 [12]). Both these sutures, but especially the tympanomastoid suture (which can best be seen in ventral view of the skull), are well ossified. Even in young animals, these two sutures - as well as the squamosomastoid suture (7 [15]) mentioned previously - are ill-defined. As stated under 7 [12] and footnote 59 before, the medial part of the squamosotympanic suture (7 [12]) may even be ossified to the retro-articular process too (vide supra).

Dorso-caudally, the semi-tubular part of the tympanic part of the temporal bone bears a deep and wide groove, the **tympanic sulcus** (*Sulcus tympanicus* **7** [26]). The sulcus extends from medial to lateral - over the width of this latero-ventrally directed semi-tubular part - forming the rostro-ventral part of the **(osseus) external ear canal** (*Meatus acusticus*

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63 The *N.A.V.* does not list a term for this large semi-tubular part of the tympanic part of the temporal bone. It is however essential to distinguish between the two parts (7 [25`] and 7 [30]) of the tympanic part of the temporal bone. It is also necessary to distinguish between the primary conducting function - conducting sound waves - and possible secondary functions as will be discussed further under **footnotes 68 & 72.**

64 A tympanomastoid suture (Sutura tympanomastoidea 7 [25``]) is not listed in the *N.A.V.* although a tympanomastoid fissure (*Fissura tympanomastoidea*) is listed.

externus **7**[27])*[65] . The canal - as completed by the contribution of the mastoid process - consists of a major lateral part (vide infra) - which is directed ventro-laterally - and a short medial part - which is directed medially. Together they form the osseus part of the **external ear** (**AURIS EXTERNA** **7**[27`]). The medial part of the canal itself is dorso-ventrally flattened and its inner dimension is approximately 9 mm x 3 mm. Medially, it projects for a short distance into the dorso-lateral part of the atrium (7[41``]) of the tympanic bulla (vide infra). The internal opening of the canal ends on a raised ridge, the **tympanic annulus** (*Anulus tympanicus* **7**[28]). The annulus (to which the tympanic membrane attaches) forms the osseus border between the external ear and the middle ear (AURIS MEDIA 7[41`])*[66] . (Also see 7[41] , vide infra.) As it appears in situ in the skull, and seen from medially, the annulus is shaped like the bearing surface of a horse's hoof with the bars dorsally and the toe ventrally. The edge of the annulus is flat and it lies in a near sagittal plane, but moderately slanted medio-rostrally. Therefore, planes drawn through the annuli of the left and the right-hand sides, would intersect each other approximately in the cranial part of the cranial cavity, in the region of the gallic crest (See 11[15] under ethmoid bone.) In young animals the major lateral part of the external ear canal itself is approximately 50 mm long. In old bulls this part of the ear canal can be more than 90 mm in length due to the increase in length of this part of the retrotympanic process *[67] . The osseus lateral opening of the external ear canal is at the **external acoustic pore** (*Porus acusticus externus* **7**[29]). The diameter of the pore - as well as the inner dimension of the major lateral part of the canal - is approximately 9 mm.

The ventral part of the semi-tubular part of the tympanic part of the temporal bone, ventral to the groove, may contain a cavity that communicates with the atrial part of the tympanic cavity. (Vide infra under 7[41``b] , and see footnote 72.)

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65 The caudal and caudo-dorsal parts of the external ear canal are formed by a contribution of the mastoid process (7[43]).

66 The terms AURIS EXTERNA (7[27`] ), AURIS MEDIA ( 7[41`]) and AURIS INTERNA (7[46]) are splanchnological terms that include more than just osteological structures. Despite that, it is convenient to use these terms and the tympanic membrane to describe the osteology better. (See also **footnote 80**.)

67 See **footnote 61** for other detail about the retrotympanic process (7[16]) and the text about its increase in length with age. The length of the retrotympanic process (an external measurement) must be distinguished from the internal measurements (such as the inner diameter) of the osseus part of the ear canal. (See also section D **: Craniometric data**, measurements §58 & §68.)

Based on the mere existence of this communicating cavity, one can assume that the semi-tubular part of the tympanic part of the temporal bone of the savannah buffalo could therefore also have a secondary resonant function * [68] .

The medial part of the tympanic part of the temporal bone, medial and medio-ventral to the styloid process (7^{45},vide infra) is the thin-walled **tympanic bulla** (*Bulla tympanica* **7** ^{30}). The bone of the bulla is so compact that it sounds shell-like when a metal instrument is tapped against it. The tympanic bulla encloses the tympanic cavity (7^{41} , vide infra). The bulla is a near spherical bulbous structure, which is obliquely flattened rostro-caudally, presenting a larger rostro-lateral and a smaller caudo-medial surface. Furthermore, the distal bulbous part (ventrally) is more dilated, and the proximal part (dorsally towards the attached end), is constricted. The proximo-distal dimension is greatest, measuring approximately 40mm to 60 mm long. In cross section, the proximal constricted part of the bulla measures approximately 30 x 20 mm, and the distal dilated part approximately 60 x 30 mm. The external surface of the bulla presents a **prominent rostro-medial ridge** (**7** $^{30`}$) and a caudo-lateral invagination (7^{35} , vide infra). The ridge and the invagination help to demarcate the rostro-lateral from the caudo-medial surfaces of the bulla **:**

The rostro-lateral surface is smooth and mildly convex. It is continuous with the rostral surface of the lateral semi-tubular conductive part of the tympanic temporal bone ($7^{25`}$, vide supra) and is fused to the infratemporal part (7^{10}) of the squamous part of the temporal bone at the squamosotympanic suture (vide supra under 7^{12}). The caudo-medial surface of the bulla is convex and totally free **:**

The proximal free margin is separated from the petrous part (7^{42}) of the temporal bone

68 The primary conducting function of the semi-tubular part ($7^{25`}$) of the tympanic part of the temporal bone has been discussed and referred to under **footnote 63**. **Footnote 72** refers to the communicating opening in the atrial part of the tympanic cavity that leads to this cavity in the ventral part of the semi-tubular part. It is not clear whether this cavity is formed by a process of "aeration" (pneumatization) in later life, or by a process of apoptosis in the young embryo. It falls beyond the scope of this study to investigate the embryological development of this part of the middle ear, or to confirm or reject the postulation that this cavity has a resonant function in the savannah buffalo. Such an extra cavity in the skull is not present in other domestic animals. Although it does not occur in all savannah buffalo skulls, it invariably communicates with the larger tympanic cavity (7^{41}). (See **footnote 81**. Also see section C **: Skull cavities**, as well as chapter four **: Discussion**, point 9.)

by a wide **petrotympanic fissure** (*Fissura petrotympanica* **7** [31]). The external wall of the bulla is also separated medially from the occipital bone by the **tympanooccipital fissure** (*Fissura tympanooccipitalis* **7** [32]). Rostro-medially, the bulla is also separated from the sphenoid bone by the **sphenotympanic fissure** (*Fissura sphenotympanica* **7** [33]). The petrotympanic, the tympanooccipital and the sphenotympanic fissures, as well as the sphenopetrous fissure (4 [13]), are continuous with the petro-occipital fissure (2 [8]). The caudo-lateral part of the petro-occipital fissure is however partially subdivided - due to the proximity of the bulla to the paracondylar process (2 [19]) of the occipital bone - dividing it into two parts * [69] . The larger medial part forms the jugular foramen (2 [10]). The smaller lateral part forms part of the distal limb (7 [83````]) of the "S-shaped" facial canal (7 [59], vide infra). The osseus walls of this part of the facial canal are therefore formed by the caudal wall of the tympanic bulla, the mastoid process and the occipital bone. The facial canal opens distally, approximately midway between the distal ends of the styloid and mastoid processes, at the **stylomastoid foramen** (*Foramen stylomastoideum* **7** [34]), on the ventral surface of the skull. Thus, the caudal and the medial walls of the bulla forms the borders of a complex fissure between the basisphenoid, the occipital and the temporal bones, to constitute a lacerated foramen medially (see 7 [1], vide supra, as well as 1 [20]), and laterally it includes the distal limb of the "S-shaped" facial canal.

Caudo-laterally, the bulla is invaginated to form a **tubular styloid sheath** (*Vagina processus styloidei* **7** [35]), the longitudinal axis of which is directed rostro-ventrally. The proximal part of the sheath holds the styloid process (vide infra under 7 [45]) of the petrous temporal bone (vide infra). The process is much shorter than the sheath. The sheath remains incomplete caudo-laterally at the original invagination point (by the styloid process). The distal patent part of the sheath - distal to the styloid process - is approximately 20 mm deep and 10 mm in diameter. It harbours the tympanohyoid (see

69 Despite the proximity of the tympanic bulla to the paracondylar process (lateral to the petro-occipital fissure), it cannot be considered as a suture because the edges of the two structures are usually smooth (and not serrated). Only in one case was local ossification seen over a small area. The space between the two bones is also filled by a type of connective tissue that differs from what is typically found in sutures. Pending histological evidence, it can therefore be regarded as a caudal part of the tympanooccipital fissure (7 [32]) - that part between the bulla and the paracondylar process of the occipital bone as well as the space lateral to it - and therefore as part of a lacerated foramen. (See also 1 [20] , 7 [1] and **footnote 56**.)

also 22[9]). Distally, the diameter of the sheath increases slightly, which would allow for a rostro-caudal pendulum-like movement of the hyoid apparatus.

The rostro-medial ridge (7[30`]) of the bulla (vide supra) ends distally in a laterally flattened but blunt, and free, **muscular process** (*Processus muscularis* **7**[36]). In some individuals the ridge is more prominent. In those cases, the process is longer, measuring up to 10 mm. The caudo-medial surface of the bulla, next to the ridge, presents two longitudinal grooves separated by a low ridge. The grooves form the medial- and lateral semi-canals which are the caudo-lateral **osseus components of the auditory tube** (*Pars ossea tubae auditivae* **7**[37]). The **medial semi-canal** (*Semicanalis tubae auditivae* **7**[38]) holds part of the Eustachian or auditory tube which connects the tympanic cavity to the nasopharynx. The **lateral semi-canal** (*Semicanalis m. tensor veli palatini* **7**[39]) fits part of the tensor muscle of the soft palate. The two semi-canals, together with their non-osseus components, form the **musculotubular canal** (*Canalis musculotubarius* **7**[40])*[70] . The grooves face the body, the wing and the pterygoid process of the basisphenoid bone that forms the dorso-rostral osseus component of the tube. (See 4[18````] under the basisphenoid bone). In some very old animals the tube can be partially subdivided longitudinally by an osseus **septum** (*Septum canalis musculotubarii* **7**[40`]). The tube opens caudally, into the atrial part of the tympanic cavity, via the rostro-medial part of the petrotympanic fissure (7[31]), to form the caudal **osseus tympanic opening** (*Ostium tympanicum tubae auditivae* **7**[40``]) of the auditory tube.

The shell-like wall of the tympanic bulla has a fairly even thickness throughout. It encloses the spacious **tympanic cavity** (*Cavum tympani* **7**[41]) as part of the **middle ear** (**AURIS MEDIA 7**[41`]). The cavity of the middle ear can be divided into a dorsal atrial part (or mesotympanicum 7[41``]), a ventral fundic part (or hypotympanicum 7[41```]) and a recess (7[41````]). The recess is positioned dorsal to the atrium. (These, as well as the other false and true cavities of the skull, are briefly reviewed again in chapter

70 7[38], 7[39] and 7[40] are non-osseus structures, but the osseus part of the auditory tube (7[37]) cannot be described well without referring to these structures too.

three, section C **: The Skull Cavities**.)

The **atrial part** or **mesotympanicum** (**7**[41``])*[71] occupies the dorsal third of the tympanic bulla. The wall of the bulla around the atrial part is incomplete dorso-medially at the petrotympanic fissure (7[31]). Rostrally, part of this fissure is the caudal opening of the musculotubular canal (7[40] , vide supra) as discussed above. The petrotympanic fissure is bordered medially - but only partially closed off - by the tympanic surface (7[83], vide infra) of the body of the petrous part of the temporal bone. Seen from internally, the wall of the tympanic bulla is concave, and being of even thickness, its inner surface mirrors or reflect much of the shape of the external surface. So, the inner surface of the tubular styloid sheath (7[35]) is etched as a cylindrical shape in the caudo-lateral wall of the bulla. Dorsally, also seen from the inside, the rostro-lateral wall bears the tympanic annulus (7[28] , vide supra) which projects medially into the mesotympanic part. The annulus is supported by septa from the lateral wall of the bulla. The proximal ends of other septa from the fundic part (vide infra under 7[41``` a]) also project dorsally into the atrial part. As seen from the atrium, the septa diverge away from the centrally positioned annulus, in a radiating fashion. These septa only partially subdivide the mesotympanic region, but divide the fundic part almost completely (vide infra). Apart from the tympanic annulus, there is another **opening on the inner rostro-lateral wall of the bulla** (**7**[41`` a] ). This opening is inconstant. It lies between the tympanic annulus (7[28] ) and the base of the tubular styloid sheath (7[35] ) and is approximately 4 mm in diameter. (Vide supra under 7[25`] .) This opening leads to a **cavity** (**7**[41`` b]) that may have **secondary resonant functions**. This cavity is situated within the semi-tubular part of the tympanic part of the temporal bone*[72] . (See figure 3.29.)

The **fundic part** or **hypotympanicum** (**7**[41```])*[73] occupies the more voluminous

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71 The *N.A.V.* does not list the term mesotympanicum (7[41``]). (See also **footnote 73** and 7[41```].)

72 The *N.A.V.* does not list a term for this opening (7[41`` a] ), nor for the cavity it leads to (7[41`` b]). Whether a cavity forms, or whether a cavity does not form, appears to be independent of age or gender. (See also **footnotes 63 & 68**.)

73 The *N.A.V.* does not list the term hypotympanicum (7[41```]). (See also **footnote 71** and 7[41``].)

ventral two thirds of the bulla. It is almost completely subdivided by radiating **septa** (*Septum bullae* **7**[41``` a])*[74] . The septa are of varying length (and sometimes even of direction), subdividing the fundus into sub-compartments or **tympanic cells** (*Cellulae tympanicae* **7**[41``` b])*[75] . Proximally, these cells communicate freely with each other at their mesotympanic ends, but distally (in the ventral part of the tympanic cavity) the compartments are more isolated. In young animals, the proximal ends of the septa end in a multitude of spicules. Boney spicules, un-associated with septa, however also project individually or in small groups from the peripheral inner wall of the bulla, or even from the walls of the septa. Spicules always project proximally, towards the mesotympanicum, in the direction of the annulus. The spicules can be either minutely thin or robust, usually ending in dilated knobs. In young animals the spicules are more delicate while in old bulls they may be either stubby or totally absent. In old animals in general, there are fewer spicules and the proximal ends of the septa are smoother.

The **epitympanic recess** (*Recessus epitympanicus* **7**[41````]) occupies a space dorsal to the tympanic annulus and dorsal to the atrium (mesotympanicum). It is much smaller than the other two parts of the tympanic cavity. Its borders cannot easily be described as it lies in an uneven recess that includes fossae on the temporal surface of the petrous part of the temporal bone. The recess and its fossae harbour the auditory ossicles (see subheading 8), the two openings of the first and second limbs of the facial canal (7[59]) as well as a fossa for the origin of the stapedius muscle *[76] . Further detail of those structures related to or facing the recess, are considered under 7[83] . (Vide infra under the petrous part of the temporal bone, and see footnote 84.) The dorsal limit of the recess forms the absolute roof of the tympanic cavity.

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74 The septa of the hypotympanicum (Septum bullae 7[41 ``` a]) should be differentiated from what might be septae in the petrous part of the temporal bone, where the petrous part joins the mastoid process. (See 7[42] to 7[47] , and **footnote 81**.)

75 The tympanic cellulae of the hypotympanicum is actually a splanchnological term, but it also needs to be used here in this osteological connotation even though it is not listed for such use in the *N.A.V.* (See **footnote 74** and also see 7[42] to 7[47] .) Distinction should be made between these sub-compartments of the tympanic cavity - the tympanic cellulae (7[41``` b]) - and the cells of the mastoid process. (See **footnote 81** and 7[46``] .)

76 See literature on Myology for detail of this muscle.

The petrous part of the temporal bone **:**

The **petrous part** (*Pars petrosa* 7[42]) of the temporal bone consists of a pyramidally shaped **body** (7[42`])*[77] with two processes, namely the mastoid and the styloid processes (7[43/45]). The body of the petrous part protrudes medially into the caudal part of the cranial cavity. **Central** (7[42``]) **and peripheral parts** (7[42```]) **of the body** can be distinguished especially after the internal structure of the bone is exposed either by sculpturing or by breaking parts away. The body presents four surfaces (vide infra under 7[48/49/51 & 83]) of which two contribute to the internal surface of the cranial cavity. The mastoid process (7[43]) of the petrous part of the temporal bone is larger than the body itself and is directed caudo-laterally. The styloid process (7[45]) of the petrous part of the temporal bone is a much smaller process and is directed ventrally. Both processes present a single external surface only.

The exposed external surface of the caudo-laterally directed **mastoid process** (*Processus mastoideus* 7[43]) is triangular *[78] in shape. This triangular surface forms the most lateral part of the nuchal surface (1[10`] ) which in old animals it is uneven and rough. The "**true**" **base** (7[43`]) of the triangular external surface of the mastoid process lies ventrally and the **apex** (7[43``]) dorsally. ("True" being based on its actual shape in surface view and three-dimensionally.) The lateral border of the whole process - and that of the caudal triangular surface - is fused to the squamous part of the temporal bone at the squamosomastoid suture (7[15]). The medial border of the whole mastoid process is fused to the paired flat parts of the occipital bone. In a nuchal view, the apex of the triangular external surface of the mastoid process, is fused to the unpaired squamous part of the occipital bone. Both fusions occur at the occipitomastoid suture. (See 2[18] under the occipital bone.) In some individuals the occipitomastoid suture presents a **mastoid foramen** (*Foramen mastoideum* 7[44]). This foramen leads ventrally into a **groove for the caudal meningeal artery** (*Sulcus a. meningea caudalis* 7[44`]). The groove is usually ill-defined and can be present unilaterally

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77 The *N.A.V.* does not recognize a separate body for the petrous bone, but only mastoid and styloid processes of the petrous part. In the savannah buffalo, three distinct parts have to be recognized.

78 The *N.A.V.* does not distinguish between the process itself and the caudal surface of it, but the latter are always implied. To ignore the difference would be to ignore the three-dimensional shape of all three parts of the mastoid part of the petrous part of the temporal bone.

only. The ventral border of the mastoid process - as well as the external surface which forms the base (7[43`]) - are fused intimately (even in young animals) to the caudal aspect of the semi-tubular part of the tympanic part of the temporal bone at the tympanomastoid suture (7[25``]). In doing so, it closes off the tympanic sulcus (7[26]) in the formation of the external ear canal (7[27]). (Also see footnotes 64 & 65.)

The ventrally directed **styloid process** (*Processus styloideus* **7**[45]) of the petrous part of the temporal bone is short and rodlike. It is situated midway between the body of the petrous bone and the caudal nuchal surface of the mastoid process. Apart from its distal end, the styloid process is surrounded by the styloid vagina (7[35]) of the tympanic bulla, except caudo-laterally at the point of invagination. The styloid process appears to be totally fused at the **petrotympanic suture** (Sutura petrotympanica **7**[45`] ) to the styloid sheath of the bulla *[79] . A lateral part of the petrotympanic suture (7[45`]) can sometimes be identified in the depths of the epitympanic recess when sections of bone have been cut away. (See figure 3.29.) Only the distal surface of the styloid process can be seen and it articulates by means of a symphysis to the proximal end of the fibro-cartilaginous tympanohyoid. (See 22[9 & 10] under the hyoid bone.)

The body of the petrous part (7[42`]) has a pyramidal shape and projects medially, as a whole, into the cranial cavity. Although it appears to "articulate" along a short distance to the parietal bone at the petroparietal suture (9[10] and see footnote 99), only the dorsal third of the petrous body is properly attached to the rest of the skull. That attachment is via its peripheral part (7[42```] , vide supra) and from there by means of the mastoid process, to the surrounding skull bones. Two thirds of the body is therefore mostly free, and thus the body of the petrous temporal bone can conveniently be subdivided into attached dorsal and free ventral sections. Based on macroscopic appearances of the bone substance which makes up the body of the petrous temporal bone itself, central (7[42``]) and peripheral (7[42```]) parts are distinguished (vide supra). The central part (7[42``]) is composed of a very dense

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[79] The petrotympanic suture (Sutura petrotympanica 7[45`]) is not listed in the *N.A.V.* It definitely does not form part of the petrotympanic fissure (7[31]).

homogenous type of bone. The peripheral part incompletely surrounds the central part - like a cortical layer would surround a medullary component - but it does not cover the central region medially nor ventro-laterally. Apart from being less dense, the peripheral part also elicits radiating characteristics. This characteristic feature can be seen best when a split surface is viewed from medially. Splitting the body can be achieved very easily by applying some external force on the body, using mechanical tools to lever it away from the surrounding skull bones. The central part of the body contains the osseus components of the semicircular canals for the vestibular part as well as the spiral cochlea for the auditory part of the vestibulocochlear organ (7$^{46`}$ , vide infra). It therefore holds all the osseus canals and ducts that harbour the inner ear (**AURIS INTERNA** **7** $^{46}$ ), including the **vestibulocochlear organ** (*Organum vestibulocochleare* **7**$^{46`}$)* [80] itself. (See also footnote 66.) Ventrally, one side of the free section of the petrous body forms part of the medial wall of the mesotympanicum (7$^{41``}$), as well as the medial and dorsal walls of the epitympanic recess (7$^{41````}$). (Vide infra under 7^{83} .)

Note : In the region where attachment between the peripheral petrous body and the mastoid process takes place, a different type of bone is found apart from what have already been described in the above. In medial view, it is that part of the pyramidally shaped petrous body that should logically be the apical part. (However, see 7^{47} below.) In young animals, it still consists of a type of trabecular spongy bone (Spongiosa trabeculosa 1$^{5`\mathbf{a}}$) that contains red bone marrow (Medulla ossium rubra 1$^{5``}$). In older but immature animals, it appears as if it might have contained yellow fat (1$^{5```}$) in un-prepared skulls. But in older animals, and especially in some old bulls, this region of the petrous bone contains large spaces that apparently were not filled by yellow fat (1$^{5```}$) at all. Prepared skulls of such individuals show that it resembles pneumatized bone with boney septa. Spreading further into both the dorsal part of the petrous body and the adjacent mastoid process, these divided spaces can then be

80 The functional vestibulocochlear organ (7$^{46`}$) consists of both osseus and non-osseus components. (See Splanchnology elsewhere.) Special anatomical techniques are required to study the detail of the osseus labyrinth (see 7^{82}) of the inner ear. It falls beyond the scope of this work to study that microscopic detail. However, on macroscopic evaluation and stereo-microscopical photography - after splitting the petrous body by mechanical force - the whole organ appears to be in par with the normal anatomical detail of mammals. (Also see **footnote 83**.)

interpreted as **mastoid cells** (7[46``])* [81] .

Being pyramidal in shape and only attached dorsally via its peripheral part - as well as having a free ventral section, which is much wider than the attached dorsal part - the body of the petrous temporal bone presents occipital, rostral, medial and ventral (or tympanic) surfaces. The medial and the rostral surfaces form part of the lateral wall of the cranial cavity. The medial surface is the larger of the two and faces the cerebellar part of the cranial cavity whereas the rostral surface faces the cerebral part of the cranial cavity. The rostral, occipital and medial surfaces are triangular in shape with the bases of each surface situated ventrally and the apices dorsally. However, it is not the dorsal but the rostro-ventral angle of all these surfaces that - by convention - forms the **apex of the petrous bone** (*Apex partis petrosae* 7[47])* [82] .

The **occipital surface** (*Facies occipitalis* 7[48]) is flat and it faces caudally to form the base of the pyramidally shaped petrous body (as per convention). Although the occipital surface is free, and is exposed in a prepared skull, it does not face the cranial cavity as meninges fills the space between this surface and the occipital bone. Ventrally, it is separated further from the occipital bone than dorsally, and that separation is part of the petro-occipital fissure (2[8]).

The **rostral surface** (*Facies rostralis partis petrosae* 7[49]) meets the medial surface (vide infra) at right angles to form the **petrosal crest** (*Crista partis petrosae* 7[50]). The crest forms the most prominent osseus border between the cerebral and the cerebellar

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81 The cells in the petrous body and mastoid process, appear to rather take origin from the mastoid process and can therefore be considered as **mastoid cells** (7[46``]) rather than petrous cells. These cells must not be confused with the *N.A.V.* term Cellulae tympanicae (7[41``` a]) which refers to the multiple sub-compartments of the tympanic cavity (listed under the Splanchnology section). (See also **footnotes 74 & 75**. Pending histological evidence, the cells may or may not have connections with other cavities in the skull. Also, see **footnote 68** regarding the possibility of the formation of spaces in other parts of the temporal bone by means of apoptosis or pneumatization. If histological evidence proofs them to be just fat containing spaces, they will in fact then only be part of another variation of spongy bone.)

82 It is confusing to adhere to the historical terminology that regards this part of the petrous temporal bone as the apex (7[47]). Even so, although the body of the petrous bone is pyramidal in shape and on gross morphology presents the apex directed dorsally, the conventional approach will be followed in this text by keeping the rostro-ventral angle of the petrous part as the apex of the petrous bone. Note that this must not be confused with the apical part of the mastoid process (7[43`]) as seen in caudal view of the nuchal surface.

parts of the cranial cavity. The crest is in line with the low ridges (2[27`]) arising from the internal occipital protuberance of the occipital bone. The rostro-lateral margin of the rostral surface "articulates" with the internal surface of the parietal bone at the petroparietal suture (Sutura petroparietalis 9[10]). (See footnote 99 under the parietal bone.)

The **medial surface** *(Facies medialis partis petrosae* **7**[51]) meets the ventral or tympanic surface (vide infra) at an acute angle to form the **ventral margin** (*Margo ventralis partis petrosae* **7**[52]) of the body of the petrous part of the temporal bone. The margin curves ventro-medially, presenting as a sharp ridge. The ventral margin and the petrosal crest meet rostrally, at the apex of the petrous bone. The tip of the apex is usually invaginated and rough, bearing two foramina **:** The one foramen leads via a canal to join the proximal limb of the facial canal **;** the other foramen leads to a canal that opens at the ventral foramen of the rostral compartment of the fundus (vide infra under 7[59```]). In some individuals, the petrous apex (7[47]) is not invaginated but ends in a sharp point. The medial surface the petrous part of the temporal bone presents a dorsal **cerebellar fossa** (*Fossa cerebellaris* **7**[53]) and a large ventral opening. The latter are the **internal acoustic meatus** (*Meatus acusticus internus* **7**[54]). The entrance to the meatus is the **internal acoustic pore** (*Porus acusticus internus* **7**[55]). The pore leads into a short **fundus** (*Fundus meatus acustici interni* **7**[56]). A **"Y-shaped" ridge** (*Crista transversa* **7**[57]) divides the dorsal part of the fundus into rostral, middle and caudal compartments (7[58], 7[60] and 7[62]) **:**

The **rostral compartment of the fundus** (**7**[58]) contains two foramina, one dorsally (or dorso-caudally) and one ventrally (or ventro-rostrally) **:** The **dorsal foramen** (*Area n. facialis* [*intermediofacialis*] **7**[58`]) leads into the **facial canal** (*Canalis facialis* **7**[59]). The canal curves laterally and caudally to form the **first curve** (*Geniculum canalis facialis* **7**[59`]) **of the proximal limb** (**7**[59``]) **of the "S-shaped" facial canal** before it opens caudo-dorsal to the epitympanic recess (7[41````]) in the roof of the tympanic cavity. (See 7[33 to 34] and 2[8], and vide infra for distal limb 7[83````].) The **ventral foramen** (**7**[59```]) of the rostral compartment leads to the canal that opens at the petrous apex (vide supra).

The **middle compartment of the fundus** (*Area vestibularis superior* **7**[60]) leads via a short canal towards the central vestibular cavity (7[77], vide infra). The central vestibular cavity contains various openings, of which three leads to the **osseus semicircular canals** (*Canalis semicircularis ossei* **7**[61]). The **semicircular canals** (*Canalis semicircularis anterior / posterior / lateralis* **7**[61\` / 61\`\` / 61\`\`\`]) lie in X, Y and Z planes, arranged at approximately 90 degrees to each other. The canals lie approximately in horizontal, transverse and sagittal planes with the horizontal plane fairly parallel to the basal axis* (**axis I**) of the bones of the cranium. The semicircular canals contain the splanchnological parts of the vestibular organ. (See Splanchnology elsewhere.) The canals lie in an area of approximately 10 x 10 x 10 mm in the central dense part of the petrous body. The diameters of the horizontal semicircular canal is smaller in diameter than those of the others* [83] .

The **caudal compartment of the internal acoustic fundus** (**7**[62]) contains two foramina, one dorsally and one ventrally. The **dorsal foramen** (*Area vestibularis inferior* **7**[62\`]) leads via a short canal towards the central vestibular cavity (Vestibulum 7[77], vide infra). The **ventral "singular" foramen** (*Foramen singulare* **7**[63]) leads to the osseus **cochlea** (*Cochlea* **7**[64]).

The osseus cochlea is a conical spiral with a **proximal base** (*Basis modioli* **7**[64\`] ) - which lies near the singular foramen (7[63] ) - and a distal apex (**7**[64\`\`]). The osseus cochlea and the cavity associated with it, are positioned in the central petrous part of the temporal bone. The cavity is in the shape of a **spiral canal** (*Canalis spiralis cochlea* **7**[65]) around a **tapering cone** (*Modiolus* **7**[66]) of bone. The cone extends from the base to the apex where it is attached to the surrounding

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83 It appears as if the spatial orientation of the semicircular canals relative to the basal axis* (**axis I**) of the skull remains the same from juveniles to aged animals. However, no special study was undertaken to elucidate the details of these canals. In the dog, the "anterior", "lateral" and "posterior" semicircular circles have diameters of 6.0, 4.5 and 3.5 mm respectively, and the canals of the circles have a diameter of approximately 0.5 mm. These osseus canals of the vestibulocochlear organ of the savannah buffalo therefore appear to be proportionally bigger and more voluminous, but in par with what is known for the dog. Tail hair of a horse can be threaded through these canals with a fair amount of ease, giving an idea of the diameter of these canals. (See **footnote 80**. Also see **footnote 186** under section D **: Craniometric data**.)

bone. Axially, the **modiolus** itself, also accommodates a cavity in the form or a **longitudinal canal** (*Canalis longitudinales modioli* **7** [67]). The longitudinal canal harbours the cochlear nerve that, via the singular foramen (7 [63]), links with the respective part of the brain in the "cranial cavity". (See section C **: Skull Cavities**.) The modiolus, apart from its basal and apical attachments, also appear to be "attached" to the outer wall of the spiral cochlear canal by the **lamina of the modiolus** (*Lamina modioli* **7** [68]). The lamina - which actually consist of two separate laminae (vide infra) - spirals three times around the modiolus. Medially, part of the osseus outer wall of the spiral canal is formed by the promontorium (7 [84], vide infra). The diameter of the **cochlea** is approximately 8 mm at the **base** (*Basis cochlea* **7** [69]) and approximately 2 - 3 mm at the **distal apex** (*Cupula cochlea* **7** [70]). The axis of the cochlea is approximately 7 mm long and it is directed rostro-laterally and slightly dorsally. The spiral of the right cochlea spirals clockwise as seen from the median plane and that of the left cochlea spirals anticlockwise as seen from the median plane. The spiralling cochlear canal (7 [65]) as formed by the lamina of the modiolus is actually subdivided into a central **osseus spiral lamina** (*Lamina spiralis ossea* **7** [71]) and a peripheral **secondary spiral lamina** (*Lamina spiralis secundaria* **7** [72]). The central border of the former is attached to the modiolus. The peripheral border of the osseus spiral lamina is free and approximates the secondary spiral lamina. The secondary spiral lamina is attached to the outer wall of the spiral cochlea. (The outer wall of the spiral cochlea is simultaneously also the inner wall of the promontorium). The osseus spiral lamina (and its secondary part) winds around the modiolus for three and a quarter turns, dividing the spiral cochlear canal incompletely into a proximal and a distal half. (Membranous components functionally separate the two halves completely and functionally in the living animal. (See Splanchnology elsewhere.) The distal half forms the **vestibular scala** (*Scala vestibuli* **7** [73]) **;** the proximal half forms the **tympanic scala** *(Scala tympani* **7** [74]). Together they form the perilymphatic space of the membranous parts of the labyrinth. (See Splanchnology elsewhere.) Apically the peripheral border of the **osseus spiral lamina** ends in a **hook** (*Hamulus laminae spiralis* **7**[75]) axial to which a **foramen** (*Helicotrema* **7**[76]) is formed. At the base of the modiolus (7[64`]), the proximal end of the osseus spiral lamina forms the caudal wall of the vestibulum (7[77], vide infra), caudo-ventral to the position of the vestibular window (7[85], vide infra), thus accounting for the extra quarter turn of the osseus spiral lamina. The vestibular scala is continuous proximally with the central vestibular cavity and therefore with the vestibular window (7[85], vide infra). At the base, the tympanic scala is continuous with the cochlear window (7[86], vide infra). Apically, the helicotrema allows free communication between the scalae, osteologically as well as functionally in the living animal.

The cavities of the osseus semicircular canals and of the spiralling cochlear canal are connected to a separate central **vestibular cavity** (*Vestibulum* **7**[77]). The vestibulum measures approximately 5 x 5 x 5 mm. Dorsally, the vestibulum is connected via a **minute canal** (*Aqueductus vestibuli* **7**[78]) to a **small opening** (*Apertura externa aqueductus vestibuli* **7**[79]) on the medial surface of the petrous pyramid. The aperture lies dorsally, on the border between the central and the peripheral parts, dorso-caudal to the cerebellar fossa (7[53]). In old bulls the distal part of the canal and the aperture can be quite large, although the diameter of the proximal part of the canal is always minute. At the base of the tympanic scala, close to the cochlear window, **another minute canal** (*Canaliculus cochlea* **7**[80]) connects the spiral cochlear canal to a **very small opening** (*Apertura externa canaliculi cochlea* **7**[81]) on the medial surface of the petrous pyramid. The aperture lies caudally, on the border between the central and the peripheral parts, caudal to the internal acoustic meatus. Together, the osseus parts of the vestibulum, semicircular canals, cochlea and the internal acoustic meatus form the **osseus labyrinth** (*Labyrinthus osseus* **7**[82]).

The **ventral** or **tympanic surface** (*Facies ventralis partis petrosae* **7**[83]) is also formed by contributions of both the central and the peripheral part types (7[42``] & 7[42```]) of the petrous part of the temporal bone. This surface faces latero-ventrally and it forms the dorso-medial wall of the meso- and epitympanic parts of the tympanic cavity. Ventrally, the free part is curved that gives this surface a semilunar outline. The curved free part coincides with the ventral margin of the body of the petrous part of the temporal bone (Margo ventralis partis petrosae 7[52], vide supra). The margin and the plane of the tympanic surface, are directed ventro-medially. The tympanic surface (7[83]) is marked by a prominence, three foramina, a groove and three fossae **:**

The larger rostral **fossa** (**7**[83`]) accommodates both the head of the malleus and the body of the incus (see 8[6] and 8[8])* [84] .

Caudo-dorsal to the epitympanic recess, in the roof of the mesotympanic part of the tympanic cavity, opens a **foramen** (**7**[83``])* [85] that leads to the proximal limb of the facial canal (7[59]). The facial canal continues in a caudo-lateral direction on the 'tympanic surface' (7[83]) as a **groove** (**7**[83```])* [86] . The ventral border of the groove lies approximately on the border between the recess and the mesotympanicum. The groove ends at the **initial part of the distal limb** (**7**[83````]) **of the "S-shaped" facial canal**. (Vide supra under 7[59], 7[59`] and 7[59``] for the other parts, but also see 7[33 - 34] and 2[8].) The groove and the "initial part" lead to the **terminal part of the distal limb of the facial canal**, between the caudal wall of the tympanic bulla, the mastoid process and the occipital bone, as the lateral part of the petro-occipital fissure. (See footnote 69.) This **terminal part of the distal limb ends at - and opens as -** the stylomastoid foramen (see 7[34]). In some old bulls the groove of the facial canal (7[83```]) can re-enter the caudal part of the petrous bone before it opens and continues in the petro-occipital fissure (2[8]).

A small fossa, the **"incusidal" fossa** (**7**[83`````])* [87] , lies in the dorso-caudal part of the epitympanic recess, near the ventral ridge of the groove (7[83```]). This fossa accommodates the short crus (8[9]) of the incus. (See also Auditory Ossicles,

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[84] The *N.A.V.* does not list a term for this larger fossa (7[83`]). Its dorso-medial wall forms the roof of the epitympanic recess.

[85] The *N.A.V.* does not list a term for this foramen (7[83``]).

[86] The *N.A.V.* does not list a term for this groove (7[83```]).

[87] The *N.A.V.* does not list a term for the fossa (7[83`````]) which accommodates the short crus of the stapes.

subheading 8.)

The convex prominence on the tympanic surface of the petrous part of the temporal bone is the **promontorium** (*Promontorium* **7**[84]). The eminence of the promontorium (measured rostro-caudally and dorso-ventrally) extends over a region of approximately 10 mm x 10 mm. The inner wall of the promontorium renders attachment to the secondary spiral lamina (7[72]) of the cochlea (7[64] , vide supra). The base of the cochlea is etched as the dorsal most eminent part of the promontorium. The apex of the cochlea is directed towards the ventral margin (Margo ventralis partis petrosae 7[52]), but it is not as clearly etched as the base. The rostral border of the promontorium borders the epitympanic recess.

The **vestibular window** (*Fenestra vestibuli* **7**[85]) lies in a depression between the dorsal most convex part of the promontorium and the epitympanic recess, facing medially. It is oval in shape and it fits the baseplate of the stapes (8[17]).

The **cochlear window** (*Fenestra cochlea* **7**[86]) is positioned caudal to the most convex part of the promontorium. The cochlear window is roundish and it faces caudally. The diameter is larger than that of the vestibular window. Both windows lie ventral to the facial canal. The vestibular and cochlear windows connect the middle ear (AURIS MEDIA 7[41`]) to the osseus cavities of the inner ear (AURIS INTERNA 7[46]).

Dorsal to the most convex part of the promontorium and dorsal to the facial canal, is the third and last fossa of the ventral or tympanic surface of the petrous part of the temporal bone. It is an ill-defined small **fossa for the stapedius muscle** (Fossa m. stapedius **7**[87])* **[88]** .

The **temporal meatus** (*Meatus temporalis* **7**[88]) is a voluminous canal ***** **[89]** that connects the

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88 The *N.A.V.* does not list the term "Fossa m. stapedius" (7[87]). It would be convenient to have this term listed.

89 The temporal meatus (Meatus temporalis 7[88]) per se, and osteologically speaking, should be regarded as a voluminous fissure between the internal surfaces of the temporal, occipital and parietal bones of that part of the cranium. The venous sinuses that it contains in the living animal will not be discussed here, but there are various diploïc canals that connect the temporal meatus to the temporal fossa and these have been described. (See 7[9``] & 7[9```] and **footnote 58**.) The temporal meatus and its diploïc canals, are homologous to the condylar canal (2[11]) and its diploïc canals. (See also **footnote 24**.) Other examples are the supraorbital canal (10[22]) and the diploïc canals (2[7``]) of the body of the occipital bone. The nutrient canal of the zygomatic bone (20[8```]), does not have such a side branch that opens on another bone.

cranial cavity with the external surface of the skull. It has a single internal opening - referred to in this description as the **"dorsal or internal" opening** (**7**[88`]) - and a paired external opening, the "ventral" opening (vide infra or see 7[24]). (Note the similarity between this internal opening and the internal opening of a large branch of the condylar canal as described under footnote 24.). The temporal meatus is approximately 55 mm long with a central dilated part. It is situated between the squamous, the petrous and the tympanic parts of the temporal bone (i.e. the ventral parts of these three bones) and between the parietal bone and the squamous part of the occipital bone (the dorsal parts of both). In young animals the internal opening lies rostro-lateral to the (dorsal) internal opening of the condylar canal (2[19`], see also occipital bone and footnote 24) but in old animals it forms the lateral part of it in a combined opening. The combined opening may be as large as 10 - 15 mm in diameter. The internal opening lies in the caudo-dorsal part of the caudal compartment of the cranial cavity (Fossa cranii caudalis 2[2`] ), dorso-lateral to the body of the petrous part of the temporal bone. The "ventral" or external opening of the temporal meatus (**not** the large side branch of the condylar canal - see 2[19`]) opens as two groups of openings, the duplicated retro-articular foramen (7[24]) on either side of the retro-articular process (7[22]). The temporal meatus is also connected via various lesser foramina to two areas on the temporal fossa. (See 7[9```] and footnote 58.)

8. THE AUDITORY OSSICLES (*OSSICULA AUDITUS*)

(See figure **3.30**. Also see 3.28 & 3.29.)

The auditory ossicles form an osseus chain of three (or possibly four) small bones (vide infra). From lateral to medial, these bones extend from the tympanic membrane - the periphery of which is attached to the tympanic annulus (7^{28}), to the vestibular window (7^{85}) of the petrous part of the temporal bone. (See also temporal bone.) From without inwards, the hammer (Malleus 8^{1}) articulates with the anvil (Incus 8^{7}) which in turn articulates with - what could be a lenticular bone (Os lenticulare 8^{11}), - and then with the stirrup (Stapes 8^{13}).

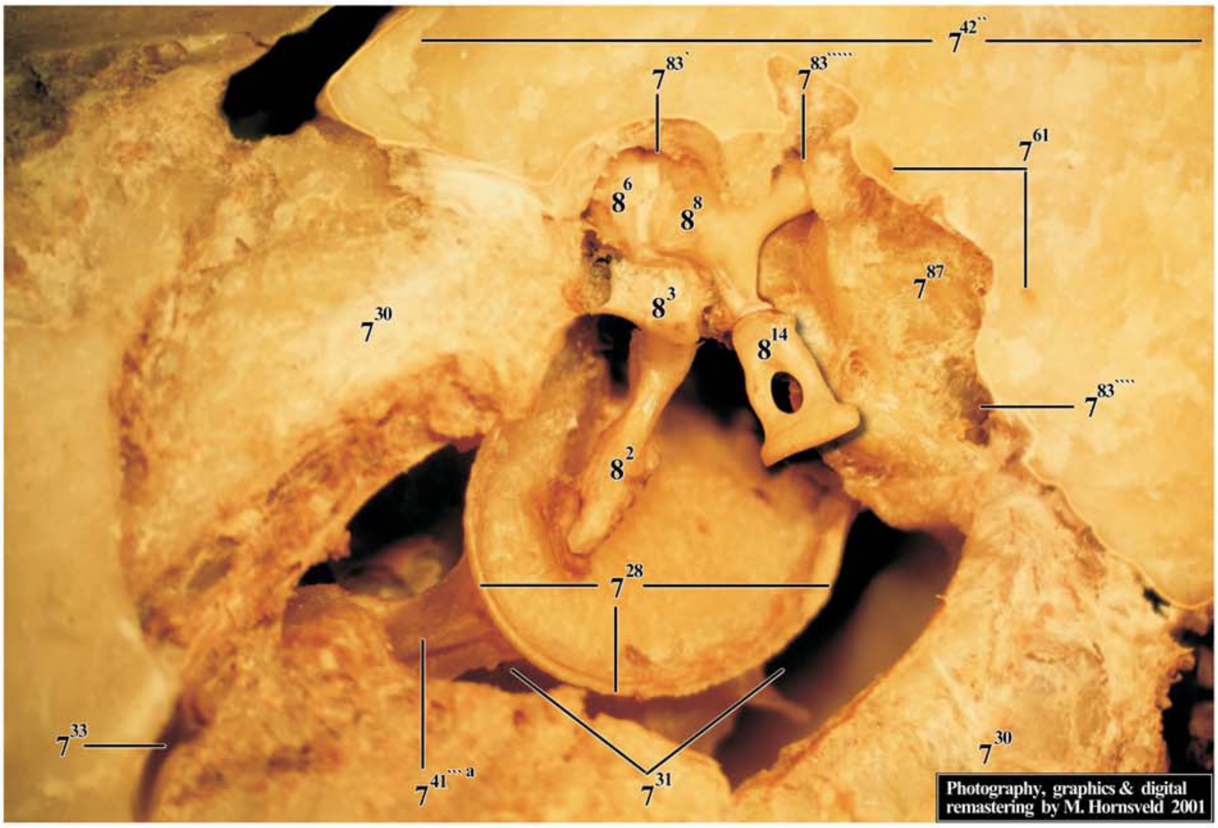
The **hammer**, or **malleus** (*Malleus* **8**^{1}), is a slender and curved bone with a total length of approximately 11 mm. The proximal part of the hammer is the **handle** (*Manubrium mallei* **8**^{2}) which (in situ) is directed rostro-ventrally. The handle is triangular in cross-section and contains a cavity. Due to preparation of the skulls, it is uncertain whether this cavity is filled with yellow bone marrow ($1^{5```}$) in the living animal or not. The handle attributes most to the length of the malleus. The **neck of the hammer** (*Collum mallei* **8**^{3}) is slender and it bears a **lateral** and a **rostral** process, as well as a **median muscular process** *(Processus lateralis / rostralis / muscularis* **8**$^{4/4`/5}$). The muscular process lies ventral to a concave part of the hammer. The curve of that line is also extended caudo-dorsally onto the body of the incus. The **head of the malleus** (*Caput mallei* **8**^{6}) bears an articular facet on its lateral surface. In situ, the neck and the head of the malleus are directed dorso-caudally.

The **anvil**, or **incus** (*Incus* **8**^{7}), does not resemble an anvil. In the savannah buffalo, the incus rather resembles a brachydont type of tooth that has two roots. In total it is approximately 5 mm long. In situ, it has a rostrally situated **body** (*Corpus incudis* **8**^{8}) and two caudally directed and diverging crura, of unequal length. The body and the distal ends of both crura, bear articulatory facets. The **short crus** (*Crus breve* **8**^{9}) is directed caudo-dorsally and it articulates with the small “incusidal” fossa (see $7^{83`````}$) in the epitympanic recess of the

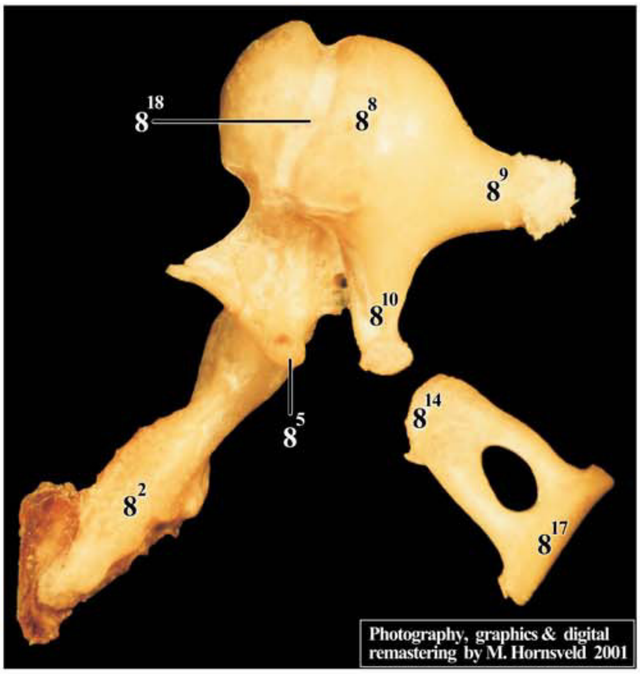
FIGURE 3.30 : OSTEOLOGY

THE AUDITORY OSSICLES IN SITU AND IN DETAILED VIEWS

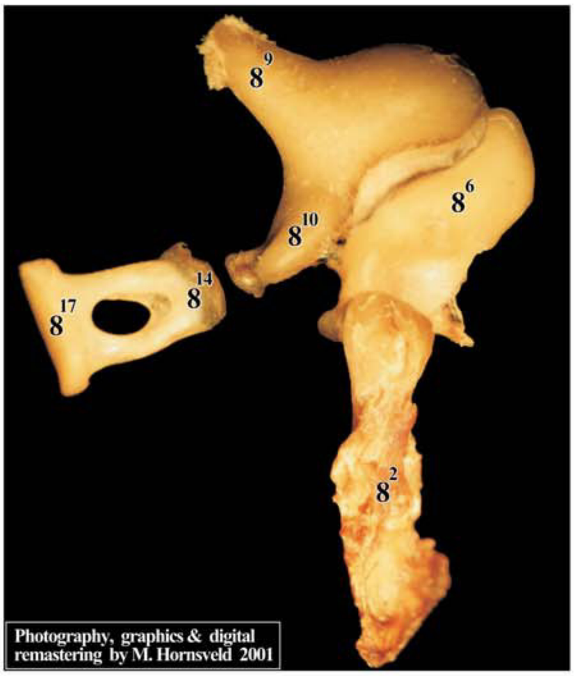
THE AUDITORY OSSICLES IN SITU : MEDIAL VIEW OF THE RIGHT EPITYMPANIC RECESS



THE AUDITORY OSSICLES : MEDIAL VIEW



THE AUDITORY OSSICLES : LATERAL VIEW



petrous temporal bone. The **long crus** (*Crus longum* **8** [10]) is divided into a proximal and a distal part. The proximal part is directed ventrally and its lateral surface is convex. The medial surface is deeply convex. Deducted from a sectional profile of this part of the crus, the mechanical strength is not weakened by being extremely concave as one would like to think, but rather enhanced (vide infra under stapes too). The distal part is delicate and it is directed medially. Topographically, the general longitudinal axis of both parts of the long crus, lies approximately parallel to the muscular process of the malleus. Distally, it appears to be fused to what could be a **lenticular bone** (*Os lenticulare* **8** [11]). If so, it then forms the **lenticular process** (*Processus lenticularis* **8** [12]) of the incus. However, because a separate lenticular bone is not clear - though it could be part of the articulatory facet only - the distal part of the long crus of the incus articulates with the head of the stapes (vide infra).

The **stapes** (*Stapes* **8** [13]) is shaped like an equestrian stirrup. Excluding the possibility of a lenticular bone, it is the most delicate auditory ossicle. The **head** (*Caput stapedis* **8** [14]) is positioned laterally (topographically), and it is connected by **rostral** and **caudal crura** (*Crus rostrale / caudale* **8** [15 / 16]) to an oval **baseplate** (*Basis stapedis* **8** [17]) that is flat. Topographically, the baseplate is situated more medially than the head, nearly in a transverse plane. The head has a proximal articular facet and a medial muscular process. The latter process can be fairly prominent. The crura are laterally flattened and curved, and they encircle a large central foramen. The inner surface of each crus - in a cross-sectional profile - is concave. The curved concave structure or the crura, together with the thin baseplate, makes the stapes very delicate, yet mechanically strong. That structure is similar to what is seen in the long crus of the incus (vide supra). Distal to the larger central foramen, the crura attach to the proximal surface of the baseplate, some distance away from the edge. The line of attachment is concentric to the ovoid periphery. The distal surface of the baseplate is flat to concave. The baseplate is not perfectly oval (in surface view) and in some individuals it can even be semilunar in shape. It fits perfectly into the vestibular (or oval) window (7 [85]). The total length of the stapes - from head to baseplate - is approximately 4 mm. The maximum diameter of the ovoid baseplate is less than 3 mm.

The **articulations** between the **malleus and the incus** (*Articulatio incudomallearis* **8**[18]) and between the **incus and the stapes** (*Articulatio incudostapedia* **8**[19]) are true **articulatory joints of the auditory ossicles** (*Articulationes ossiculorum auditus* **8**[20]). In most older animals, it appears as if the joint between the malleus and incus have lost much of their synovial character. In one case studied, the stapes was 'fused' to the vestibular window (7[85]) to form what could be a **tympanostapedial syndesmosis** (*Syndesmosis tympanostapedia* **8**[21])* [90] .

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90 No histology was done to differentiate a tympanostapedial syndesmosis from a synostosis. No histology was also done to confirm whether the attached malleus and incus bones are artefacts of preparation, or whether they were syndesmoses or synostoses.

9. THE PARIETAL BONE

(*OS PARIETALE*)

(See figure **3.31**. Also see 3.1, 3.3 - 3.5, 3.8, 3.16, 3.17, 3.26, 3.27 & 3.35.)

The parietal bone forms the lesser caudal part of the roof and the lateral walls of the cranium externally, as well as an even larger part internally. The external parts present as two laterally situated temporal parts, but the nuchal part is single. The paired temporal parts lie in near sagittal planes whereas the nuchal part lies in a near transverse plane. The nuchal part most probable was also formed originally by fusion of paired parts, sometime during very early development that even preceded the formation and fusion of the temporal parts (vide infra). In the median plane therefore, evidence of the original antimeres of the once paired parietal bones that fused so completely to each other, remains only internally, as the **sagittal suture** (*Sutura sagittalis* **9** ^{1})* [91] . Although difficult to see, other circumstantial evidence concerning the antimeric nature of the parietal bone and the sagittal suture also remains. That can be seen for instance in the remnants of the double layered nature of the septum that divides the parietal part of the frontal sinus (see 9 $^{10`}$ and 9 ^{11}). It can also be deducted from the clear rostral continuation of the sagittal suture in the frontal bone region * [92]. Advanced ossification of the parietal part of the sagittal suture must have occurred either prenatally or early postnatally, as no other signs of that suture can even be seen in the skulls of animals as young as three to four months. And, based on other circumstantial evidence, the parietal bones themselves have also fused even earlier in life with the interparietal bones or smaller remnants of it. (See subheading 3 **:** The Interparietal Bone.) Thus, all the parietal and probable interparietal components of the nuchal surface (1 $^{10`}$) dorsal to the nuchal crest, presents

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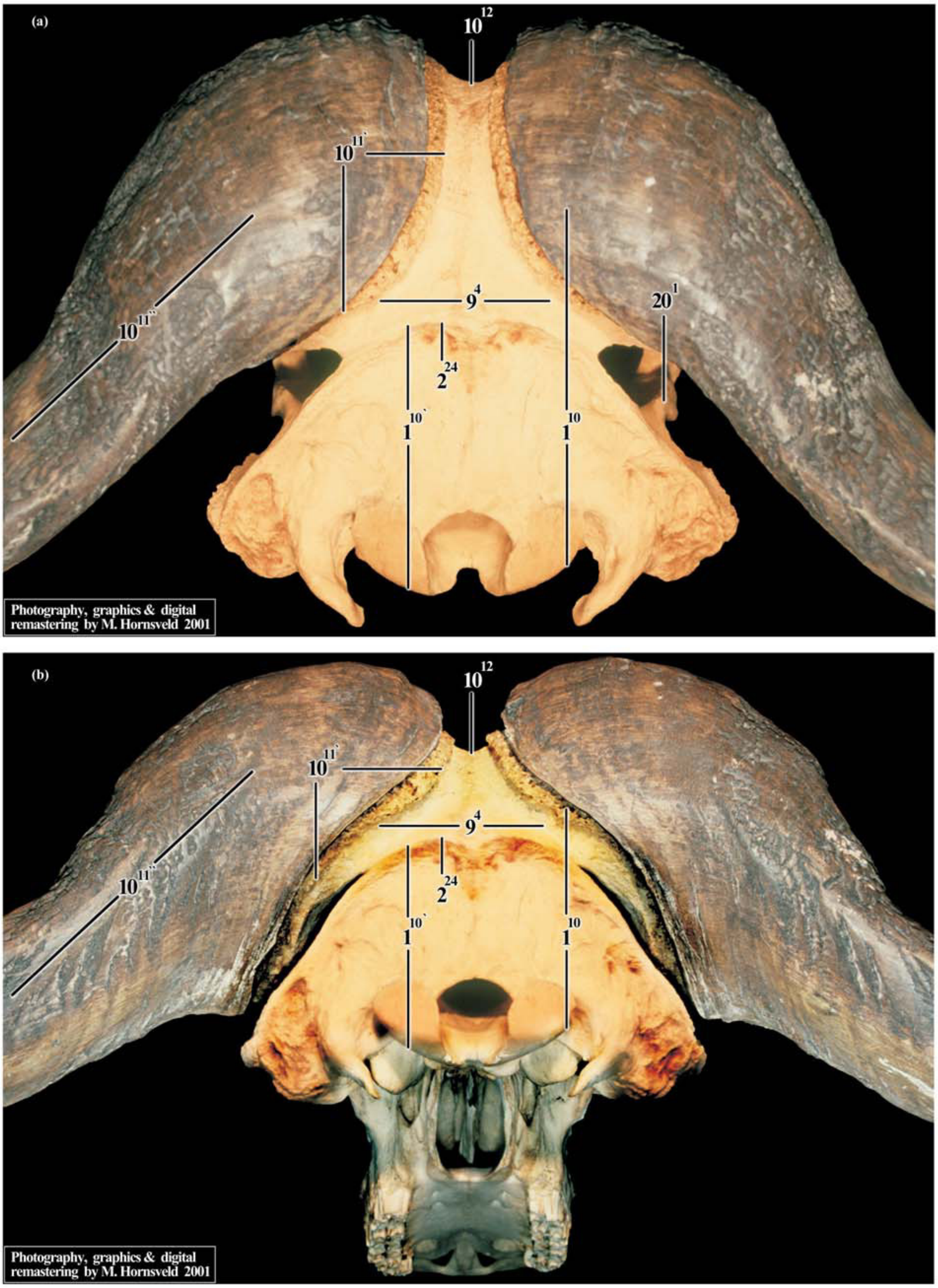
91 The *N.A.V.* states that the sagittal suture (Sutura sagittalis 9 ^{1}) only refers to that part of the suture between the parietal bones (i.e. an interparietal suture). (See also **footnote 92**, 9 ^{11} and the interfrontal suture 10 ^{4} .)

92 Skulls of animals younger than 3 - 4 months have not been studied to investigate the details of the formation of all the bones that contribute to the formation of the sagittal suture in the parietal region / nuchal plane. (See also **footnote 25**.) However, the interfrontal suture (10 ^{4}), which is the rostral continuation of the sagittal suture, is seen in the skulls of young animals. The interfrontal suture ossifies progressively in a rostral direction.

FIGURE 3.31 : OSTEOLOGY

THE *OCCIPUT* OF AN OLD BULL IN (a) CAUDAL AND (b) CAUDO-VENTRAL VIEWS



externally as a single unpaired parietal bone * [93] . Despite these intricate fusions of all the components of the parietal bone, it retains a small part of the frontal sinus complex. (See 9[10`] - 9[11``] .)

Note : As stated under subheadings 4 and 5 for the basisphenoid and presphenoid bones, it will be noticed that if skulls of young animals are compared with skulls of older animals, and considered in lateral and medial views, then the registration of the internal and external surfaces of the wings of the basis- and presphenoid bones become ever more distorted with age. Similarly, the external and the internal surfaces of the parietal bone show the same distortion phenomenon. Even though this occurs to a lesser extent in the case of the parietal bone, this de-registration with age makes an understanding of the appearance of sutures relevant to these surfaces, difficult to comprehend three-dimensionally. Figures 3.16 and 3.17 should be consulted when dealing with this.

The **external surface** (*Facies externa* **9**[2]) of the parietal bone is divided into concave **temporal parts or planes** (*Planum temporale* **9**[3]) laterally (in sagittal planes), and a transverse **nuchal part or plane** (*Planum nuchale* **9**[4]) caudally. The nuchal plane has a variable surface profile depending on age. Caudally, the temporal and nuchal planes of the parietal bone meet in a fairly acute angle at the temporal line. As seen from laterally, the parietal part of the temporal line (7[8]) - as it is continued on the temporal plane of the parietal bone - always has a dorsal curve in all age groups. That is despite great changes in the skull shape due to cornual process enlargement. When the skulls of young animals are considered either from laterally or from caudally, both the temporal and the nuchal planes have convex dorsal borders. These borders form the **frontal margin** (*Margo frontalis* **9**[5]) of the parietal bone. Along the whole length of both parts of the margin, the parietal bone is fused to the antimeric parts of the frontal bone at the **frontoparietal suture** (Sutura

93 In animals younger than approximately 3 - 4 months (and even prenatally), the sagittal suture could thus include both an interparietal as well as an inter-interparietal suture. (See 9[11] and also **footnote 28**.)

frontoparietalis **9**[5`])*[94] . The temporal and nuchal planes of the parietal bone are fused ventrally - along their **squamous** and **occipital margins** (*Margo squamosus* **9**[6] and *Margo occipitalis* **9**[7]) - to the squamous parts of the temporal and occipital bones respectively. The respective sutures involved are the temporoparietal (7[5])*[95] and occipitoparietal sutures (2[23])*[96] .

In lateral view, the temporal part (9[3]) of the parietal bone forms the dorsal lesser half of the temporal fossa (1[9]). It is concave from dorsal to ventral, facing in some measures ventro-laterally in older animals. Dorsally, the frontal margin borders the base of the cornual processes (10[11]) of the frontal bone. Rostrally -as seen in lateral view - the frontal margin might be marked by a large sphenoidal fontanel (1[17``]) which is seen in animals of approximately two years old. (See also frontal and presphenoid bones for the particulars of this fontanel. Also see footnote 42.) In the specific age group of animals where the fontanelle is present, it consists of what appears to be secondarily developed cartilage that is similar to hyaline cartilage. In some individuals it appears as if this fontanelle - as seen externally in the temporal fossa - only involves the frontal bone, and neither the frontoparietal suture (9[5`]) nor the parietal bones are involved at all. One or more foramina - usually as part of a group of up to three or four openings - can be present on the temporal part of the parietal bone. These foramina lie caudo-ventrally on or near the temporoparietal suture. They belong to the caudo-dorsal grouping of foramina (7[9``]), as was described under the squamous part of the temporal bone, that may overlap onto the parietal bone. (See footnote 58.). They connect the temporal fossa, via diploïc canals, to the dorsal part of

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94 The frontoparietal suture (9[5`] ) is not listed in the *N.A.V.* Although the frontoparietal suture could instead be numbered and described under the frontal bone, it demands some comments here under the parietal bone **: Footnote 28** comments among others on the external part of the frontoparietal fontanelle (1[17`]), a structure that cannot be distinguished from the cartilaginous part of the frontoparietal suture in animals as young as 3 - 4 months of age. By deduction, a real fontanelle never appears to form. At the second year of age, the external part of the suture is already ossified. The internal part of the frontoparietal suture remains visible. In median sections of some old animals, traces of the frontoparietal suture can sometimes be discerned for some distance, extending from the internal surface towards the external surface.

95 The temporoparietal suture (7[5]) is not listed in the *N.A.V.* (See also **footnote 57**.)

96 The *N.A.V.* only lists an occipitointerparietal suture (Sutura occipitointerparietalis), not an occipitoparietal suture (Sutura occipitoparietalis 2[23]). The central part of the suture may indeed be the remains of the sutura occipitointerparietalis if the interparietal bones did in a fact fuse to the parietal bones. However, this study excludes a study on the ontogenetic fusion of the bones that contribute to the formation of the occiput during pre- and early postnatal development. (See also **footnote 25**.)

the temporal meatus (7^{88}), close to its internal opening ($7^{88'}$). (See footnote 89 under the temporal bone.)

In caudal view, the nuchal plane (9^{4}) forms a single triangular surface even though it might consist out of at least two antimeres, indistinguishable from each other. In young animals, the plane is essentially convex, with a central flat to concave area. In old animals however, it is reshaped to be concave entirely. Therefore, this plane of the parietal bone faces caudo-dorsally in younger animals but eventually directly caudally in older animals. Considering young animals, the base or occipital margin of this triangular surface is concave. The apical part of the nuchal plane projects dorsally and almost rostrally. This apical part of the nuchal plane can then be considered as the **proper parietal plane** (*Planum parietale* **$9^{7'}$**) of the parietal bone ***** [97]. Together the single nuchal-cum-parietal planes ($9^{7'}$ & 9^{4}) form the dorsal lesser part of the occiput (1^{10}), dorsal to the nuchal crest. (See 2^{20} for the major ventral part of the nuchal surface $1^{10'}$.) In young animals, the frontal margins (prior to their ossification), are wedged between the caudal borders of the frontal bones (10^{5}). In very young animals these frontal margins are fairly straight. Even before immature stages are reached, these margins become more and more concave due to the enlargement of the frontal bones and the developing cornual processes. This happens at the expense of especially the parietal but eventually also the nuchal planes. After approximately the second year of age, the frontal margin at the frontoparietal suture ($9^{5'}$) can hardly be distinguished anymore. In animals as young as three to four months of age, the frontoparietal fontanelle ($1^{17'}$) is already very small and it is doubtful whether a true fontanelle could ever have formed before that age. (See figure 3.8.) The occipital margin at the occipitoparietal suture (2^{23}) disappears due to complete ossification. The occipitoparietal suture ossifies externally between the ages of 16 - 24 months. Internally however, evidence of the suture remains as

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97 To distinguish a parietal plane for the parietal bone also, is according to the *N.A.V.* Although it does not clearly form such a separate part in the savannah buffalo, it is convenient for descriptive purposes to regard it as such. The *N.A.V.* also refers to this part as the "frontal angle"of the parietal plane ($9^{7'}$). In young savannah buffalos between the ages of 16 to 24 months, the frontal angle can still be discerned, but of the whole parietal plane, nothing remains in old animals. Both the parietal and nuchal planes ($9^{7'\&4}$) are totally reshaped with age. The nuchal plane is remodelled to form a wide groove. The parietal plane becomes totally displaced by the corneal processes of the frontal bone. It is strongly suggested to refer to the nuchal part of the groove (**see next footnote**) as the parietal sulcus (**Sulcus parietalis**) and to the central remains of the parietal part that becomes incorporated into the frontal bone, as the caudal contribution to the **Sulcus intercornualis**. (See 10^{12} and **footnote 102**.)

a deep groove or recess. The process of ossification of the latter suture occurs before fusion of the frontoparietal suture (9[5`]). The nuchal plane of the parietal bone continues to decreases in size and surface area, especially in males. In older animals, that part of the nuchal plane that remains, eventually only separates the base of the cornual processes from the nuchal crest itself. Due to the remodelling over years of aging, the whole nuchal plane of the parietal bone then appears as a transverse groove. The axis of the groove lies in a horizontal plane and the concave surface of the plane then essentially faces caudally. In old bulls, the groove is narrower (approximately 15 - 20 mm) and pronouncedly more concave than in old cows. Where the grooves of the left and the right-hand sides meet, it is continuous dorsally with the intercornual groove (10[12]) of the frontal bone *****[98] .

The **internal surface** (*Facies interna* **9**[8]) of the parietal bone is concave and forms the mid-section of the cranial cavity (Fossa cranii media 4[1`]) dorsally as well as laterally. The area of the internal surface of the parietal bone is extensive, contributing more to the inner wall of the cranial cavity than any of the other cranial bones. The internal surface is marked by the **negative impressions** of the opposing parts of the **cerebral hemispheres** and the blood vessels in the interposed meninges (*Impressiones digitatae* **9**[8`], *Sulci arteriosi* **9**[8``] and *Sulci venosi* **9**[8```]). Dorsally, where the left and the right parietal bones are fused, the median plane is marked by a shallow **dorsal sagittal groove** (*Sulcus sinus sagittalis dorsalis* **9**[9]) and the absence of a sagittal suture. (Vide supra under 9[1] .) Rostrally the groove narrows down but is continued onto the dorsal sagittal groove of the frontal bone. Contrary to the state of the sagittal suture in the parietal region, the interfrontal suture (10[4]) remains visible. (See footnote 100 under the frontal bone.) The undivided internal surface of the parietal bone is the internal equivalent of both the temporal, nuchal and proper parietal planes (9[3] , 9[4] and 9[7`]) of the external surface. Subsequently, it appears much more extensive than all the external planes of the parietal bone put together. Similar to the situation of unequal registration between internal and external surfaces of the

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98 The cornual processes of the frontal bone of old bulls, extends so far caudally that they reach the level of the nuchal plane. The intercornual groove thereby also extends to the nuchal region, but it is the parietal groove that physically separates the contributions of the frontal bone from the other bones of the occiput (1[10]). (See the **previous footnote**, as well as **footnote 102**.)

sphenoid wings, the surfaces of the parietal bone also become ever more disrupted with age. Regardless of that, and despite age, the ventral border of the internal surface always extends much further ventrally, than the externally situated temporoparietal suture (7 [5]) - if that suture can be taken as an arbitrary level ventrally. (See figures 3.16 & 3.17). The internal surface of the parietal bone is fused - or rather it articulates, and over time fuses to various degrees - with the internal laminae of five other cranial bones in more or less five equidistant sections. These sections are situated ventrally, caudo-ventrally, caudo-dorsally, rostro-ventrally and rostro-dorsally, and articulation is as follows **:**

Ventrally it articulates but is never completely fused to the wing of the basisphenoid bone at the basisphenoidal part of the sphenoparietal suture (4 [11]). (Also see footnote 29.)

Caudo-ventrally it "articulates" with the petrous part of the temporal bone at the **petroparietal suture** (Sutura petroparietalis **9** [10])* [99].

The internal surface of the parietal bone is fused caudo-dorsally to the squamous part of the occipital bone at the occipitoparietal suture (2 [23]). The dorso-medial part of this suture appears as a deep groove in most animals. However, in some individuals the groove is filled by an osseus structure which could only be a remnant of the interparietal bone. (See subheading three **:** The Interparietal Bone and footnotes 25, 28 and 91 - 93.)

The latero-ventral part of the occipitoparietal suture borders the temporal meatus (7 [88]) rostrally. (See temporal and occipital bones and footnote 89.)

The rostro-ventral border of the internal surface of the parietal bone articulates but never completely fuses to the wing of the presphenoid bone at a presphenoidal part of the sphenoparietal suture (4 [11]). (See also footnotes 29 & 39.)

The rostro-dorsal margin of the internal surface of the parietal bone articulates but never completely fuses to the frontal bone at the frontoparietal suture (9 [5`]). (See footnote 94.)

The diploë (1 [5]) of the parietal bone is a compact type of spongy trabecula (Spongiosa trabeculosa 1 [5`a]). It separates the internal and external layers (Lamina interna / externa 1 [3/4]) of compact bone (Substantia compacta 1 [3`/4`]). The diploë contains mostly yellow bone

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99 The petroparietal suture (Sutura petroparietalis 9 [10]) is not listed in the *N.A.V.* This suture does not always give the impression that it can be classified as a suture, as the "articulation" between the respective bones appears to be either fissure-like in most individuals, or as if the bones are just in apposition to each other. A petroparietal fissure is also not listed in the *N.A.V.*

marrow (Medulla ossium flava 1[5```]) but also some red bone marrow (Medulla ossium rubra 1[5``]) near the lamina interna of young animals. The trabecula of the diploë is best developed rostrally near the median plane where the laminae can be 40 - 60 mm apart. Starting approximately at the age of 16 months, the diploë of the parietal bone becomes aerated from rostrally, starting on either side of the median plane, to form the sinus of the parietal bone. This sinus is a caudal extension of the sinus complex of the frontal bone (Sinus frontalis 10[31]), forming the **parietal part of the frontal sinus** (**9**[10`]). The left and the right-hand sides of this part of the sinus are separated from each other in the median plane by a **septum** of the original left and right antimeres of the parietal bone, to form a **double layered structure** (*Septum sinuum frontalium* **9**[11]). Caudally, this septum is incomplete (**9**[11`]). (See footnotes 27, 28, 91 - 93 and 108.) The parietal parts of the frontal sinus complex are incompletely subdivided by **many irregular plates of bone** (*Lamellae intrasinuales* **9**[12]) that project into it. Rostrally the sinus is continuous with the frontal sinus (10[31]) and caudally with the (usually unpaired) sinus of the occipital bone. (See Sinus frontalis caudalis 2[32] under the occipital bone.) These interconnected sinuses form part of the paranasal sinuses (1[6]). These are briefly discussed again in chapter three, section C **: The Skull Cavities**.

10. THE FRONTAL BONE

(*OS FRONTALE*)

(See figures **3.32 - 3.35**. Also see 3.5, 3.26, 3.31, 3.36, 3.37, 3.40 & 3.41.)

The frontal bone forms the major part of the roof (Calvaria 1 [11]) of the cranium externally, a small part of the wall of the cranial cavity internally and the medial part of the boney orbit (13 [21]). It also has a minor contribution to the formation of the zygomatic arch (20 [1]). The frontal bone harbours the greatest component of the voluminous frontal sinus complex between the internal surfaces of the external and internal laminae. It also forms the base of the cornual process that - especially in bulls - can take on massive proportions. The frontal bone is traditionally divided into a squamous component, temporal and internal surfaces, nasal and orbital parts and the cornual process. It is convenient to describe all the parts of the frontal bone of the savannah buffalo under the external and the internal surfaces **:**

The external surface of the frontal bone **:**

The **external surface** (*Facies externa* **10** [1]) of the lamina externa of the frontal bone is divided into "flat" (or squamous), temporal, orbital and nasal parts **:**

The **squamous part** (*Squama frontalis* **10** [2]) bears the cornual process, which is present in both genders. The squamous part of the frontal bone can be regarded as "flat" only in very young animals. Thereafter, the continuous development of the cornual process affects the shape and size of this part of the frontal bone tremendously. Reshaping of the squamous part is so much, that very little of its original shape can be distinguished in old animals. That occurs primarily due to the massive enlargement of especially the base of the cornual process (10 [11`]) at the expense of more peripheral parts of the frontal bone. Furthermore, enlargement of the squamous part also occurs at the expense of other bones of the skull, especially that of the parietal bone, which becomes displaced nuchally. (See parietal bone.) In old bulls, the caudal-most part of the frontal bone and the cornual process may become so enlarged that it even extends to the level of the nuchal surface (1 [10`]). Eventually, the

FIGURE 3.32 : OSTEOLOGY

THE SKULL OF AN OLD MATURE BULL (DORSAL VIEW)

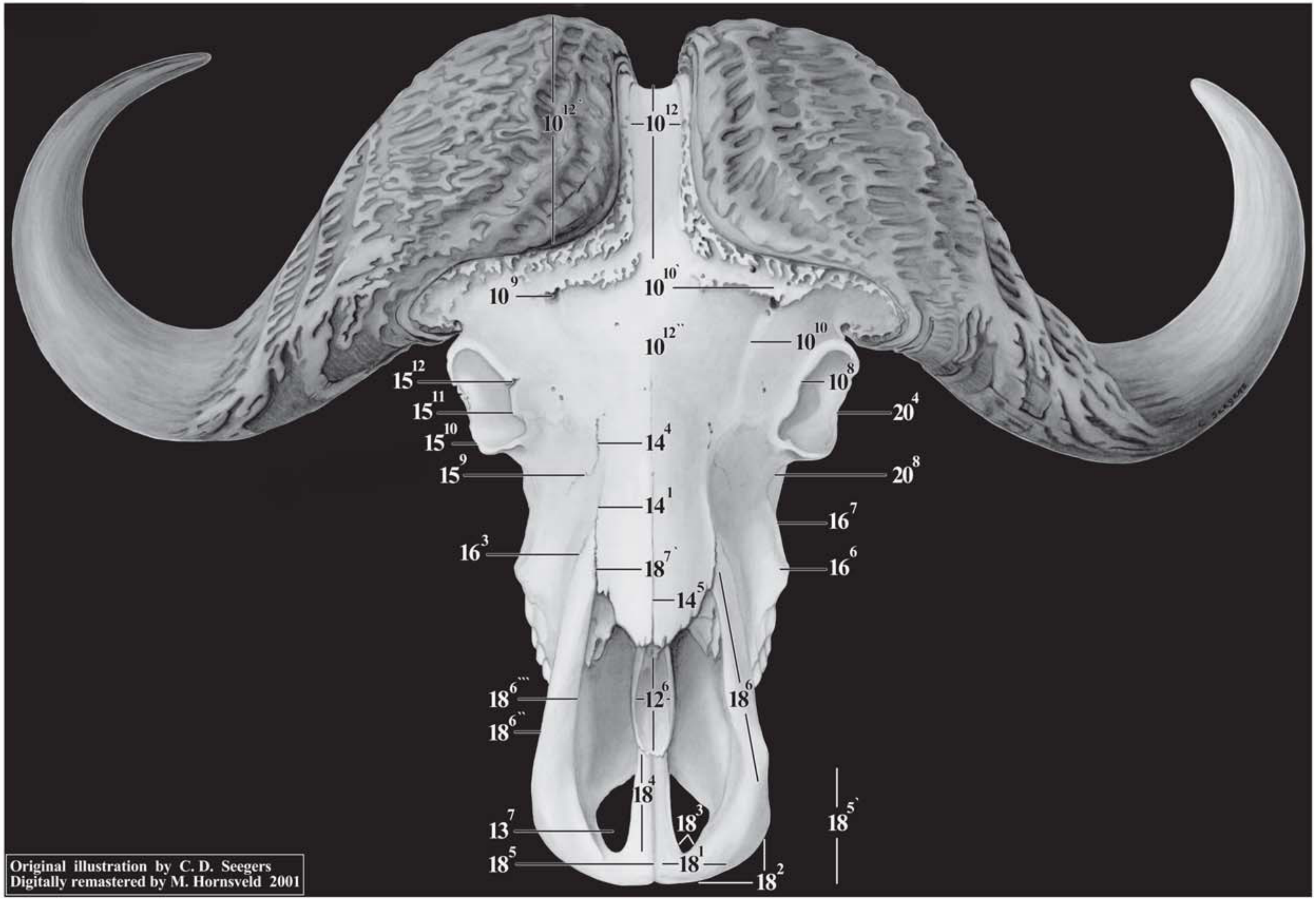


FIGURE 3.32 : OSTEOLOGY
THE SKULL OF AN OLD MATURE BULL (DORSAL VIEW)

FIGURE 3.33 : OSTEOLOGY

SKULL OF AN IMMATURE COW (DORSAL VIEW)

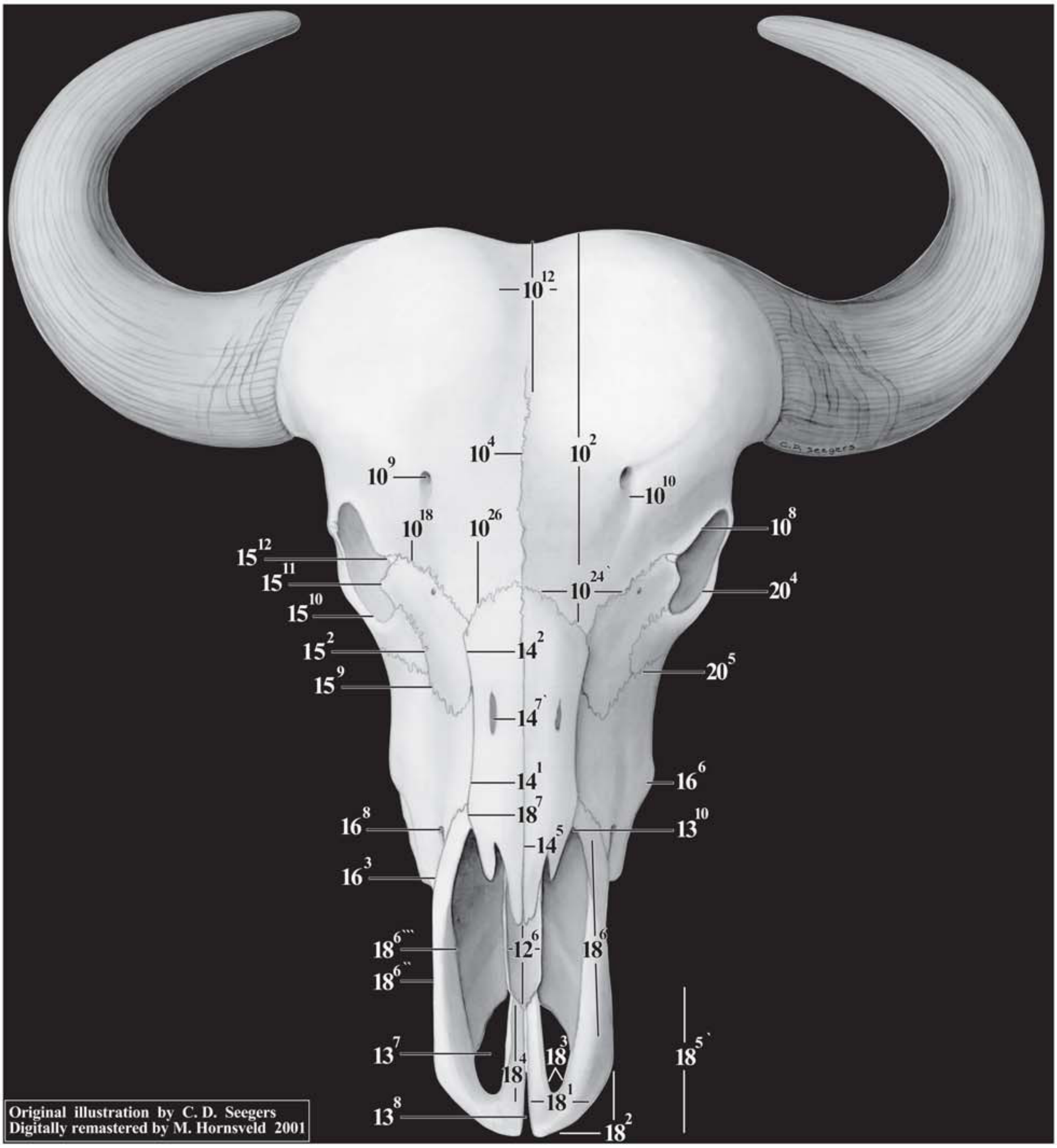


FIGURE 3.34 : OSTEOLOGY

SKULL OF AN IMMATURE COW (LATERAL VIEW)

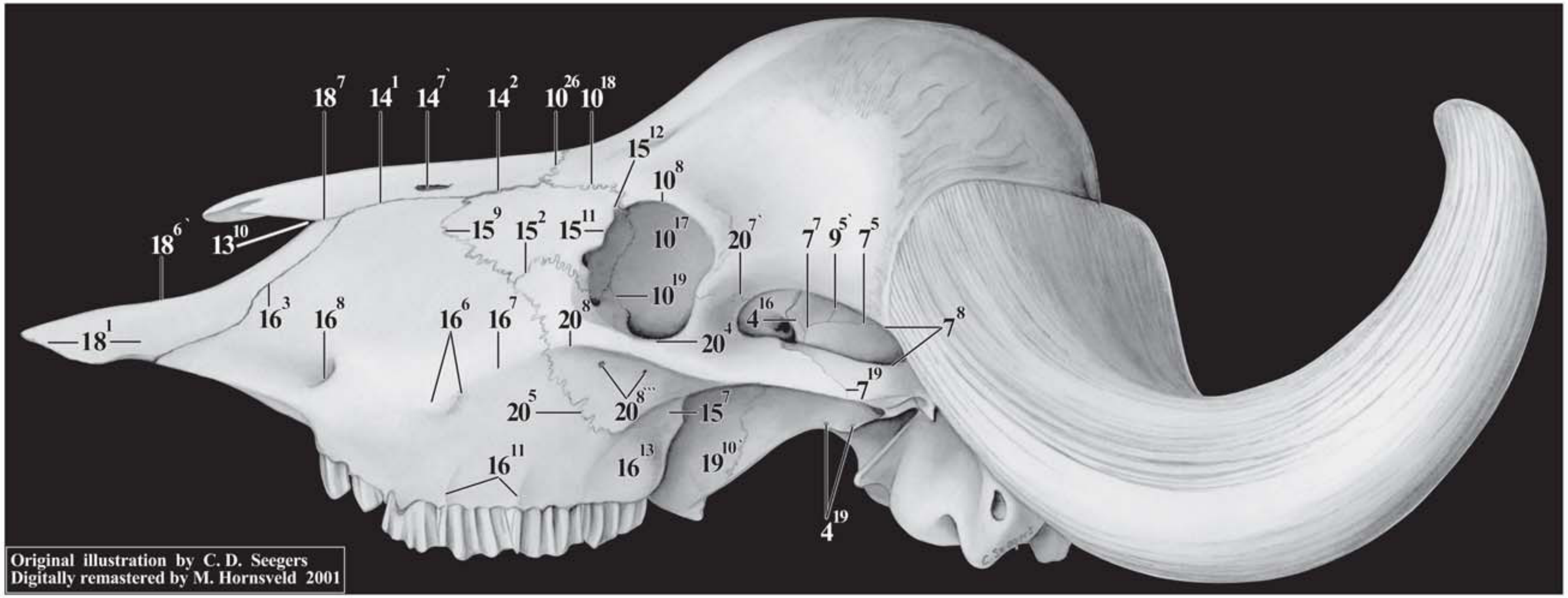
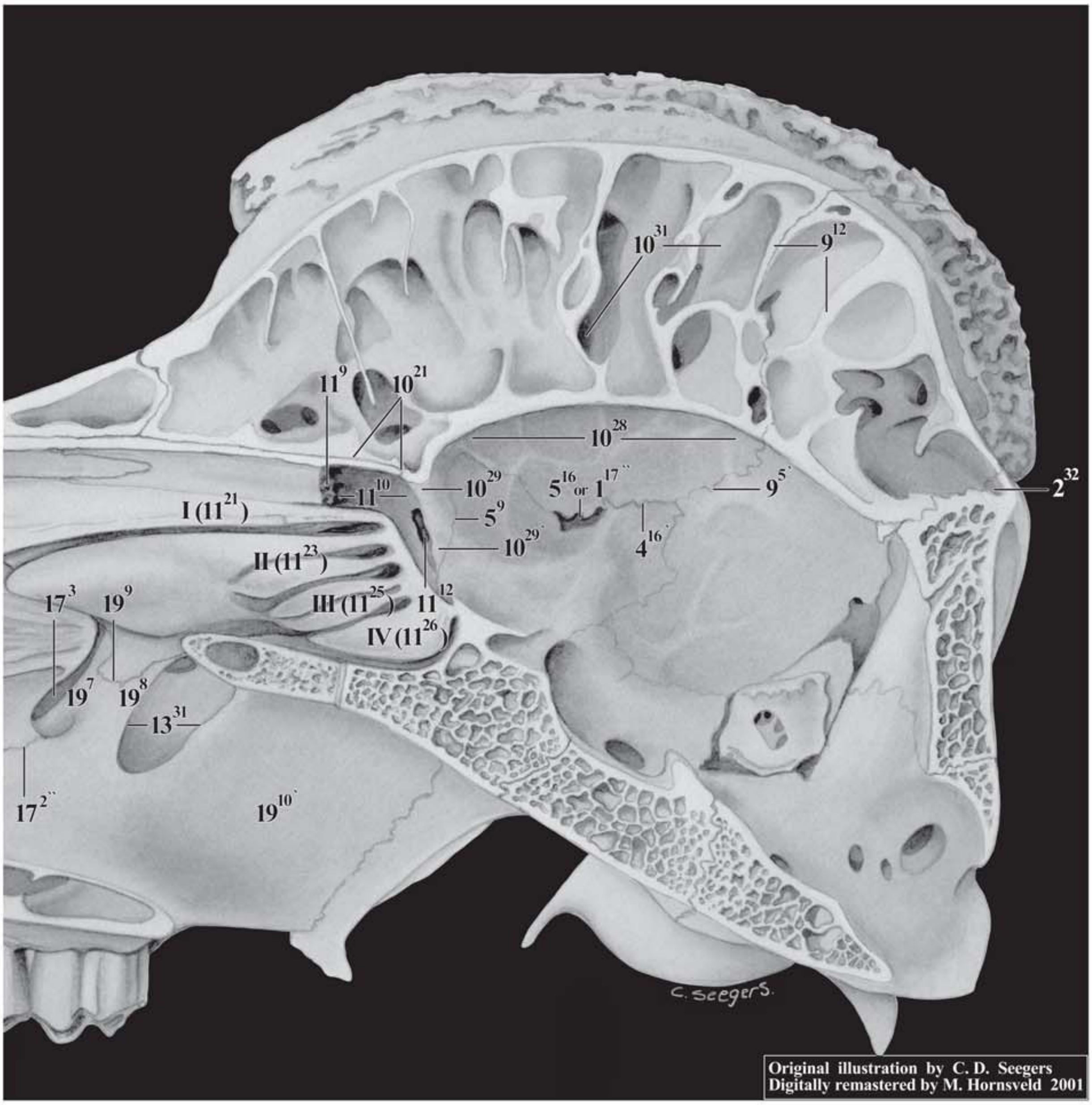


FIGURE 3.34 : OSTEOLOGY
SKULL OF AN IMMATURE COW (LATERAL VIEW)

FIGURE 3.35 : OSTEOLOGY

VIEW FIVE OF RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW)



squamous part of the frontal bone - and incorporated into it the base of the cornual processes - becomes increasingly convex or dome-shaped. Eventually, the squamous part dominates the entire external [neuro-]cranium as a whole. The squamous part of the frontal bone has median, caudal, rostral and lateral borders. These borders, and the subdivision of the lateral border, are best studied in dorsal view. It is achieved most effectively by comparing the skulls of young and old animals. It must be noted first that the rostral border of the external surface of the frontal bone articulates with the nasal and lacrimal bones of the face. Even though this rostral border is continuous with the squamous part of the frontal bone, it is discussed separately under the nasal part of the frontal bone. (Vide infra under 10[24] .) The other borders of the antimeric squamous parts of the frontal bone are therefore as follows **:**

Medially, at the frontal part of the **sagittal margin** (*Margo sagittalis* **10**[3]), the caudal half of the **interfrontal suture** (*Sutura interfrontalis* **10**[4])* [100] cannot be seen externally after the age of approximately two years. That is because the suture ossifies progressively in a rostral direction. (See also sagittal suture 9[1] under the parietal bone.) Internally, the whole interfrontal suture remains visible (vide infra under the internal surface 10[28]).

The caudal or **parietal margin** (*Margo parietalis* **10**[5]) is fused to the parietal bone at the frontoparietal suture (9[5`]). The external part of this suture cannot be seen after approximately the second year of age. (See footnotes 94, 97 & 98.)

The lateral border of the squamous part of the frontal bone is divided by the ventrally projecting **zygomatic process** (*Processus zygomaticus* **10**[6]), into a smaller rostral, and a much larger caudal part. This division for descriptive purposes, is only applicable when very young animals are considered. The caudal part of the lateral border cannot be distinguished in immature or older animals.

The rostral part forms the dorsal half of the lateral angle of the boney orbit (see 10[8]

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[100] The *N.A.V.* states that in domestic animals, the frontal bones are considered as paired bones, and that the suture between them should be termed the interfrontal suture (Sutura interfrontalis 10[4]). The sagittal suture (Sutura sagittalis 9[1]) refers to that part of the suture in the median plane between the parietal bones - it can however not be seen in the skulls of savannah buffalos older than approximately 3 - 4 months of age.

& 13[21]). The caudal part of the lateral border eventually becomes totally incorporated in the cornual process.

The zygomatic process (10[6]) of the frontal bone contributes to the formation of the zygomatic arch (20[1]). The zygomatic process is fused to the frontal process of the zygomatic bone (20[7]) at the frontozygomatic suture (20[7`]). Together, they form the lateral osseus wall of the boney orbit (13[21]). As animals age, the rostro-caudal dimension of this combined process increases approximately four-fold - and mainly in a rostral direction - from approximately 10 mm to more than 40 mm. It is most prominent in old animals, especially old bulls, and it accentuates the protruding supraorbital margin laterally. The lateral surface of the process is continuous with the lateral surface (20[2]) of the zygomatic bone. The medial surface of the process is concave, and at its base, it harbours an ill-defined **shallow concavity for the lacrimal gland** (*Fossa glandulae lacrimalis* **10**[7]).

The rostral part of the lateral border - rostral to the zygomatic process - meets the orbital surface of the orbital part of the frontal bone (vide infra under 10[17]) at the **supraorbital margin** (*Margo supraorbitalis* **10**[8]). This margin also becomes increasingly prominent with age to accentuate the protruding supraorbital margin dorsally, especially so in old bulls. (Also see 15[10] and 20[4] under the lacrimal and zygomatic bones respectively, for similar changes in the infraorbital margin). The **supraorbital foramen** (*Foramen supraorbitale* **10**[9]) opens approximately at the junction of the squamous and nasal parts (10[24] , vide infra) of the frontal bone, almost halfway between the median plane and the supraorbital margin. The foramen can be either single or double. When two foramina are found, their openings are of unequal size. Rostral and caudal to the foramen an inconspicuous **supraorbital groove** (*Sulcus supraorbitalis* **10**[10]) can be seen, especially in young animals. In old bulls, the base of the cornual process itself, or additional **osseus deposits** (**10**[10`]) on and around the cornual base, can cover the caudal part of the groove and the foramen partially or completely. (See also 10[22] and 13[29] for the supraorbital canal, and 10[12] for the development of the cornual process of the frontal bone.)

The larger caudal part of the lateral border of the squamous part of the frontal bone - caudal to the zygomatic process - only exists in very young animals as said above. It meets the temporal surface (Facies temporalis 10^{14}) of the frontal bone at the temporal line (7^{8}). The temporal line of the frontal bone is rounded and continues rostrally onto the caudal margin of the zygomatic process (10^{6}) where the line becomes more distinct. The temporal line of the frontal bone is also continued caudally onto the parietal bone. (See Linea temporalis 7^{8} under the parietal bone.) The temporal line of the frontal bone becomes incorporated, progressively from caudal to rostral, into the ventral aspect of the base of the cornual process due to the continuous enlargement of the process in aging animals. In old bulls, the whole lateral border of the squamous part of the frontal bone is eventually completely taken up into the ventral aspect of the base of the cornual process. In some old bulls the temporal line - or what remains of it on the ventral aspect of the cornual process - approaches the temporal line of the squamous part of the temporal bone. (See also 7^{8} under the temporal bone, and also see measurement 39 under section D **: Craniometric data**.) Eventually, the cornual process obscures the temporal fossa from lateral view.

The **cornual process** (*Processus cornualis* **10** ^{11}) of bulls and cows, forms the osseus core for the horn. The cornual process is the most striking feature of the frontal bone in mature animals, especially bulls. The cornual process can be divided into a **proximal base** (*Corona processus cornualis* **10**$^{11`}$) and a tapering **distal free columnar (conical) part** (*Collum processus cornualis* **10** $^{11``}$)***** [101]. The base eventually incorporates most of the squamous part of the frontal bone, while the columnar part of the cornual process is free and curved. In mature animals the distal part of the column is more acutely curved than proximally towards the base. The

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101 No clear distinction can be made between a corona (Corona processus cornualis $10^{11`}$) and column (Collum processus cornualis $10^{11``}$). These *N.A.V.* terms therefore do not fit the morphology of the cornual process of the savannah buffalo well. A proximal base and a distal free part of the cornual process - **Basis processus cornualis** and **Pars libera processus cornualis** - are suggested to be more appropriate terms.

development of the cornual process is rapid initially, commencing at birth and growing throughout life. However, after maturity, the growth rate appears to slow down. The base of the cornual process in bulls continues to increase in diameter. Increase in the length of the cornual process is achieved by addition that occurs at the base. Apart from this longitudinal growth, an increase in the diameter of the base also occurs simultaneously. Enlargement of the base eventually incorporates and extends over most of the external layer of the squamous part of the frontal bone. Medially, between the bases of the left and right cornual processes of both genders, the squamous part of the frontal bones' external lamina is fairly flat in young animals, but due to basal expansion in older animals, especially in bulls, an **intercornual groove** (Sulcus intercornualis **10** [12])* [102] is formed. The intercornual groove is also much more marked in bulls than in cows. The basal attachment of the cornual process not only increases in area with age as described in all of the above, but is also repositioned with respect to its placement on the squamous part of the frontal bone. This repositioning is therefore in relation to the rest of the skull and by that it also affects the direction of the free part. In young animals the horn originates as a small bud in the skin that overlies a particular part of the squamous part of the frontal bone. That bud initially forms a solid protrusion of bone from the external surface. The cornual process subsequently evaginates as a full thickness of the external lamina at the caudo-lateral part of the squamous part of the frontal bone (and not as a separate ossification centre). In mature animals however, the cornual process ultimately takes origin from the complete squamous part, in a definite lateral setting. Additional growth at the ventral aspect of the base, causes the distal free part to curve dorsally, giving the constant curving of the cornual process. The continuous repositioning and the additional growth at the basal attachment of the process, alters the direction and the general position of the corneal process's relative position to the skull. The end effect of that is as follows **:**

The direction of the proximal end of the cornual process is directed caudo-

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102 The *N.A.V.* only lists the term intercornual protuberance (*Protuberantia intercornualis*) which is not applicable for the situation in the savannah buffalo. The term intercornual sulcus (**Sulcus intercornualis** 10 [12]) is strongly proposed. (See also **footnotes 97 & 98**.)

dorsally in very young animals, then caudo-laterally, thereafter caudo-ventrally and eventually in typical mature old bulls, ventro-laterally. The distal free part of the horn covering the cornual process - which in young calves are directed outwards and upwards - would finally be directed inwards in mature animals.

In the living animal, the horn follows the curvatures of the cornual process as the development of both parts are totally interrelated **:**

The direction, shape and size of the cornual process as covered by horn, is well correlated with age and gender. These changes, including those caused by longitudinal and basal diameter growth, are constant and can be used as criteria of sexual dimorphism in the savannah buffalo. It can also be used to estimate the age of living animals under field conditions by comparing the horns of peer group sizes. In bulls the convexity of the dome-shaped part of the external lamina of the frontal bone exceeds that of cows. The cornual processes and overlying horn in bulls are massive and bulky. In cows the overlying horn is not as bulky at the base, and the horns are more slender, but the lengths can equal that of males. Especially in older bulls, the base of the cornual process covers the temporal fossa laterally.

Besides these growth processes already described above, the base of the cornual process plus the overlying horn, also enlarges in a rostral direction at the expense of the squamous part of the frontal bone. Eventually, the cornual base and horn therefore extend from the parietal margin - at the caudal extremity of the frontal bone - to the base of the zygomatic process (10^6) at the rostral end of the frontal bone.

The proximal part of the free part of the cornual process, is dorso-ventrally flattened (especially in mature bulls) and bears rostral and caudal ridges. The horns reflect the same dorso-ventral flattening, and rostral and caudal ridges are also formed. These ridges can best be seen on cross sections of horn. The caudal ridge is often more pronounced.

Apart from all the above already said about the cornual growth processes, additional growth not related to basal diameter increases or longitudinal growth, is also seen in males. It is a type of excessive growth that takes place at the dorso-medial part of the base of the process. Growth in this region incorporate the more medial aspect of the squamous part of the frontal bone and increases the dorso-ventral dimension in this region much more than in cows. In bulls this excessive growth of cornual process and horn, contributes to form the so-called "**boss**" (**10** [12`]) of the horns in living animals. In bulls therefore (if both antimeres are considered) the squamous part of the frontal bone rostral to the bases of the cornual processes, and medial to the supraorbital foramina, consequently become concave to form a single frontal concavity (1 [14]). A smaller area of this concavity - between the supraorbital foramina, the bases of the cornual processes and the nasal bones - are often smoother and delineates the **glabella** (**10** [12``])* [103] . The glabella effectively lies in the centre of the frontal fossa (1 [14]). Regardless of the extent of the formation of the "boss" in living bulls, the osseus bases of the left and of the right cornual processes, always remain separated from each other by the (median) intercornual groove (10 [12]). In old bulls the groove is approximately 20 - 30 mm wide. Caudally the groove is continuous with the parietal groove situated between the frontal and the occipital bones. (See footnote 97 under the parietal bone.) Rostrally, the intercornual groove ends in the frontal fossa and the glabella. Whereas the surfaces of the frontal fossa, the glabella, the intercornual groove (as well as the suggested parietal sulcus - see footnotes 97 & 98) is even and smooth, the surface of the cornual process per se is uneven, especially in animals older than approximately two and a half year of age. The surfaces of the base and the proximal part of the cornual process, is very rough in old bulls.

The changes in the shape of the squamous frontal bone - to become more dome-shaped as the animal ages - also play a role in the constant redirection of the cornual process of both genders. Individual variations occur in both genders. Such variations among bulls explain why the frontal fossa and the glabella are better defined in some males. In cows, the frontal fossa, the glabella and the demarcation between the intercornual groove and the bases of the cornual processes, are not as clearly defined

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103 The *N.A.V.* does not list a glabella (10 [12``]). Having this term listed would however be convenient.

as in bulls. In cows, the intercornual groove is much wider and more shallow. Caudally, it also joins the parietal grooves on the caudal nuchal surface of the skull as it does in males.

A **thick layer of connective tissue** (**10** 12```) separates the rough surface of the cornual process from the horn. The connective tissue layer is much thicker in bulls than in cows.

The cornual process is pneumatized by a **cornual diverticulum** (Diverticulum cornuale **10** 13)* [104] of the frontal sinus. (Vide infra under 10 31 .) The diverticulum starts to aerate the cornual process from approximately 16 months of age. It rapidly enlarges and at the age of approximately two years it has totally displaced the diploïc bone of the corneal process base. In old bulls the diverticulum extends for approximately 60 to 100 mm beyond the lateral width of the skull - taken at the level of the zygomatic arch - into the distal free part of the cornual process. (Also see FINAL COMMENT 13 and LIST OF INDEXES under section D **: Craniometric data**.)

The **temporal surface** (*Facies temporalis* **10** 14) is the smallest of the four parts of the frontal bone. It is concave from dorsal to ventral, facing ventro-laterally. It forms the rostro-dorsal part of the temporal fossa (Fossa temporalis 1 9). (See also parietal and temporal bones.) The caudal margin of the temporal surface of the frontal bone is fused to the temporal surface of the parietal bone at the frontoparietal suture (9 5` and also see footnote 94). This suture might be marked by a large sphenoidal fontanel (1 17``) which is best seen in animals of approximately two years old. (See presphenoid bone under 5 16 for details on this fontanel on an internal view of the cranial cavity, and also see footnote 42.) However, in some individuals, it appears as if this fontanel - as seen in the temporal fossa - only involves the temporal surface of the frontal bone (and not the suture or the parietal bone at all). This region in the temporal fossa around the fontanel, is always marked by the openings of two diploïc canals (2 7``). The internal openings of these diploïc canals are

104 The *N.A.V.* does not list a cornual diverticulum (10 13) for the frontal sinus. Having this term listed would however be convenient.

found in the cranial cavity, on or near the spheno-sphenoidal suture, lateral to the internal opening of the combined round and orbital foramen (Foramen orbitorotundum 4 [12]). Both the external and the internal openings of these diploïc canals are usually marked by deep grooves (4 [12`]) that lead away from the openings. (See the paragraph that follows after the asterisk for footnote 31, as well as footnote 31 itself.)

The ventral margin of the temporal surface is fused caudally for a short distance to the squamous part of the temporal bone at the squamosofrontal suture (Sutura squamosofrontalis 7 [7]) and rostral to that, to the wing of the basisphenoid bone at the sphenofrontal suture (Sutura sphenofrontalis 4 [16]). (See also temporal and basisphenoid bones). Rostrally, the temporal surface of the frontal bone joins the orbital surface of the frontal bone at the **orbitotemporal crest** (*Crista orbitotemporalis* **10** [15]). The crest is blunt dorso-laterally, sharp ventro-medially and rounded centrally. When the crest itself is considered, its concave curvature from dorsal to ventral describes an even arch. The orbitotemporal crest demarcates the temporal fossa from the boney orbit. If an imaginary line is drawn and extended from the orbitotemporal crest in a ventral direction, it continues onto the pterygoid crest (4 [17]) of the basisphenoid bone. Together these crests demarcate the caudal border of the medial wall of the boney orbit (13 [21]). (Also see 5 [18] for the ventral demarcation.)

The **orbital surface** (*Facies orbitalis* **10** [16]) of the **orbital part** (*Pars orbitalis* **10** [17]) of the frontal bone is concave in all directions and it forms the dorsal and dorso-medial parts of the boney orbit (13 [21]). The rostral margin is fused dorsally and ventrally to the orbital parts of the lacrimal and palatine bones, at the **frontolacrimal** (*Sutura frontolacrimalis* **10** [18]) and **frontopalatine** (*Sutura frontopalatina* **10** [19]) sutures respectively. The ventral margin of the orbital part is fused mainly to the dorsal border of the wing of the presphenoid bone at the presphenoidal part of the sphenofrontal suture (see 4 [16`] ). That part of the ventral margin of the orbital surface that has a deep **sphenoidal incision** (*Incisura sphenoidalis* **10** [20] ) caudally, is fused to the process-like part (see 5 [17`]) of the wing of the presphenoid bone. Rostrally and caudally (caudal to the sphenoid incision), the ventral border of the orbital surface of the frontal bone is fused for a short distance to the ethmoid and basisphenoid bones respectively at the ventral section of the **frontoethmoidal suture** (*Sutura frontoethmoidalis* **10** [21]) and to the basisphenoidal part of the sphenofrontal suture (Sutura sphenofrontalis 4 [16]). The particular part of the ethmoid bone involved (11 [5]) in the former suture, may however be so small in some animals that the frontal bone may then contribute to a section of the dorsal quadrant of the sphenopalatine foramen (13 [31]). (See also 11 [5], 19 [17] and in particular 5 [21], under the ethmoid, palatine and basisphenoid bones respectively for further detail.) Rostro-ventrally, near the ventral margin, the ventral orbital ridge (5 [18]) - the larger part of which also extends over the wing of the presphenoid bone - divides the orbital surface of the frontal bone, into a major dorsal part and a very small ventral part. The latter face ventrally and it forms part of the dorsal aspect of the pterygopalatine fossa (13 [30]). (See also presphenoid bone.) The surface of the orbital part of the frontal bone - apart from being concave in all directions - is marked by the following **:** A larger central foramen, a smaller foramen near the ventral margin and an inconspicuous concavity - or fovea - rostro-dorsally.

The **large central foramen** (**10** [22])* [105] (not illustrated), leads via the **supraorbital canal** (*Canalis supraorbitalis* **10** [22`]) (and see 13 [29]) to the supraorbital foramen (10 [9], vide supra). A caudally directed branch of the supraorbital canal leads directly into the rostral part of the frontal sinus, into which it opens * [106]. The smaller foramen that lie just rostral to the sphenoid incisure and rostro-dorsal to the rostral opening of the optic canal (13 [26]) - near the sphenoidal incisure - is the external opening of the ethmoid foramen (Foramen ethmoidale 11 [12]). This foramen may be paired (Foramina ethmoidalia 11 [12`]) in some animals. The ill-defined **trochlear fovea** (*Fovea trochlearis* **10** [23]) lies halfway between the central foramen (10 [22]) and the medial angle of the boney orbit. The orbital surface is continuous dorso-laterally with the medial surface of the lateral osseus wall of the boney orbit (13 [21]), formed by the zygomatic processes of the frontal (10 [6])

105 The *N.A.V.* only lists the supraorbital canal and the supraorbital foramen, but not this large foramen that leads to the canal from the side of the boney orbit. It would be convenient to allocate an appropriate term for it, also seen from the point of view that side-branching of the canal occurs. (See **next footnote**, and also see **footnote 126**.)

106 The caudal branch of the supraorbital canal apparently carries an artery for the nutrient supply of the mucous membrane that lines the frontal sinus. It can be regarded as a diploïc canal (2 [7``]) or a nutrient canal (2 [7````]). (See the **previous footnote** and **footnote 126**.)

and zygomatic bones (20[7]). The medial surface of the orbital part of the frontal bone per se, forms part of the lateral wall of the ethmoid cells (11[4]). (See footnotes 107, 112, 124, point 23 under the **Discussion**, chapter four, as well as figure 3.36.) The medial surface of the orbital part is fused via septa to reciprocal septa of the orbital plate of the ethmoid bone to form the proper ethmoid cells (11[4]).

The **nasal part** (*Pars nasalis* **10**[24]) of the frontal bone is small. Although it is a part of a bone of the [neuro-]cranium, it contributes to a small facial part of the skull. (See also ethmoid bone.) Projecting rostrally from the squamous part, it presents a **larger external** (**10**[24`]) and a **smaller internal surface** (**10**[25]). This smaller internal surface of the nasal part must not be confused with the internal surface (10[28]) of the frontal bone that forms part of the cranial cavity - vide infra. The external surface is triangular, the apical part of which forms a caudo-dorsal part of the facial surface, rostro-lateral to the glabella (10[12``] , vide supra). It is fused laterally at the frontolacrimal suture (Sutura frontolacrimalis 10[25]) to the lacrimal bone and medially at the **frontonasal suture** (*Sutura frontonasalis* **10**[26]) to the nasal bone. The frontolacrimal suture ossifies late in life. However, the **nasal margin** (*Margo nasalis* **10**[27]) - as the most rostral part of the frontal bone - is always discernable even in very old animals by ways of the frontonasal suture (10[26]) which remains incompletely ossified. The nasal margin ends rostrally at the nasomaxillary fissure (14[3]) which also remains un-ossified even in very old bulls.

In medial view, the internal surface of the nasal part (10[25]) may articulate incompletely with the ethmoid bone at a dorsal section of the frontoethmoidal suture (10[21]) to form a <u>temporary ethmoidonasal fissure</u> (14[9]) in young animals between approximately 16 and 24 months of age. (See also 11[7] under the ethmoid bone and footnote 125.) Ventrally, the nasal part of the frontal bone is fused via septa, to reciprocal septa of the fundic part of the tectorial plate of the ethmoid bone, to form cells. (See paragraphs following 11[2] .) The cells form part of the rostral compartment of the frontal sinus complex (vide infra under 10[31]).

The internal surface of the frontal bone **:**

The **internal surface** (*Facies interna* **10**[28]) of the frontal bone is much smaller in area than the external surface. That is directly the opposite of the situation of the parietal bone. The internal surface is concave in all directions and forms the roof and part of the lateral walls of the rostral part of the cranial cavity (Fossa cranii rostralis 5[12]). Rostro-dorsally, the internal surface bears a ridge which fades out laterally and ventrally. The ridge forms the **frontal part of a partial constriction** (**10**[29]). It demarcates the roof of the cranial cavity from the ethmoidal fossae (11[10]). Rostral to the constriction, the internal surface of the frontal bone thus forms the roof (and a smaller lateral part) of the ethmoidal fossae. The exact contributions of the frontal bone to the ethmoidal fossa cannot be clearly determined due to ossification of most of the internal parts of the frontoethmoidal suture (10[21]). The **ethmoidal parts of the partial constriction** (**10**[29`]) are less prominent laterally and ventrally. (See also footnotes 43 & 46 regarding the variations in position of the suture and the constriction.) Caudal to the constriction, the internal surface of the frontal bone - as seen in a median view of a halved skull - has caudal, lateral, rostral and dorsal borders **:**

The caudal border of the internal surface of the frontal bone is wide and convex and is fused to the parietal bone at an internal part of the frontoparietal suture (Sutura frontoparietalis 9[5`]). (See also footnote 94.)

The lateral (i.e. the latero-ventral) border is convex caudally (see 5[14]) and concave rostrally (see 5[15]) and is fused to the wing of the presphenoid bone at an internal part of the presphenoidal part of the sphenofrontal suture (4[16`]). Remnants of the sphenoidal fontanel (1[17``]) can sometimes be seen on this suture line even in old animals, resembling a sphenofrontal fissure. See 5[16] for the situation in younger animals, footnotes 41 & 42, and point 2 of the **Discussion**, chapter four. The fontanel may ossify partially to form what could be considered as a sphenofrontal fissure (5[16]). This part of the sphenofrontal suture may also appear in old animals like any other suture that is not completely ossified. Alternatively, the cartilage may ossify from a central point, to leave a circumscribed osseus scar (5[16``]) that would represent a Wormian bone. (See footnote 28.)

The **rostral border** (*Margo ethmoidalis* **10**[30]) of the internal surface is narrow and the frontoethmoidal suture (10 [21]) between the internal lamina of the frontal bone and the cribiform plate ossifies early in life. (See also 11 [9] .) Even in animals as young as approximately three to four months of age, this suture is difficult to see and skulls have to be cut delicately in special planes before small un-ossified cartilaginous parts of the frontoethmoidal suture can be discerned *[107] . In skulls of old animals, often the only remains of the frontoethmoidal suture in the ethmoid fossa, can be seen when the skull is cut in a paramedian plane. That remnant of the suture then lies dorsally, on the cut surface of the dorsal wall of the ethmoid fossa.

Dorsally, the medial borders of the internal surfaces of the left and the right antimeres of the frontal bone are raised and fused to each other in the median plane at the interfrontal suture (10[4]). Rostro-dorsally, the medial borders forms a single ridge, but caudally the elevated medial borders are separated from each other by a shallow median groove. The groove between the two ridges widens further caudally and is continued onto the parietal bone, to join the dorsal sagittal groove (Sulcus sinus sagittalis dorsalis 9[9]). To recap, the interfrontal suture on the external surface ossifies early as discussed under the external surface of the frontal bone (vide supra). Only the rostral half can still be seen in animals of approximately 2 years of age. However, on the internal surface of the frontal bone, the interfrontal suture can be seen in the dorsal sagittal groove even in old animals. However, partially ossified parts of the falx cerebri (of the dura mater), may conceal both the groove and the suture. (Also see 2[30] .) The internal surface is marked by the impressions of the cerebral hemispheres and the blood vessels interposed in the covering meninges (Impressiones digitatae 9 [8`], Sulci arteriosi 9 [8``] and Sulci venosi 9 [8```]).The digital impressions on the internal lamina of the frontal bone are more distinctly etched than those of the other bones that line the cranial cavity.

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107 The other components of the frontoethmoidal suture (10[21]) that might remain visible are between the frontal bone and the lamina tectoria (11[2]) and between the orbital part (11[17]) of the frontal bone and the baseplate (11[8]) of the ethmoid bone. However, they were found to be all hardly discernable in the skulls studied. The suture between the orbital part of the frontal bone and the orbital plate (11[3]) of the ethmoid bone was not studied specifically into further detail as nothing more could be seen macroscopically. (Also see the paragraph in which the ethmoidonasal suture (11[7]) is discussed.)

The internal and external layers (Lamina interna / externa)(1 [3 / 4]) of the frontal bone are separated from each other by the voluminous frontal part of the **frontal sinus** (*Sinus frontalis* **10** [31]), forming a frontal sinus complex * [108] . In old bulls the layers of the sinus are approximately 60 mm apart medially, and approximately 90 mm laterally. The latter measurement is taken vertically at the base of the cornual process, and on the level of the zygomatic arch. The volume of the sinus increases with age and it extends into the cornual process. (Vide supra under 10 [13] .) Mainly perpendicular, but also randomly scattered intrasinal lamellae (9 [12]), connect the internal and external laminae of the frontal bone. These lamellae subdivide the sinus and the cornual diverticulum incompletely. The lamellae render tremendous mechanical strength to the Calvaria (1 [11]) and the cornual processes. The sinuses of the left and the right-hand sides are completely separated from each other in the median plane by a double layered septum (Septum sinuum frontalium 9 [11]). The septa of the left and right antimeres of the frontal and nasal bones (and also what remains of that septum of the parietal bone), are continuous with each other to form the paired or double layered septum as referred to above. It divides the frontal sinus complex into left and right-hand sides, except caudally at the occipital bone (see 2 [32]), where the occipital part of the sinus is undivided as is most often seen. Rostrally, the sinus communicates via a **large opening** (**10** [31`]) of approximately 10 x 40 mm with the sinus of the dorsal nasal concha (11 [21]) to form a conchofrontal sinus (*Sinus conchofrontalis* **10** [32])* [109] . The frontal sinus also communicates via **multiple smaller openings** that varies between 2 to 9 mm in diameter (*Aperturae sinuum frontalium* **10** [33]) with various ethmoidal meatuses, and therefore with the nasal cavity. These openings are perforations of the tectorial and orbital laminae (11 [2 & 3]) of the ethmoid bone. Caudally the frontal sinus communicates with the sinus of the parietal bone (9 [10`]).

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108 The frontal sinus complex consists of frontal (10 [31]), parietal (9 [10`]), occipital (2 [32]), nasal (14 [10]), dorsal conchal (11 [22]) and lacrimal (15 [16]) components. The nasal sinus (Sinus nasalis 14 [10]) is not listed in the *N.A.V.* It would be convenient to have the term listed. (See also **footnote 27**.)

109 A conchofrontal sinus (10 [32]) is more typically found in the domestic horse, but the term is applicable here. The opening that connects the two parts of the sinus can therefore also be termed a conchofrontal aperture (*Apertura conchofrontalis*). (See also **footnote 110**.)

11. THE ETHMOID BONE
(*OS ETHMOIDALE*)

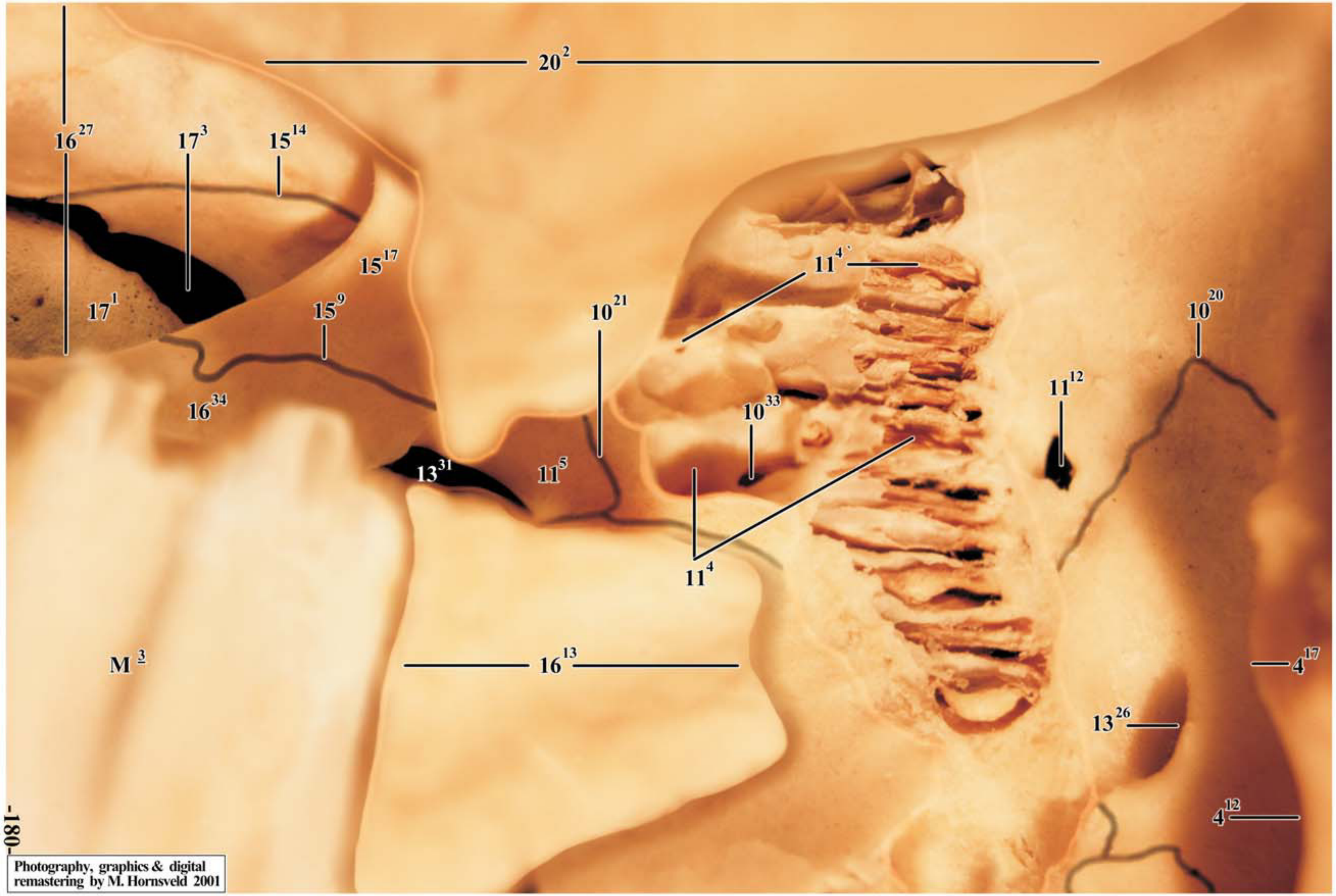
(See figures **3.35 - 3.37**. Also see 3.8. 3.9, 3.20 & 3.40.)

The ethmoid bone is traditionally considered as an unpaired bone of the [neuro-]cranium. But it has both paired and unpaired components, (see **Discussion**, point 8), and furthermore, although it is a cranial bone, it lies mostly within the facial part of the skull. In the savannah buffalo it appears as if intrinsic fusion of cartilaginous parts occurs during its ontogenetic development, as well as extrinsic fusion to other cranial bones. Subsequent ossification of coalesced central parts are followed by centrifugal spreading of ossification into the paired peripheral parts of the ethmoid bone. The degree of fusion between different parts of the ethmoid itself and to surrounding bones further away from the centre of coalescence, varies a lot. The whole spectrum, from temporary to permanent fissures, suture lines that are maintained (even if not always very clearly), and even complete ossification of sutures - without leaving any trace of the original suture - is therefore found in the ethmoid bone. All these factors therefore, makes an understanding of the morphology of this bone - and how it relates to surrounding bones - a complex issue. The following two paragraphs give further basic information on the ethmoid bone. The paragraphs also give an introduction to the different parts of the ethmoid bone, and how these parts are fused to each other, and to other bones of the skull **:**

In external appearance, the ethmoid bone is roughly cone-shaped, with the dorsal part (the roof) of the cone larger and the ventral part (the floor) smaller. The open end of the cone is directed rostrally. The cone-shaped peripheral part forms the unpaired component, whereas the contents of the cone are made up by the paired parts of the ethmoid bone. Regarding the peripheral part of the ethmoid, the internal boundaries roughly follow the contours of the external boundaries inside the [viscero-]cranium. This is because the thickness of the peripheral wall is even as it consists out of three plate-like structures, namely tectorial, orbital and basal plates. These plates relate topographically to the dorsal, lateral and ventral

FIGURE 3.36 : OSTEOLOGY

THE BONEY ORBIT AT APPROXIMATELY 2 $\frac{1}{2}$ YEARS OF AGE : LEFT LATERAL VIEW OF THE (PROPER) ETHMOIDAL CELLS. OVERLYING BONE HAS BEEN SCULPTURED AWAY



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.36 : OSTEOLOGY
THE BONEY ORBIT AT APPROXIMATELY 2 $\frac{1}{2}$ YEARS OF AGE : LEFT LATERAL VIEW OF THE (PROPER) ETHMOIDAL CELLS. OVERLYING BONE HAS BEEN SCULPTURED AWAY

FIGURE 3.37 : OSTEOLOGY

CONTRIBUTIONS OF THE ETHMOID AND OTHER BONES TO THE FORMATION OF AN INFRAORBITAL PILLAR AND A BONEY CANAL
MOST OF THE DORSAL AND VENTRAL CONCHAL BONES HAVE BEEN REMOVED (MEDIAL VIEW)

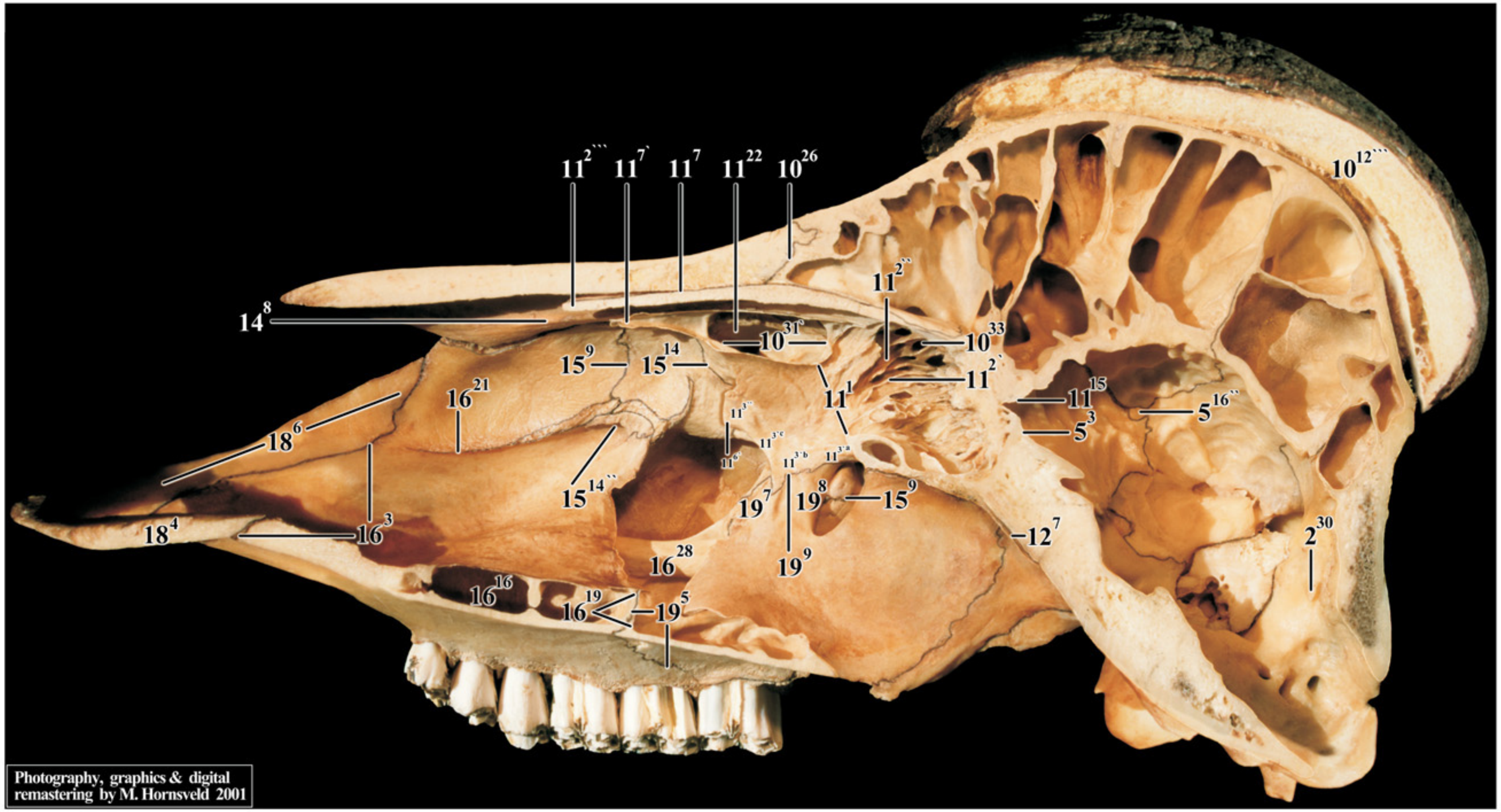


FIGURE 3.37 : OSTEOLOGY

CONTRIBUTIONS OF THE ETHMOID AND OTHER BONES TO THE FORMATION OF AN INFRAORBITAL PILLAR AND A BONEY CANAL
MOST OF THE DORSAL AND VENTRAL CONCHAL BONES HAVE BEEN REMOVED (MEDIAL VIEW)

components of the [viscero-]cranium. Situated in the caudal part of the nasal cavity, the cone shaped part of the ethmoid encloses a cavity, most of which forms the caudal (or fundic) parts of the nasal cavity (vide infra). This cavity however is mostly occupied by the paired components of the ethmoid bone. The paired parts are bilaterally symmetrical, and form the ethmoidal turbinates. The turbinates are delicate and each resembles a shell in some respects (vide infra). The cavities so encircled - but not totally enclosed by the peripheral boundary of the ethmoid bone - plus the paired parts, are divided into left and right antimeres by an unpaired median or perpendicular plate. Caudally (at the apical end of this cone-shaped bone) a single transverse part of the ethmoid - consisting out of bilaterally symmetrical halves - forms the cribiform plate. The latter plate separates the nasal cavity from the cranial cavity. The divided cavities in front, the divided cribiform plate, and the paired turbinates of the ethmoid bone, are all indicative of the paired nature of the ethmoid bone. Unpaired parts on the other hand - like the cone itself and a single rostral process of its tectorial plates (vide infra), and the single perpendicular plate - are reminiscent of the unpaired components of this bone * [110] .

In contrast to the delicately thin dorsal and lateral peripheral walls of the ethmoid bone, the perpendicular plate is thick. The transverse part consists out of compact bone, yet is perforated. The basal plates are more intimately fused to the surrounding bones of the skull than any of the other ethmoid parts. The basal plates therefore form an integral part of the internal laminae of these bones they are is fused to, and by that closes the coned ethmoid bone off ventrally. The tectorial, orbital and with some imagination the basal plates too, have internal concave and external convex surfaces as can be expected from a cone shaped structure. The internal surfaces of the different plates are continuous with each other without any clear boundary. The combined form of the internal surface of the ethmoid bone is more responsible for coining the ethmoid as cone-shaped than the external surface. An **internal constriction** (**11** [1]) partially divides that part of the nasal cavity enclosed by the

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[110] It was not the intention of this study to go into the details of the ontogenetic development of all the bones of the skull. Compared with what is known of the development of skulls of other domestic animals and man, similarities and differences were interpreted for the savannah buffalo.

ethmoid bone, into caudal fundic and rostral nasal sections* [111] . Excluding a single and minor contribution from the tectorial plate, the walls of the rostral nasal section are formed by the orbital plates only and it forms part of the caudo-lateral wall of the proper nasal cavity. (See also palatine bone for other parts.) The walls of the caudal fundic section of the ethmoid-enclosed cavity is composed of all the plates of the ethmoid bone. Together, they all enclose the blind ending and most caudal part of the nasal cavity, the nasal fundus (Fundus nasi 13 [13]). For descriptive purposes, it is convenient to clearly distinguish the caudal fundic from the rostral nasal parts for each of the tectorial, orbital and basal plates. The fundus accommodate approximately 24 horizontally arranged turbinates or nasal conchae of ethmoid origin (vide infra). The turbinates are attached to the lateral, dorsal and caudal walls of the fundus only. From these attachments, the turbinates project medially, and by that they partially subdivide the cavity of the fundus into ethmoidal meatuses (vide infra under 11 [17]). Two of these turbinates are much more elongated than the others and project rostrally. Limited by the caudal boundary of the cone, these elongated turbinates project beyond the rostral limits of the fundus, right into the proper part of the nasal cavity. Except ventrally - where the basal plate is fused directly to the presphenoid, palatine and frontal bones - the external surfaces of particularly the fundic parts of the tectorial and orbital plates, are fused by means of a multitude of septa to reciprocal septa from the nasal, squamous and orbital parts of the frontal bone, and also the lacrimal bone. The septa subdivide peripherally situated compartments of aerated bone - which surrounds most of the fundus - into smaller sub-compartments or cells. (Vide infra under 11 [4] .)

With the above as a broad introduction to the ethmoid bone, details can now be discussed by considering the surfaces, borders, particular contributions & fusions, of each of the plates **:**

The plates of the ethmoid bone **:**

The dorsal **tectorial plate** (*Lamina tectoria* **11** [2]) forms the roof of the coned part of the

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111 The nasal fundus (Fundus nasi 13 [13]) is not listed in the *N.A.V.* The presence of an internal constriction (11 [1]) in the savannah buffalo, clearly separates the caudal end of the nasal cavity from the more caudally situated nasal fundus. The caudal border of the nasal fundus is formed by the cribiform plate (11 [9]) and the rostral border lies at the level of the rostral end of the rostrum presphenoidale (5 [8]). For descriptive purposes of the ethmoid bone, listing the Fundus nasi as official term would be convenient. The term nasal fundus (13 [13]) is used as such under the Introduction to the Facial bones, subsection 13. Relevant matters of the ethmoid bone are therefore repeated under **footnote 121**.

ethmoid bone. It is divided into nasal and fundic sections. The fundic section will be described first **:**

The internal surface of the fundic section of the tectorial plate is subdivided by the attachments of the base-plates or **basal laminae** (**11**[2`]) of ethmoid turbinates (vide infra under 11[16]) into **grooves** (**11**[2``], vide infra). The grooves form the peripheral boundaries of the dorsally situated ethmoidal meatuses (11[17], vide infra).

The external surface of the fundic section of the tectorial plate is fused by means of septa, to reciprocal septa of the cranial and facial parts of the frontal bone. Due to complete ossification and the complexity of the frontoethmoidal suture (10[21]) along all these septa, this suture is beyond tracing. The septa subdivide peripherally situated compartments of aerated bone dorsal to the tectorial plate into ethmoidal cells (11[4]). These cells cannot always be clearly differentiated from cells associated with the adjacent orbital plate. Peripherally, the cells are continuous with the rostral compartment of the frontal sinus complex. The tectorial plate itself is perforated by approximately 10 foramina. The foramina not only connect associated cells - and therefore the frontal sinus complex - to the nasal fundus, but in some instances also to spaces enclosed by dorsally situated ethmoid turbinates. (Vide infra under 11[16] and see 10[33] as well as footnotes 109 & 113.)

Medially, the left and the right tectorial plates contribute to a single but rather long and slender **rostral process** (**11**[2```]). This process tapers down rostrally, to end beyond the borders of the fundus. The process thereby forms a sole nasal section contributed to by both tectorial plate antimeres. Caudally the process is approximately 20 mm wide and **V - shaped** in cross section. Dorsally, the outer or external surface of this process is fused to the caudal half of the internasal suture (14[5]) at a median part of the ethmoidonasal suture (11[7]). Ventrally, paramedian parts of the internal surfaces of this process borders the dorsal nasal meatus of the left and right nasal cavities. One must realize that medio-ventrally, the rostral process (11[2```]) - of paired origin - is continuous with the perpendicular plate that is of unpaired origin. This occurs without any signs of a suture. Due to the rostrally advancing ossification of the perpendicular plate (see 11[13`]), the process would end further rostrally in the skulls of older animals when compared to that of young animals.

The lateral **orbital plate** (*Lamina orbitalis* **11**[3]) consists of a caudal fundic section and a rostral nasal section, to form the lateral wall of the coned ethmoid bone in both these sections. The fundic and nasal sections of the orbital plate, covers the interior of the internal surface of a large area of the caudal nasal cavity, by "lining" it. The internal surface of the nasal section of the orbital plate (11[3]) has a much larger surface area than the nasal part of the tectorial plate. This surface presents **ventral** (**11**[3`]), **rostral** (**11**[3``]) and **dorsal** (**11**[3```]) **borders**. The ventral border is subdivided again into **caudal** (**11**[3`a]), **middle** (**11**[3`b]) and **rostral thirds** (**11**[3`c]) (Vide infra.) Before these can be discussed, the fundic section of the orbital plate has to be described first **:**

The external surface of the fundic section of the orbital plate is fused by means of the septa similar to those of the tectorial plate (vide supra). In this instance, the cells are situated laterally, between the fundic section of the ethmoid and the orbital part of the frontal bone (10[17]). Because they can be differentiated with more ease from the smaller subdivisions of the frontal sinus complex, they form the **ethmoidal cells proper** (*Cellulae ethmoidales* **11**[4])* [112]. The fundic section of the orbital plate is also perforated by approximately 10 foramina. These foramina vary in diameter from approximately 2 to 9 mm and they are often oval in shape. The foramina not only connect the associated cells to the nasal fundus (i.e. the ethmoidal meatuses), but sometimes also to spaces enclosed by the ethmoidal turbinates (vide infra), in a similar way as with the tectorial plate * [113]. (Vide infra under 11[16], but also see 10[33], as well as footnote 109.)

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112 In animals of approximately 2 years of age, osteolytic activity around the cells or on the orbital surface of the orbital part of the frontal bone (or even at both places), may expose some ethmoid cells in prepared skulls. These unobvious changes can best be seen when the medial wall of the boney orbit (13[21]) is viewed from laterally and on close inspection. (See also **footnote 124** for a similar situation in the nasal bone. Increased osteolytic activity of the peri-and endosteum can be expected to occur in ages when remodelling of bone occurs fast. See chapter four **: Discussion**, point 23.)

113 The foramina of the orbital and tectorial plates make up the multiple smaller openings referred to under the frontal bone (Aperturae sinuum frontalium 10[33]). (See also **footnote 97**.)

The internal surface of the fundic section of the orbital plate is also subdivided by the attachments of the base-plates or basal laminae ($11^{2'}$) of the ethmoid turbinates into grooves ($11^{2''}$). The grooves form the peripheral boundaries of laterally situated ethmoidal meatuses (vide infra under 11^{17}).

The external surface of the nasal section of the orbital plate is fused by means of the septa of its associated and overlying ethmoidal cells, to **reciprocal septa of the lacrimal bone** (**11**$^{4'}$) rostrally, and to the nasal and frontal bones dorsally (see second paragraph following 15^{16}). The sutures involved are the lacrimoethmoidal (15^{14}), ethmoidonasal (11^{7}) and the rostral part of the frontoethmoidal (10^{21}) sutures respectively. The cells are generally larger than those around the tectorial plate, and they communicate directly with the overlying sinuses of the frontal and nasal bones and with the dorsal compartment of the lacrimal sinus ($15^{16'}$ - see lacrimal and frontal bones).

The internal surface of the nasal section of the orbital plate (11^{3}), can best be described in a median view of a halved skull of which the conchae have been removed. (See figure 3.37.) As stated above, it presents ventral ($11^{3'}$), rostral ($11^{3''}$) and dorsal ($11^{3'''}$) borders, with the ventral subdivided into caudal ($11^{3'\mathbf{a}}$), middle ($11^{3'\mathbf{b}}$) and rostral ($11^{3'\mathbf{c}}$) thirds **:**

The caudal third ($11^{3'\mathbf{a}}$) of the ventral border is fused to the orbital process (19^{16}) of the palatine bone at the palatoethmoidal suture (Sutura palatoethmoidalis 19^{9}) and to the orbital surface of the frontal bone at a ventral section of the frontoethmoidal suture (Sutura frontoethmoidalis 10^{21}) to form the roof of the dorsal quadrant (or the edge) of the sphenopalatine foramen (13^{31}). (See also the paragraph following 19^{17} under the palatine bone and illustrations of lateral views of the skull.) Therefore a small area of the ethmoid bone is visible on the external surface of the skull when the pterygopalatine fossa (13^{30}) is exposed for lateral view. By deduction, it appears as if this external part of the ethmoid bone must have been the region where ontogenetic fusion between orbital and basal plates have occurred. This **particular region of the ethmoid bone** (**11**^{5}) is fused to the apex of the external surface of the wing of the presphenoid bone at an externally visible part of the sphenoethmoidal suture (Sutura sphenoethmoidalis). (See also 5 [9] and 5 [21] under the presphenoid bone, 10 [21] under the frontal bone, and also consult figures 3.20 & 3.26.)

The middle third (11 [3`b] ) is fused to the palatine part of an infraorbital pillar at the palatoethmoidal suture (19 [9] ). (Also see 15 [17`] and footnote 132 under the lacrimal bone as well as 19 [7 & 8] and consult figure 3.40.)

The ventral margin of the rostral third (11 [3`c]) is free and it forms the caudo-dorsal border of a <u>large and permanent compound fissure</u> between the ethmoid bone itself and the palatine, ventral conchal and lacrimal bones. (See 17 [3] as well as text preceding footnote 143. See also footnote 144, and also see palatine, ventral conchal and lacrimal bones.) In old animals the ventral margin of the rostral third can be very short or even absent * [114] . The rostral border (11 [3``]) of the internal surface of the nasal section of the orbital plate differs from the (flattened) edges of the other borders in that it is **deeply grooved** (**11** [6]) from dorsal to ventral. The groove is bordered medially and laterally by a **medial free** (**11** [6`]) and a **lateral fused side** (**11** [6``]) respectively. The free side can be either sharp or rounded. It forms the caudal part of the incomplete medial wall of a boney canal (17 [5]). (Also see footnotes 144 & 145 under ventral conchal bone where this canal is discussed.) In some old animals the medial free part (11 [6`]) of it can extend rostrally towards the body of the ventral conchal bone, to form a more complete medial osseus border for the boney canal (17 [5]). The lateral side (11 [6``]) is either fused to the nasal surface of the lacrimal bone, or to the caudal border of the internal lamina of the lacrimal bone at the lacrimoethmoidal suture (15 [14] , see also lacrimal bone). Or, as a third alternative in some animals, the latter suture is incomplete, and a <u>small but permanent lacrimoethmoidal fissure</u> (not illustrated) may remain. (See 15 [14`] as well as footnote 130.)

The lateral aspect of the dorsal border (11 [3```]) is fused rostrally to the nasal bone

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[114] This might be an indicator of age.

and caudally to the frontal bone at the **ethmoidonasal suture** (*Sutura ethmoidonasalis* **11**[7]) and the dorsal section of the frontoethmoidal suture (10[21]) respectively (vide supra and see also nasal and frontal bones). In young animals, between the ages of approximately 16 to 24 months, the former suture may be incomplete and a temporary ethmoidonasal fissure can be seen. (See 14[9] under the nasal bone, 10[24] under the frontal bone, footnote 125, 11[14``] for the perpendicular plates' part of the ethmoidonasal suture, and consult figure 3.9.)

Dorso-rostrally, the orbital lamina of the ethmoid bone has a **slender rostral (paramedian) process** (**11**[7`]). This slender paramedian process tapers rostrally into a point, similar to the process of the tectorial plate (11[2```] , vide supra) but more rounded. In old animals it can extend rostrally up to the level of the nasoincisive incisure (13[10]). It is fused laterally to the ethmoid crest (14[8]) of the nasal bone. Medially, the process and a large surface area of the orbital plate renders attachment for the dorsal nasal concha (vide infra under 11[21]).

In one old bull studied, the slender paramedian processes (11[7`]) of the orbital plates and the rostral process of the tectorial plates (11[2```] , vide supra) were fused into a single combined but wider structure. It appeared therefore as if the tectorial plate in that case also had a complete rostral nasal section and not just a fundic section with a rostral process. In that particular bull with this aberration, the combined much wider process, also extended rostrally, and also only to the level of the nasoincisive incisure (13[10])*[115] .

The ventral **basal plate** (*Lamina basalis* **11**[8]) has a fundic section only.

The dorsal internal surface forms the floor of the nasal fundus (13[13]) to the right and to the left of the nasal septum (vide infra). The ventral external surface of this plate is fused to the

115 The aberration found in the case of one bull, might be an indicator of age or just a rare exception to the rule. It does appear however in general, as if the rostral process (11[2```]) and the slender paramedian process (11[7`]) - and the extent to which they project rostrally either on an individual base or when fused to each other - are rather factors of advancing stages of ossification of the perpendicular plate. That aberration may also be linked to a larger than normal dorsal nasal concha.

rostrum [prae-]sphenoidale and rostrally it is also fused to the wings of the vomer (see also vomer). Even in animals as young as approximately three to four months of age, the sutures between the base plate, the vomer and the rostrum of the presphenoid bone (Sutura vomeroethmoidalis 12 [10] and Sutura sphenoethmoidalis 5 [9]) are hardly visible. (See also presphenoid bone and vomer.) In animals of approximately 16 months and older, these sutures cannot positively be identified anymore. Those parts of these sutures are therefore described as "invisible" sutures to distinguish them from other more visible components of these sutures. (See also footnote 38.) However, the particular part of the ethmoid bone (11 [5]) which is visible externally in the pterygopalatine fossa, may be an external part of the ontogenetically fused orbital and base plates that usually forms the dorsal quadrant of the sphenopalatine foramen (13 [31]).

The internal surface of the basal plate is subdivided by the attachments of the base-plates or basal laminae (11 [2`]) of the ethmoid turbinates into grooves (vide supra under 11 [2``]). The grooves form the peripheral boundaries of ventrally situated ethmoidal meatuses. A caudo-medial ethmoidal meatus may be more voluminous in some animals to form an enlarged recess. The recess then displaces the cortical layer of the basal plate of the ethmoid bone as well as the trabecular spongy bone of the body of the presphenoid bone. The large recess can then extend caudally up to the level of the optic canal (see 5 [7]) and the orbitosphenoidal crest (5 [4]). If a presphenoidal sinus (5 [10]) is simultaneously present in the rostrum of the presphenoid bone, it is then also displaced caudally by that enlarged recess. Such a recess can be present uni - or bilaterally, and accommodates an enlarged endoturbinate IV. (See 11 [18] and 11 [26] .)

The **cribiform plate** (*Lamina cribrosa* **11** [9]) lies in a transverse plane, forming the caudal wall of the nasal fundus (13 [13]). The plane of the cribiform plate is slanted rostro-dorsally at approximately 45 degrees (with the skull in the datum plane). The caudal surface of the cribiform plate is exposed to viewed from the cranial cavity through the partial constriction (10 [29]). The rostral surface of the cribiform plate can also be visualized but only after all the ethmoturbinalia have been broken away. The respective surfaces of the cribiform plate form the rostral boundary of the cranial cavity and the caudal boundary of the nasal cavity.

The rostral surface of the cribiform plate is divided into left and right convex halves by the caudal end of the perpendicular plate. Each half is oval in shape being wider dorsally than ventrally. The plate is perforated by groups of foramina. The groups of foramina are arranged around the caudal ends of the ethmoid turbinates where they attach to the rostral surface of the cribiform plate (vide infra). The turbinate attachments are arranged in clusters and therefore the rostral surface of the cribiform plate is irregularly grooved. The convex dorsal, ventral and lateral margins of the cribiform plate are fused to the frontal bone, the wing of the presphenoid bone and the body of the presphenoid bone respectively. These parts of the frontoethmoidal (10[21]) and sphenoethmoidal (5[9]) sutures have the tendency to ossify early in life. In animals of approximately 16 months and older, only that part of the sphenoethmoidal suture between the wing of the presphenoid and the lateral convex margin of the cribiform plate, may remain visible. More parts of these sutures can be seen in animals of approximately three to four months of age, but even then they are so ill defined that no positive identification of any other specific sutures can easily be made macroscopically.

The caudal surfaces of the bilaterally symmetrical halves of the cribiform plate are concave. They form the rostral borders of **ethmoidal fossae** (*Fossae ethmoidales* **11**[10]), as separated by the gallic crest (vide infra under 11[15]). The fossae harbour the **most rostral extent of the cranial cavity** (**11**[11]). It is demarcated from the rostral part of the cranial cavity (5[12]) by the frontal and ethmoidal parts of the partial constriction (10[29] & 10[29`]). (Also see footnotes 43 & 46.) The constriction emphasises the ethmoidal fossae, clearly demarcating it from the rostral part of the cranial cavity. (See also 5[12] for the Fossa cranii rostralis, 4[1`] for the Fossa cranii media and 2[2`] for the Fossa cranii caudalis.) Usually, a single **ethmoid foramen** (*Foramen ethmoidale* **11**[12])(see also 13[27]) opens rostral to the constriction in the lateral walls of the fossae. In some sub-adults it may be paired to form **ethmoidal foramina** (*Foramina ethmoidalia* **11**[12`]). The foramen or foramina connect the cranial cavity to the orbit. (See 13[21], and also the orbital part of the frontal bone 10[17].)

Dorso-laterally, the ethmoidal fossae are somewhat wider, reflecting the oval shape of the rostral surface of the cribiform plate.

The **perpendicular plate** (*Lamina perpendicularis* **11** [13]) is an unpaired flat part of the ethmoid bone. It is roughly rectangular in a lateral profile, and it lies in the median plane. In young animals of approximately three to four months of age, it is cartilaginous except a very small caudal part directly in front of the gallic crest (11 [15] , vide infra). In growing animals, the perpendicular plate gradually becomes **ossified along a constantly advancing, and well defined, almost vertical line** (**11** [13`]). (See footnote 116.) However, even in old animals the most rostral part remains cartilaginous (see 11 [14``] , vide infra). In sub-adults and mature animals, the ossified left and right surfaces (facing the ipsilateral nasal cavities) are slightly concave (bilaterally) and the plate presents well demarcated dorsal, caudal, ventral and rostral borders. The plate then extends from the rostral end of the cranial cavity (from the gallic crest) to the level of the nasoincisive incisure (13 [10] and also see the nasal bone) to form - with contributions from the rostrum of the presphenoid bone as well as from the vomer - the **combined osseus part of the nasal septum** (*Septum nasi osseum* **11** [14]). (See also vomer and presphenoid bones as well as 13 [11] .) In old bulls the perpendicular plate measures approximately 200 mm long by 60 mm high. The thickness of the perpendicular plate varies from approximately 3 mm in the bi-concave centre to more than 10 mm along the peripheral borders. (In old bulls the ventral part of the plate can be as thick as 15 mm.) The ossified nasal septum as a whole consists of two layers of compact bone on the outside (Substantia compacta 1 [3`/4`]) with spongy bone (Substantia spongiosa 1 [5`] ) between these layers. Dorsally, rostrally and ventrally the spongy bone is of a trabecular type (Spongiosa trabeculosa 1 [5`a]). Caudo-ventrally, the trabecular spongy bone is continuous with the trabecula of the body and the rostrum of the presphenoid bone. (See also presphenoid bone and footnote 38)* [116] .

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[116] It appears as if the ossification of the presphenoid bone, the rostrum [prae-]sphenoidale as well as the perpendicular lamina of the ethmoid bone is continuous, i.e. without the intervention of a sphenoethmoidal suture or a synchondrosis. Dissections on the calves of three to four months of age, at least seem to confirm a single coalesced cartilaginous centre for these parts. In animals of that young age, only the gallic crest and a small caudal part of the perpendicular lamina are ossified and the continuity of the cartilaginous rostrum [prae-]sphenoidale and perpendicular lamina as a uniform structure can be clearly seen. (See figure 3.8). Deducted from the above, one can reason that the yet-to-ossify part of the perpendicular plate as a whole, may be considered as a synchondrosis per se, even in the absence of any bones more rostral than the perpendicular plate itself. (See **footnote 38**.) At three to four months of age, the cribiform - and basal plates, and all the smaller endo- and ectoturbinates, are also still cartilaginous. Further details of the ossification stages of the tectorial - and orbital plates were not studied.

Centrally, the perpendicular lamina may only be bi-lamellar (without a trabecular component), or the lamellae may even be fused to each other, to form a single layer of compact bone.

The **dorsal border of the perpendicular plate** (**11** [14`]) is continuous with the rostral process (11 [2```]) of the tectorial plate (vide supra) which, in aberrant cases, can also be fused to the paramedian process of the orbital plates (see under 11 [7`]). Whatever the scenario, the dorsal border of the ossified part of the perpendicular plate articulates via the process of the tectorial plate (11 [2```]) with the ventral margin of the internasal suture (14 [5] , see nasal bone) at the perpendicular plates' part of the ethmoidonasal suture (11 [7]).
The **osseus rostral border of the perpendicular plate** (**11** [14``]) is "free" and it can be either straight or convex, often sloping ventrally in younger animals. The rostral part of the septum consists out of a brittle type of spongy bone. Obviously, in the live animal, this rostral part is continuous with the cartilaginous part of the nasal septum and is actually never a free border.

The **ventral part of the perpendicular plate** (**11** [14```]) is held in the middle and rostral sections of the vomeral or [septal] groove. (See 12 [6] under the vomer.) The lateral edges of the perpendicular plate, near the ventral border, are incompletely or only partially fused to the vertical part of the wings and the dorsal margin of the keel of the middle and rostral sections of the vomer (see vomeroethmoidal suture 12 [10]). The absolute ventral margin of the perpendicular plate is however free along its length. It remains separated from the most ventral part of the sulcus of the vomer to form the rostral part of the roof of a longitudinal canal, the vomeral canal (12 [11] and also see vomer). Caudally, the absolutely free ventral margin of the perpendicular lamina of the ethmoid bone is continuous with the ventral free margin of the presphenoid bone. In that region, the ventral margin of the presphenoid body therefore forms the caudal part of the roof of the vomeral canal (see paragraph following 5 [1]).

The **caudal border of the perpendicular plate** (**11** [14````]) is intimately fused to the cribiform plate, presenting on the caudal surface of the cribiform plate as a prominent free ridge, the **gallic crest** (*Crista galli* **11** [15]). This crest divides the caudal surface of the cribiform plate into right and left antimeres of the ethmoidal fossa (11 [10] , vide supra). Ventrally, the gallic crest is continuous with the sphenoidal crest (5 [3]) of the presphenoid bone. At the caudo-ventral angle of the perpendicular plate, no sutures whatsoever are formed between the perpendicular plate, the presphenoid bone, the tectorial, orbital, basal or cribiform plates. (See 11 [5] and footnotes 116 & 38.)

The combined osseus parts of the nasal septum (11 [14]), including the yet-to-be ossified part of the perpendicular plate, divides the nasal cavity in the median plane. The sides of the combined septum, face the ipsilateral common nasal meatuses to the left or the right respectively. (See Splanchnology elsewhere and 13 [11] under the Introduction to the Facial bones.)

The turbinates of the ethmoid bone **:**

The turbinate parts of the ethmoid bone are the most obvious and therefore the most striking parts of the ethmoid bone. They form the nasal conchae.

In general, the conchae are arranged as bilaterally symmetrically pairs of scrolls of bone, formed by internal folds or primary invaginations of the fundic section of the ethmoid bone. These - mostly horizontally orientated - invaginations, mainly take origin from the tectorial and orbital plates, and project medially into the nasal cavity. Each invagination has at least one proximal bi-lamellar attached end, or basal laminae (11 [2`]), and a distal free end. The free ends are dilated to various degrees, forming the conchae or turbinate bones itself. The turbinates, as spacious invaginations, enclose cavities of their own, or may communicate with the frontal sinus complex. Caudally, the primary invaginations and basal laminae of the tectorial and orbital plates are continuous caudally with folds of bone that ends on the rostral surface of the cribiform plate (vide supra). Together all the turbinates and their basal laminae form the **ethmoid turbinalia** (*Ethmoturbinalia* **11** [16]). The ethmoturbinalia subdivides the cavity of the nasal fundus into sub-compartments or **ethmoidal meatuses** (*Meatus ethmoidales* **11** [17]) which end in grooves on the insides of the tectorial and orbital plates (see 11[2``]). The basal laminae - most of which loses their bi-lamellar nature - separate the turbinates from the peripheral wall of the fundus for varying distances. The dilated parts of the turbinates are therefore positioned either more medially or more peripherally depending on the width of the basal laminae. These positions determine their classification **:** The most medial ones - which are also dilated more and which directly face the nasal septum and therefore the common nasal meatus (see also nasal cavity) - are classified as **endoturbinates** (*Endoturbinalia* **11**[18]). Decreasing in size from dorsal to ventral, they are numbered from I to IV (vide infra under 11[21/23/25/26])*[117]. All the other turbinates (approximately 20) are positioned more peripherally. They are much less dilated and can be very small and somewhat contorted. They do not face the common meatus (vide infra and see 13[17]) but each other and the fundic wall, to form **ectoturbinates** (*Ectoturbinalia* **11**[19]). Secondary (see 11[23`]) and tertiary evaginations of the ethmoidal meatuses - back into the dilated parts of the turbinates - form a complex of spaces. These evaginations can be either caudal or rostral in position, or over the length of the turbinates. Such evaginations may create the false impressions of subdivided or doubled ethmoturbinalia. Together, the complex of ethmoidal meatuses forms the **ethmoidal labyrinth** (*Labyrinthus ethmoidalis* **11**[20]). Endoturbinates I and II project rostrally beyond the fundic part of the ethmoid bone (vide supra). The former turbinate is fused laterally to the orbital plate (vide supra). The rostral parts (of both I and II) are porous.

The dorsal endoturbinate (**endoturbinate I**) forms the **dorsal nasal concha** (*Concha nasalis dorsalis* **11**[21]). Its basal lamina is attached via the slender rostral process (11[7`]) of the orbital plate to the ethmoid crest (14[8]) of the nasal bone (vide supra). The dorsal nasal concha encloses a large cavity, the **dorsal conchal sinus** (*Sinus conchae dorsalis* **11**[22]). The sinus communicates laterally by means of the large conchofrontal aperture in the lateral wall of the concha, with the rostral part of the frontal sinus complex. (See 10[31] and also see footnote 109.) Together they form the conchofrontal sinus (10[32]). Via the aperture it also

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117 By convention, the endoturbinates (11[18]) are shown in Roman numerals whereas the ectoturbinates (see 11[19]) are indicated in Arabic numerals, starting dorsally.

communicates indirectly with the dorsal compartment of the lacrimal sinus (15[16`]), but also with the nasal sinus (14[10]) when the later is present. (See also frontal, lacrimal and nasal bones.) A perpendicular septum - which is incomplete and inconstant - can subdivide the sinus partially into lateral and medial compartments. Rostrally the concha tapers to a sharp point to end at the level of the nasoincisive incisure (13[10]).

The second endoturbinate (**endoturbinate II**) forms the **middle nasal concha** (*Concha nasalis media* **11**[23]). It projects rostrally to the caudo-dorsal end of the ventral nasal concha (17[10]). The middle nasal concha is divided into caudal and rostral parts. The caudal part appears doubled because its medial surface presents a clear **secondary evagination** (**11**[23`]) of the common nasal meatus. The dilated rostral part encloses a cavity that forms the **middle conchal sinus** (*Sinus conchae media* **11**[24]). The middle conchal sinus appears in some animals to be an enclosed space, whereas in others is communicates caudally via a small opening with an ethmoidal meatus.

In medial view, the dorsal concha separates the dorsal nasal meatus (Meatus nasi dorsalis 13[14]) from the middle nasal meatus (Meatus nasi medius 13[15]). The middle nasal concha divides the caudal part of the middle nasal meatus into dorsal and ventral branches (13[15`] and 13[15``]). The dorsal branch (13[15`]) ends blindly at the cribiform plate. The ventral branch (13[15``]) continues between the middle and the ventral conchal bones to join the caudal part of the nasal cavity at the nasopharyngeal meatus (Meatus nasopharyngeus 13[6]). The rostral part of the middle nasal meatus is situated between the dorsal (11[21]) and the ventral (17[10]) nasal conchae. Individually, the dorsal, middle and the ventral nasal meatuses, communicates freely with the common nasal meatus (Meatus nasi communis 13[17]), and by that indirectly with each other.

The third endoturbinate - **endoturbinate III** - (**11**[25]) is small. Its medial surface also presents a secondary evagination of the meatus, giving the false impression that it is a doubled concha too.

Endoturbinate IV (**11**[26]) is usually the smallest of the endoturbinates. However in some individuals it is enlarged (not illustrated), in which case it extends caudo-ventrally. This occurs at the expense of the size of the rostrum of the presphenoid bone. (Vide supra in the second paragraph following 11[8] , and also see presphenoid bone.)

The spaces surrounded by Endoturbinates III and IV, and by the ectoturbinates, communicate with the ethmoidal cells that surround the ethmoid bone. In turn, they once again communicate via multiple smaller openings (10[33]) with the labyrinth of ethmoid meatuses (11[20]).

12. THE VOMER

(*VOMER*)

(See figures **3.38 & 3.39**. Also see 3.1, 3.8, 3.32, 3.33, 3.60 & 3.63.)

The vomer is considered to be an unpaired bone, yet it has an unpaired **keel** (*Crista vomeris* **12**[1]) ventrally and paired **wings** (*Ala vomeris* **12**[2]) dorsally. The whole vomer is longitudinally oriented in the skull with the keel in the median plane. For descriptive purposes, the vomer can be divided into caudal, middle and rostral sections. These sections are of unequal length and the divisions apply to both the keel and the wings. Two discretionary criteria are used for this. The one is obtained from a convenient point on the wings, the other from the way the keel is fused to the boney palate **:**

A **horizontal ridge** (**12**[3] , vide infra) on the lateral surface of the wings serves as reference point to divide the caudal from the middle sections of the vomer. This horizontal ridge also forms a division point rostral and caudal to which the wings of the vomer lie in sagittal and horizontal planes respectively.

The **division between the middle and the rostral sections** (**12**[3`]) of the vomer are determined by the junction of the free and the fused parts of the ventral margin of the keel.

Transverse sections of the whole vomer in the caudal, middle and rostral sections are “T”, “Y” and “U” shaped respectively. The discussion that follows will consider the caudal, middle and rostral sections of the keel first, and then the wings **:**

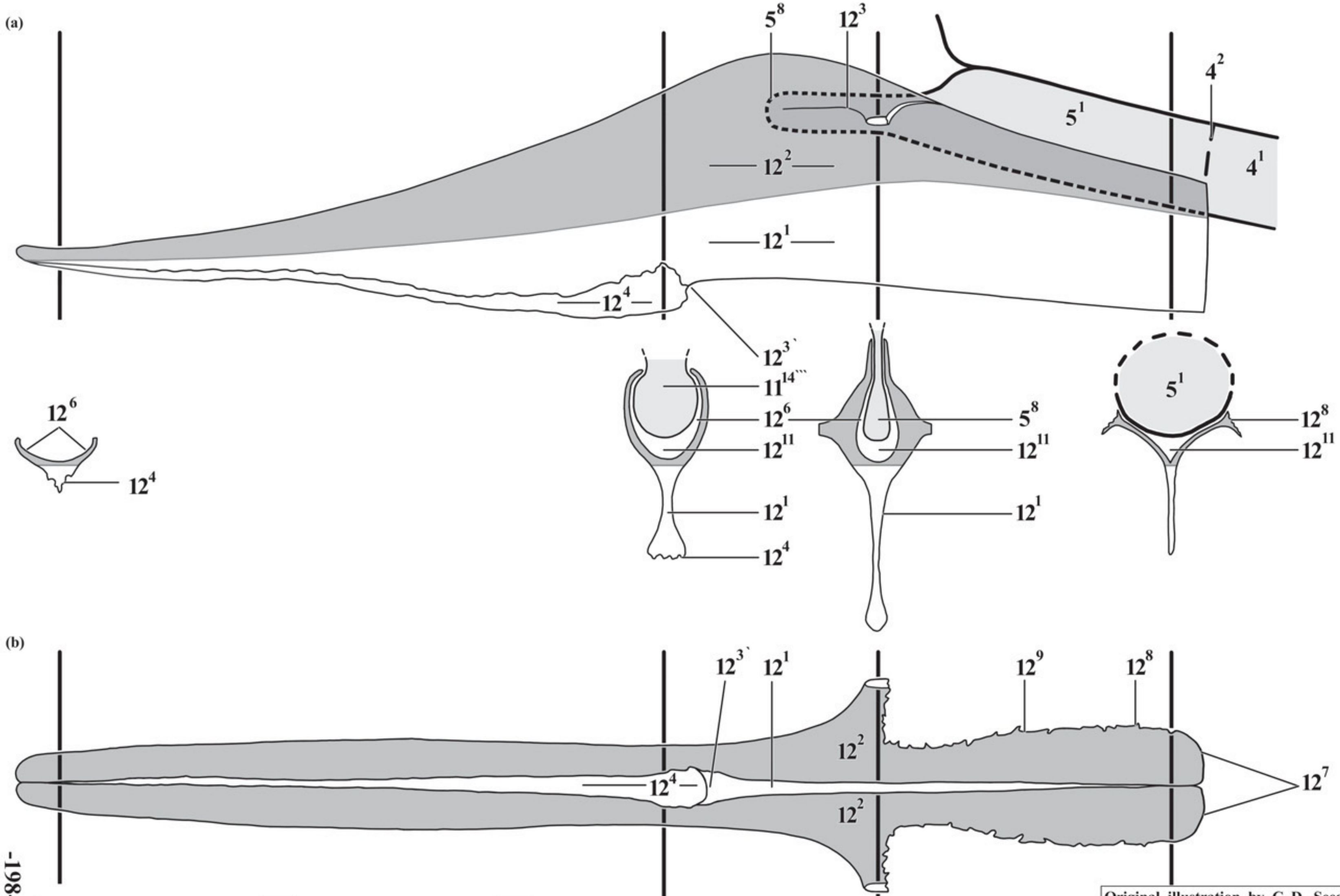
<u>The keel of the vomer</u> **:**

The keel is the most prominent part of the vomer. It is slender, laterally flattened and presents three margins. The caudal and the ventral margins are obvious to see. The third margin lies dorsally, in a groove formed between the wings of the vomer. The centre of the groove is taken as the dorsal margin of the keel. Even though the wings are incompletely (or in areas only partially) fused to the perpendicular plate of the ethmoid bone (11[13]), the central part

FIGURE 3.38 : OSTEOLOGY

LATERAL (a), VENTRAL (b) AND CROSS SECTIONAL VIEWS OF THE VOMER (SEMI-SCHEMATIC)

FIGURE 3.38 : OSTEOLOGY
LATERAL (a), VENTRAL (b) AND CROSS SECTIONAL VIEWS OF THE VOMER (SEMI-SCHEMATIC)

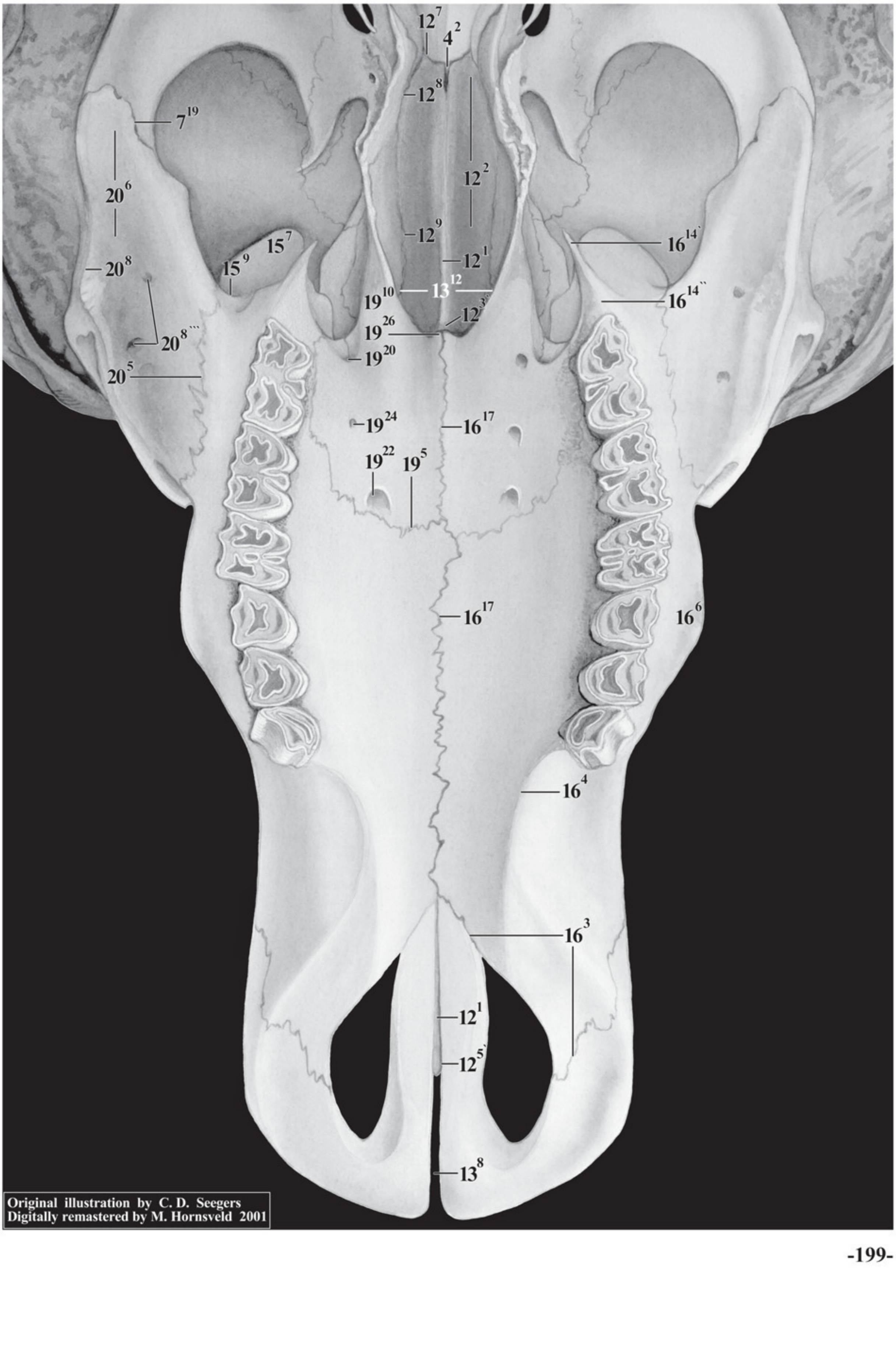


Vomer wings   Vomer keel   Basisphenoid body and perpendicular lamina of ethmoid bone

Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.39 : OSTEOLOGY

VIEW FIVE OF THE SKULL OF A MATURE BULL : THE CAUDAL VOMER IN SITU (VENTRAL VIEW)



of the groove, remains unfused and free. The exposed surfaces on the lateral sides of the keel face towards the left and right antimeres of the nasal cavity. These surfaces are roughly triangular in shape and are continuous with the lateral or the ventral (exposed) surfaces of the wings (vide infra). The middle and the caudal free sections of the keel, incompletely divides the osseus part of the caudal nasal opening or boney choana (Choana 13 [12])

The ventral margin of the rostral section of the keel is fused at the **vomeromaxillary suture** (*Sutura vomeromaxillaris* **12** [4]) to the median palatine suture of the boney palate. This suture lies partially embedded into the raised and prominently crested dorsal part of the median palatine suture (see 16 [23] under the maxilla). The ventral margin of the keel thereby becomes partially included into the boney palate itself. Furthermore, in some old bulls and even in some old cows, the most rostral part of the keel can be seen to extend rostrally beyond the maxillary part of the median palatine suture. In those cases it is then also fused to the caudal parts of the palatine processes of the incisive bone at the **vomeroincisive suture** (*Sutura vomeroincisiva* **12** [5]). This **specific fusion of the rostral end of the keel of the vomer** (**12** [5`]) is age related. Effectively, in older animals therefore, the vomer unquestionably contributes to the formation of the osseus rostral third of the boney palate. A small part of the keel can therefore, in those cases, be seen in ventral views of the palate. In actual fact, the vomeroincisive sutures are then seen on both sides of this visible part of the keel. Because the keel has a median position, the two sutures are therefore in paramedian positions. In prepared skulls of younger animals, it appears as if the vomer does not extend as far rostrally, but that is due to the palatine parts of the vomer and incisive bones that have not ossified yet. And therefore in those cases, the vomeroincisive suture appears to be not present in all cases. What is more important regarding these sutures, is that because these parts of the vomer and incisive bone do ossify in all cases - but only at a late stage in life - the interincisive fissure (13 [8]) is a actually a misnomer in the savannah buffalo. (See incisive bone, footnote 146 as well as **Discussion**, chapter four, point 15.)

The caudal section of the keel of the vomer is delicately thin and tends to disintegrate during the preparation of skulls. The caudal margin of the keel ends at a vertical line and is free.

The wings of the vomer **:**

The wings of the vomer are also divided into caudal, middle and rostral sections by the same discretionary points as discussed. (See 12[2] and12[3] above.) In the caudal section, the wings lie in near horizontally planes, but in the middle and rostral parts they lie in near sagittal planes (vide infra). The wings take origin from the dorsal end of the keel, presenting a free and a fused surface. In the rostral two sections, the free surfaces face laterally (towards the nasal cavity), whereas in the caudal section, the free surfaces face ventrally. And thus, in the middle and rostral sections, the wings present a dorsal margin, but in the caudal section, the wings present a lateral border. The dorsal margin of the keel, as well as the medial surfaces of the wings - at their bases - remain free and unfused. Together they form a longitudinal **vomeral** or **[septal] groove** (*Sulcus vomeris* [*septalis*] **12**[6]). The vomeral or [septal] groove is much deeper in the caudal part of the middle section of the vomer. Rostrally the groove is shallow but can be 10 - 15mm wide, depending on the thickness of the ventral part of the perpendicular plate of the ethmoid bone (11[14```]) which it holds. The rostral, middle and caudal parts of the [septal] groove, forms the floor of a longitudinal canal (vide infra under 12[11]).

The dorsal surface of the wings in the caudal section of the vomer is fused to the body (and the rostrum) of the presphenoid bone at the **vomerosphenoidal suture** (*Sutura vomerosphenoidalis* **12**[7]). The central part of the vomeral or [septal] groove - opposite the absolute ventro-medial margin of the body of the presphenoid bone - also remains unfused. That is therefore similar to the unfused central part of the groove, in the middle and rostral sections of the vomer (vide supra). The ventral surfaces of the wings of the caudal section, face ventrally towards the nasopharyngeal meatus (13[6]). The lateral border of the caudal section of the wings of the vomer, is fused (from caudal to rostral) to the larger process of the pterygoid bone, the perpendicular plate of the palatine bone and to the basal plate of the ethmoid bone. The respective sutures involved are the **vomero-pterygoidal suture** (*Sutura* *vomero-pterygoidalis* **12** [8])*[118], the **vomeropalatine suture** (*Sutura vomeropalatina* **12** [9]) and the **vomeroethmoidal suture** (*Sutura vomeroethmoidalis* **12** [10]). Although the former two sutures are clear to see even in old animals, the latter vomeroethmoidal suture cannot be seen. (Vide infra and also see pterygoid, palatine and ethmoid bones.) The vomerosphenoidal suture (12 [7]), at the caudal border of the wings, is always clearly visible. The suture lies superimposed over the intersphenoidal synchondrosis (4 [2]), or, in old animals, over the intersphenoidal synostosis (1 [19`]). (See also Hormion (H)*# and measurement §50 a & b, under section D **: Craniometric data**.)

The medial surfaces of the wings of the middle and rostral sections or the vomer, are fused to various degrees to the ventro-lateral aspects of the perpendicular plate of the ethmoid bone and to the rostrum of the presphenoid bone respectively. Rostrally, this fusion is usually incomplete. In the middle, it can be partial to complete, and caudally - especially in the region of the rostrum [prae-]sphenoidale - the fusion is intimate and complete. Even in animals as young as approximately three to four months of age, the sutures between the wings and the rostrum (at the vomerosphenoidal suture 12 [7]) and the ethmoid (at the vomeroethmoidal suture 12 [10]), are hardly visible. In animals of approximately 16 months of age, the vomeroethmoidal suture (12 [10]) cannot positively be identified anymore. (See footnote 38 and the paragraph following 11 [8] under the ethmoid bone.) In total contrast, is that neither the ventral margin of the perpendicular plate nor the rostrum or body of the presphenoid bone is fused in that region of the absolute median plane that faces the vomeral or [septal] groove. Together, these unfused margins form the roof of a longitudinal canal. The roof and the floor of this longitudinal canal form the respective boundaries of the **vomeral canal** (Canalis vomeris **12** [11])*[119]. The canal is therefore unpaired, lies in the

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118 The vomero-pterygoidal suture (Sutura vomero-pterygoidalis 12 [8]) is not listed in the *N.A.V.* (See also **footnote 42**.)

119 This longitudinal vomeral canal (Canalis vomeris 12 [11]) must not be confused with the vomeral or [septal] groove although the latter forms the floor of this canal. A vomeral canal is not listed in the *N.A.V.* (See also **footnote 36**.) On macroscopic dissection of two latex injected specimens of approximately 3 - 4 months old, it was found that this canal contains adipose tissue, two small arteries and some delicate loose connective tissue. No nerves were observed macroscopically. On these dissections it was also shown that ossification between the vomer (on the one side), and the presphenoid bone and the perpendicular plate of the ethmoid bone (on the other side), was incomplete. That status quo of the degree of fusion between these bones, remains like that till maturity.

median plane and extends over the whole length of the vomer. Caudally, the canal measures 2 - 3 mm in diameter in prepared skulls of old animals. In the middle and rostral sections of the vomer, the canal is much more voluminous.

The horizontal ridge (12[3] , vide supra) on the lateral surfaces of the vomer wings, arise at the level of the rostral end of the presphenoid bone but peters out further rostrally, to end in the region of the middle section of the vomer. The free edges of the horizontal ridges divide the lateral surfaces of the wings of this middle section into dorsal and ventral parts. The ventral part is continuous with - and in the same plane as - the ventral surface of the wing of the caudal section. The dorsal part is not only continuous with the lateral surface of the wing in the middle section, but caudo-laterally (dorsal to the free edge), it is also continuous with the internal surface of the basal plate of the ethmoid bone, and thus with the nasal fundus (13[13]).

The wings of the middle and rostral sections, and the keel of the caudal and middle sections, together with the whole perpendicular plate of the ethmoid bone - including the rostrum of the presphenoid bone - forms the osseus part of the nasal septum (Septum nasi osseum 13[11]).

The height of the keel as well as the height of the wings of the middle section of the vomer, exceeds the dimensions of wings-and-keels in the other two sections. The heights of the keel and the wings taper off rostrally. In lateral view, the vomer ends in a sharp point, but in dorsal view it is rounded.

The vomer extends from the rostral end of the basisphenoid bone, nearly to the apex of the skull, making it the longest of the cranial bones. Even though it is traditionally classified as a cranial bone, it does not contribute to the formation of the internal wall of the cranial cavity at all, and very little to the external wall.

13. INTRODUCTION TO THE FACIAL BONES (*OSSA FACIEI*)

(See figures **3.40 - 3.51**. Also see 3.7, 3.8, 3.11, 3.16, 3.17, 3.25, 3.32 - 3.34, 3.37 & 3.39.)

Counting the hyoid as a single bone, the nine **bones of the face** (*Ossa faciei* **13**[1]) are arranged around the nasal and oral cavities, forming the osseus face (*Facies* **13**[1`]). The bones of the face consist of the nasal, the lacrimal, the maxillary, the ventral nasal conchal, the incisive, the palatine, the zygomatic, the mandibular and the hyoid bones. They are all paired bones that fuse to their counterparts in the median plane. Of those, the body of the hyoid apparatus is an exception in that it is unpaired and that it lies over the median plane. (The hyoid also has paired antimeric parts.) With contributions of some bones of the cranium they form the **visceral part** (**[viscero-]cranium** **13**[2])* [120] of the skull. (See also 1[22] for [neuro-]cranium.)

The cribiform plate of the ethmoid bone (11[9]) separates the cranial cavity (1[1`]) from the nasal cavity. The **boney palate** (*Palatum osseum* **13**[3]) separates the **nasal cavity** (*Cavum nasi* **13**[4]) from the **oral cavity** (*Cavum oris* **13**[5]). Caudally, the palate is incomplete and the nasal cavity joins the nasopharynx via the **nasopharyngeal opening** (*Meatus nasopharyngeus* **13**[6]). Rostrally, the osseus palate seems incomplete in prepared skulls, due to the **palatine fissures** and the **interincisive fissure** (*Fissura palatina* / *Fissura interincisiva* **13**[7 / 8]) that can be seen at times. In the living animal, the nasally situated and paired vomero-nasal organs, drain via the incisive ducts, through the cartilage filled paramedian palatine fissures, to the oral cavity. How much of this cartilage belongs to the tubular part of the vomero-nasal organ, and how much belong to the palatine fissure itself, needs to be established histologically. That should prove whether it is a misnomer to recognize the palatine fissure. The interincisive fissure however, proofs to be a misnomer in the savannah buffalo as the interincisive suture does ossify later in life. (See incisive bone,

120 The term [viscero-]cranium (13[2]) is not listed as *N.A.V.* term. Nor is the term [neuro-]cranium (1[22]) listed, but these are handy alternative terms to use instead of "face" (Ossa faciei 13[1]) and "cranium"(Ossa cranii 1[1]), to distinguish the two parts of the skull when reference is made to both in the same text.

vomer and footnote 146.)

The nasal cavity is bounded dorsally by the nasal and frontal bones and laterally by the incisive, maxillary, lacrimal and palatine bones. Rostrally, the edge of the unpaired boney entrance to the nasal cavity, the **osseus rostral nasal opening** (*Apertura nasi ossea* **13** ^{9}), is bounded by the incisive and nasal bones and sometimes also partially by the maxillary bone. The dorso-lateral angle of the aperture includes the **nasoincisive incisure** (*Incisura nasoincisiva* **13** ^{10}).

Four cranial bones namely the frontal, ethmoid, vomer and presphenoid bones, extend rostrally into the facial region, contributing partially in the formation of the face. Although the frontal bone forms part of the facial surface externally, it does not contribute to the walls of the nasal cavity internally. Similarly, the zygomatic bone - as a facial bone - contributes to the formation of the facial surface (externally), but it does not contribute to the internal surface of the wall of the nasal cavity. In the nasal cavity, parts of the above mentioned cranial bones namely the ethmoid, the vomer and the presphenoid bones, form an incomplete but combined **boney nasal septum** (*Septum nasi osseum* **13** ^{11}) in the median plane. (See also 11 ^{14} , 5 ^{8} and the vomer.) Caudally, the combined septum incompletely divides the nasopharyngeal opening (13 ^{6}) as the keel of the vomer is not fused to the caudal palatine part of the boney palate. At the nasopharyngeal opening, the vomer only partially divides the roof of the **osseus caudal nasal opening** (*Choana* **13** ^{12}) which - at least osteologically speaking - remains undivided. Caudo-dorsally, the nasal septum divides the blind ending **nasal fundus** (Fundus nasi **13** ^{13})* [121] into right and left compartments. Each half of the nasal cavity is further subdivided - by the ventral and ethmoidal conchae I & II - into **dorsal, medial, ventral** and **common nasal meatuses** (*Meatus nasi dorsalis / medius / ventralis / communis* **13** $^{14/15/16/17}$). The middle nasal meatus is divided into **dorsal** and **ventral branches** (**13** $^{15`}$ and **13** $^{15``}$) by the middle nasal concha. The nasal fundus is subdivided by the ethmoturbinalia

121 The term Fundus nasi (13 ^{13}) is not listed in the *N.A.V.* The nasal fundus is the most caudal part of the nasal cavity, caudal to the internal constriction (11 ^{1}) which also divides the tectorial and orbital plates of the ethmoid bone into rostral nasal and caudal fundic sections. Apart from the dorsal and middle nasal conchae that also project rostrally beyond the borders of the nasal fundus, the fundus renders attachment to all 24 ethmoturbinalia. (See **footnote 111**.)

into ethmoidal meatuses (11 [17]). The subdivisions of the nasal cavity and the nasal fundus are incomplete as none of the conchae reach - or are fused - to the nasal septum. Therefore, all the nasal meatuses communicate medially with each other.

The mandible and the hyoid apparatus form the rostral and the caudal components respectively of the ventral part of the face. The antimeres of the mandible articulate caudally by means of paired synovial joints (1 [21]) of an incongruent sellar or saddle type with the squamous parts of the temporal bone. Articulation is via articular discs, and the rigid intermandibular suture makes it a functional condylar joint. The hyoid lies more caudally, between the rami of the mandible, and articulates by means of a fibro- cartilaginous joint (1 [18]) of a symphysis type (22 [10]), with the petrous part of the temporal bone. The symphysis does not ossify even at old age. A whole range of other articulation types, is encountered in the mandible and the hyoid apparatus **:** Rostrally, the intermandibular joint is a synchondrosis (1 [19] & 21 [28]) in young animals. Later in life, it appears to change either via a symphysis type of articulation (22 [10]) - or even a syndesmosis (22 [6]) - rarely to ossify into a partial synostosis (1 [19`] ). The types of articulations between the hyoid bones include synchondrosis (1 [19] & 22 [2`]), synovial joints (1 [21] , 22 [3`] & 22 [4``]) and a dense fibrous joint (1 [15]) of a syndesmotic type (22 [6]). The synchondrotic joints between the body of the hyoid bone and the thyrohyoid bones, ossify in late adulthood to form synostoses (1 [19`] , and also see 22 [2`] under the hyoid bone). The articulations between the bones of the face as well as their articulation with the cranial bones, are by means of fibrous joints (1 [15]) of different suture types (Sutura 1 [16]). Most of the sutures of the [viscero-]cranium, remain visible to various degrees throughout life. Some sutures fuse earlier in life, others only ossify very late in life or never at all, even in very old animals. The nasomaxillary and nasolacrimal sutures remain wide to form what could be regarded as permanent **nasomaxillary** and **nasolacrimal fissures** *(Fissura nasomaxillaris / nasolacrimalis* **13** [18/19]). These, as well as permanent fissures of the cranium and face, remain as fissures even in the skulls of very old savannah buffalo bulls. The nasolacrimal fissure, the interincisive "fissures" and the nasal septum (perpendicular plate of the ethmoid bone) are the last cartilaginous remnants of the original primordial skull to ossify. The palatine fissure never becomes closed off by ossification of its cartilage, not even in old animals.

The **orbital margin** (*Margo orbitalis* **13**[20]) is formed by the frontal, lacrimal and zygomatic bones. The walls of the **boney orbit** (*Orbita* **13**[21]) are formed by the frontal, lacrimal and zygomatic bones, as well as by a very small contribution from the palatine bone. Dorsal, medial, lateral and ventral parts (*Paries dorsalis /medialis /lateralis /ventralis* **13**[22 /23 /24 /25]) of the orbit, form from contributions of the various bones discussed above, but laterally and ventrally the osseus orbital wall is incomplete. The orbit is connected to the cranial cavity by the **optic canal** (*Canalis opticus* **13**[26]) and the **ethmoid foramen** (*Foramen ethmoidale* **13**[27]). (See also 11[12] and 11[12`] .) The orbit is connected to the nasal cavity by the **nasolacrimal canal** (*Canalis nasolacrimalis* **13**[28] )* [122] but also to the dorsum of the skull, by the **supraorbital canal** (*Canalis supraorbitalis* **13**[29] ). (See also 10[22`] under the frontal bone as well as footnote 105.)

Ventral to the orbit, the medial wall of the large **pterygopalatine fossa** (*Fossa pterygopalatina* **13**[30]) is formed by the palatine bone of the face together with the basisphenoid, presphenoid and pterygoid bones of the cranium. The fossa is connected to the cranial cavity by the **combined orbital and round foramen** (Foramen orbitorotundum 4[12]), to the nasal cavity by the very large **sphenopalatine foramen** (*Foramen sphenopalatinum* **13**[31]), to the facial surface of the maxilla by the **infraorbital canal** (*Canalis infraorbitalis* **13**[32]) and to the oral cavity by the **major palatine canal** (*Canalis palatinus major* **13**[33]). (Also see 16[28] and 19[21] for duplication of numbers 13[32] & 13[33] .) The contributions of the vomer and the pterygoid bone to the [viscero-]cranium, and not to the [neuro-]cranium, question the traditional classification of these bones as cranial bones.

The diploë of the nasal, maxillary, palatine and lacrimal bones are aerated to form paranasal sinuses. The sinuses are more voluminous caudally than rostrally to contribute largely to the pyramidal shape of the face. (See also subsection one for a synopsis of the cranial bones, as well as section B **: The Skull as a Whole**.) No **rostral bone** (*Os rostale* **13**[34]) or any other visceral bone - apart from sutural bones (see footnote 28) - was found in the head of the savannah buffalo.

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122 See **footnote 126** regarding the confusing issue around the (naso-)lacrimal canal that contains the membranous nasolacrimal duct.

14. THE NASAL BONE

(*OS NASALE*)

(See figures **3.41 & 3.42**. Also see 3.11, 3.32 - 3.34 & 3.37.)

The nasal bone is an elongated bone, having parallel lateral and medial sides. The nasal bone forms the dorsal third of the face. The dorsal surface of the nasal bone can be either flat or convex. Especially in some old bulls, the convexity of the nasal bone can be disfigured to form a distinctive feature that can be described as a "Roman nose".

The rostral end of the nasal bone is free and it has a shorter lateral and a longer medial process. The lateral border of the lateral process forms the dorsal border of the nasoincisive incisure (Incisura nasoincisiva 13^{10}). This lateral process of the nasal bone decrease in size with age, increasing the angle of the incisure and therefore also the size of the rostral nasal osseus opening (13^{9}).

The lateral border of the nasal bone articulates rostrally with the maxillary bone at the **nasomaxillary suture** (*Sutura nasomaxillaris* **14** ^{1}) and caudally with the lacrimal bone at the **nasolacrimal suture** (*Sutura nasolacrimalis* **14** ^{2}). (See also maxilla and lacrimal bones.) The sutures are wide and they form the **nasomaxillary** and the **nasolacrimal fissures** (*Fissura nasomaxillaris* / *nasolacrimalis* **14** $^{3/4}$) respectively. The latter fissure remains un-ossified even in very old bulls ***** [123] .

The caudal border of the nasal bone is fused to the nasal margin (10^{27}) of the (larger)

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123 In some animals, the lateral border of the nasal bone is not only fused to the maxilla and the lacrimal bones with the potential to leave nasomaxillary and nasolacrimal fissures **:** Rostral to the nasomaxillary suture, the nasal bone may in some cases also be fused for a short distance to the nasal process of the incisive bone at the nasoincisive suture (18^{7}). (Also see 16^{3} under the maxilla.) This occurs when the nasal process of the incisive bone (18^{6}) is longer than usual. A nasoincisive suture may also become a nasoincisive fissure ($18^{7'}$), which logically would be a rostral extension of a nasomaxillary fissure (14^{3}). A nasoincisive fissure ($18^{7'}$) is not listed in the *N.A.V.* The variable length of the nasal process of the incisive bone may affect the size of the rostral nasal osseus opening (13^{9}) and the angle of the nasoincisive incisure. (See also section D **: Craniometric data**, FINAL COMMENT 14 and measurement §70.) A nasoincisive suture is typically found in the goat. (See also chapter four **: Discussion**, point 4.) In young calves of approximately 3 to 4 months of age, a large part of the nasal bone near the nasomaxillary suture, appears un-ossified. (See figure 3.8.) This un-ossified part at the rostral end of the nasal bone, may be an early indicator of a nasoincisive fissure to form in later life.

external nasal part of the frontal bone (10 [24`]) at the frontonasal suture (Sutura frontonasalis 10 [26]). (See also frontal bone.)

The left and right nasal bones are fused along their medial borders at the **internasal suture** (*Sutura internasalis* **14** [5]). The internasal suture - at the internal surface of the medial borders of the nasal bone antimeres - is fused ventrally to either the tectorial or the perpendicular plates of the ethmoid bone, at the perpendicular plates' part of the ethmoidonasal suture (Sutura ethmoidonasalis 11 [7]). This fusion between the nasal bone and the ethmoid is either directly to the unpaired long and slender rostral process of the tectorial plate of the ethmoid bone (11 [2```]) (in the caudal part of the internasal suture) or directly to the cartilaginous part of the perpendicular plate (in the rostral part of the nasal septum). (See also under 11 [13] up to 11 [14``] for variations in degrees of ossification of the perpendicular plate, and footnote 115 for age significance of the length of the rostral processes of the ethmoid bone.)

In a cross section of the nasal bone, the **external surface** (*Facies externa* **14** [6]) of the nasal bone is prominently convex from medial to lateral. The **internal surface** (*Facies interna* **14** [7]) is concave and it follows the contours of the external surface fairly well, although these surfaces are not exactly parallel to each other in all ages and over the whole length of the bone. In young animals of approximately two years of age, the internal surface is excavated to such an extent - due to remodelling of especially the central part of the bone - that this surface breaks through onto the external surface, creating a **temporary longitudinal nasal fissure** (**14** [7`])* [124] . The medial and the lateral borders of the internal surface of the nasal bone are raised, to form two parallel longitudinal ridges. The lateral ridge on the internal surface of the nasal bone is more prominent and it forms the **ethmoidal crest** (*Crista ethmoidalis* **14** [8]). The rostral part of the crest is free, especially in young animals, but the caudal part is always fused for a variable distance at the ethmoidonasal suture (Sutura

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124 The temporary longitudinal nasal fissure of the nasal bone is not a true fissure. That is because it does not lie on a suture line, but almost in the centre of the bone itself. It appears to be caused by increased osteolytic activity of the peri-and endosteum in animals of approximately 2 years of age, when remodelling of bone occurs fast. (See **footnote 112** for similar cases involving the ethmoid and orbital parts of the frontal bone. Also see **Discussion**, chapter four, point 23.)

ethmoidonasalis 11 [7]) to the dorsal nasal concha (11 [21]). This fusion to the dorsal nasal concha is via the slender rostral (paramedian) process (11 [7`]) of the orbital lamina. In older animals, the rostral part of the crest can also be fused to this process when the dorsal concha is large. (See footnote 115). In young animals between the ages of approximately 16 to 24 months, the suture may be incomplete and a **temporary ethmoidonasal fissure** (Fissura ethmoidonasalis **14** [9])* [125] can form. (See also paragraph following 10 [24] under the frontal bone, as well as 11 [7] for the ethmoidonasal suture under the ethmoid bone.) Caudally, the internal surface of the nasal bone dorso-medial to the crest, is usually only partially covered by the orbital and the tectorial plates of the ethmoid bone. In some extremely old animals - or specific individuals where these parts of the ethmoid bone are more extensive - the internal surface of the nasal bone can be covered further rostrally than usual by these plates. Covering of the interior of the internal surface of the nasal bone can then extend up to the level of the nasoincisive incisure (13 [10]). (Also see ethmoid bone and footnote 115.)

The caudal part of the nasal bone can be aerated in some animals to form a **nasal sinus** (Sinus nasalis **14** [10]). (See footnote 27.) It communicates laterally with the dorsal part of the lacrimal sinus (15 [16`]) and the dorsal conchal sinus (11 [22]) and indirectly therefore also with the frontal sinus. The nasal sinus therefore constitutes a nasal part of the frontal sinus complex (Sinus frontalis 10 [31]). (See footnote 108.) A double layered median septum (9 [11]) separates the left and right sinuses of the nasal bones as it does for the other components of the frontal sinus complex. The nasal sinuses can be present even in young heifers of approximately 16 months of age.

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125 The ethmoidonasal fissure (Fissura ethmoidonasalis 14 [9]) is not listed in the *N.A.V.* In the live animal, mucoperiosteum and a layer of nasal mucosa, closes off this temporary fissure. No histology was done to determine the extent of the cartilaginous component of the fissure at that age. (See also **footnotes 130 & 144**.)

15. THE LACRIMAL BONE

(*OS LACRIMALE*)

(See figures **3.26, 3.32 - 3.34, 3.36, 3.37 & 3.40**. Also see 3.39.)

The external and internal layers (Lamina externa / interna 1 $^{3/4}$) of the lacrimal bone contribute to form smaller parts of the orbit, the face and the nasal wall. The lacrimal bone is aerated by two different sinus complexes. Only at the rostral borders are the laminae not separated from each other. Elsewhere, the diploë has been displaced by the sinus complexes, leaving only a single firm septum of bone that lies essentially in the middle of the bone. Functionally, the septum of bone not only separates the two sinus complexes, but also renders strength by connecting the widely separated internal surfaces of both the external and the internal laminae. The external surface of the external lamina, forms the ventral and ventro-medial parts (Paries ventralis 13 ^{23}) of the boney orbit (13 ^{21}), and a caudal part of the face (vide infra under 15 ^{1} and 15 ^{8}). The external surface of the internal lamina forms a caudal part of the lateral nasal wall (vide infra under 15 ^{13}). A process of the lacrimal bone contributes to the formation of a boney pillar-like strut. (See the 'infraorbital pillar' under 15 ^{17} and footnote 132.) This pillar renders biomechanical support to the caudal ipsilateral superior dental arch.

The **orbital surface** (*Facies orbitalis* **15** ^{1}) is concave. Medially it is fused to the orbital part and process respectively of the frontal (10 ^{16}) and palatine bones (19 ^{16}) at the frontolacrimal (Sutura frontolacrimalis 10 ^{18}) and palatolacrimal sutures (Sutura palatolacrimalis 19 ^{17}). Laterally it is fused to the orbital part (20 ^{3}) of the zygomatic bone at the **lacrimozygomatic suture** (*Sutura lacrimozygomatica* **15** ^{2}). (See also zygomatic bone.) For descriptive purposes, it is convenient to divide the orbital surface of the lacrimal bone into rostro-medial and caudo-ventral parts **:**

The rostro-medial part forms part of the ventro-medial wall of the boney orbit (13 ^{21}). It has two shallow fossae. The **fossa for the ventral oblique muscle of the eye** (*Fossa m. obliqui* *ventralis* **15** [3]) lies near the orbital process of the palatine bone and the **fossa for the lacrimal sac** (*Fossa sacci lacrimalis* **15**[4]) lies near the orbital margin. None of these fossae are clearly defined. In old animals the fossa for the lacrimal sac is 10 - 15 mm away from the orbital margin. The fossa of the lacrimal sack leads to the **lacrimal foramen** (*Foramen lacrimale* **15** [5]), and the foramen continues further rostrally as the boney part of the **lacrimal canal** (*Canalis lacrimalis* **15** [6]). The canal is situated within the external lamina of the lacrimal bone. (Vide infra for the rostral opening of the (naso-)lacrimal canal under 15 [14``])* **[126]** .

The caudo-ventral part of the orbital surface of the lacrimal bone forms the ventral wall of the boney orbit (13 [25]). A caudal projection of the caudo-ventral part, forms the free and blunt ending, but thin walled, **lacrimal bulla** (*Bulla lacrimalis* **15**[7]). In young animals the wall of the bulla is membranous. It lies directly dorsal - but in close proximity to - the maxillary tuber. The bulla projects caudally beyond the level of the maxillary tuber (16 [13]) except when the latter contains developing molar teeth. (See the maxilla.) In old animals, the lacrimal bulla is evenly ossified and consists of compact bone. On close inspection of the lacrimal bulla, a lacrimomaxillary suture (vide infra under 15 [9]) may be found as proof that the ventral half of the bulla of some old animals is in fact formed by a dorsal part of the maxillary tuber * **[127]** . The medial surface of the bulla faces the pterygopalatine fossa (13 [30]) whilst the lateral surface faces the temporal process of the zygomatic arch. (See also 20 [6] under the zygomatic bone.)

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126 The *N.A.V.* lists both a Canalis nasolacrimalis (13 [28] under the **Introduction to bones of the face**) as well as a Canalis lacrimalis (15 [6]) under the maxilla and under the lacrimal bones. The *N.A.V.* correctly also lists a **Ductus nasolacrimalis** under the Splanchnology. It would be less confusing to use one term only - the Canalis nasolacrimalis - for the osseus canal as also referred to under **footnote 122**. Furthermore, the *N.A.V.* presently lists the Foramen lacrimale as the caudal osseus opening (15 [5]) but no term is listed for the rostral opening (15 [14``]). It would therefore be less confusing if this shortcoming can be corrected too, by listing two osteological terms for these openings. In line with the latest terminology on human osteology, it is suggested to list the rostral and the caudal openings of the nasolacrimal canal as the **Ostium canalis nasolacrimalis rostrale / caudale** respectively. The canal is approximately 30 - 35 mm long in the savannah buffalo. The caudal opening is round and measures approximately 5 - 8 mm in diameter. The rostral opening lies immediately ventral to the level of the conchal crest (16 [21]), is oval, and measures approximately 8 mm by 15 mm. The level of the (naso-)lacrimal canal (15 [6]) forms the dorsal border of the proper part of the maxillary sinus (16 [26`]). (See also **footnotes 37, 105 & 106** regarding the supraorbital and optic canals where definitive terms should also be allocated to the respective ends of each of these osseus canals.)

127 An evenly ossified lacrimal bulla 15 [7] - that is also fused to the maxillary tuber (16 [13]) - is a good indicator of an aged animal.

The **facial surface** (*Facies facialis* **15**[8]) is concave from rostral to caudal and it has lateral, medial and rostral borders **:**

The lateral border (**15**[8`]) is fused to the facial surface of the zygomatic bone at the facial part of the lacrimozygomatic suture (15[2] , vide supra).

The medial border has rostral and caudal parts. The rostral part (**15**[8``]) is fused rostrally to the nasal bone at the nasolacrimal suture (Sutura nasolacrimalis 14[2]). Caudally, the medial border (**15**[8```]) of the lacrimal bone is fused to the nasal part of the frontal bone at the frontolacrimal suture (Sutura frontolacrimalis 10[18]). The nasolacrimal suture remains un-ossified even in very old bulls, forming a nasolacrimal fissure (Fissura nasolacrimalis 14[4]).

The rostral border (**15**[8````]) of the facial surface of the lacrimal bone is fused at the **lacrimomaxillary suture** (*Sutura lacrimomaxillaris* **15**[9]) to the maxilla.

The orbital and the facial surfaces of the lacrimal bone meet each other at the medial angle of the **infraorbital margin** (*Margo infraorbitalis* **15**[10])* [128] . The margin becomes increasingly prominent with age, especially in bulls. The **caudal lacrimal process** (*Processus lacrimalis caudalis* **15**[11]) projects laterally from this margin. In old animals the process has the tendency to blend with the protruding orbital margin. Dorsal to the process, a deep notch, the **infratrochlear incisure** (*Incisura infratrochlearis* **15**[12]), separates the infra- and supraorbital margins. The notch usually lies directly on the frontolacrimal suture (10[18]). In some very old animals with markedly protruding orbital margins, the incisure can be absent.

The **nasal surface** (*Facies nasalis* **15**[13]) of the internal lamina of the lacrimal bone has caudal, dorsal, rostral and ventral margins. The nasal surface and its margins can only be seen on a median view of the skull after the dorsal, middle and ventral conchal

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128 The infraorbital margin (Margo infraorbitalis 15[10]) is also listed under the zygomatic bone (under 20[4]). The supraorbital margin (10[8]) also becomes increasingly prominent with age. A complete protruding orbital margin is characteristic of old bulls.

bones have been removed **:**

The internal lamina of the nasal surface is fused caudally to the ethmoid bone and dorsally to the nasal bone. The sutures involved are the **lacrimoethmoidal suture** (Sutura lacrimoethmoidale **15** [14])* [129] and the nasolacrimal suture or fissure (Sutura / Fissura nasolacrimalis 14 [2 / 4]) respectively. (See also ethmoid and nasal bones.) In some animals the lacrimoethmoidal suture is incomplete to form a **small but permanent lacrimoethmoidal fissure** (Fissura lacrimoethmoidale **15** [14`])* [130] . (This fissure is not illustrated but see paragraph preceding 11 [7] .)

The rostral borders of the nasal and facial surfaces of the lacrimal bone coincide with each other, because the rostral part of the bone is not separated by diploë. The rostral ends of both these surfaces are fused - sharing the same suture - to a non-aerated part of the maxilla, at the lacrimomaxillary suture (15 [9] , vide supra). This suture can therefore be seen on medial and lateral views in very much the same place. The **rostral opening** (**15** [14``]) **of the boney part of the (naso-)lacrimal canal** ends - on the nasal side of the maxilla - on the lacrimomaxillary suture, just ventral to the level of the conchal crest of the maxilla (16 [21]). (Also see 16 [22] and footnote 126.)

The ventral margin of the nasal surface of the lacrimal bone is free along its whole length and it forms the dorso-rostral border of the larger permanent compound fissure of the lateral nasal wall between the lacrimal bone itself, the ethmoid, the palatine and the ventral conchal bones. (See the respective bones, 17 [3] , as well as footnotes 143 & 144.)

Rostro-ventrally a small area of the internal lamina of the lacrimal bone is fused in a sagittal plane to the body and process of the ventral nasal conchal bone at the **lacrimoconchal suture** (*Sutura lacrimoconchalis* **15** [15]). Caudal to this, the nasal

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129 The lacrimoethmoidal suture (Sutura lacrimoethmoidale 15 [14]) is not listed in the *N.A.V.*

130 The lacrimoethmoidal fissure (Fissura lacrimoethmoidale 15 [14`]) is not listed in the *N.A.V.* In the live animal, mucoperiosteum and a layer of nasal mucosa closes off this fissure. No histology was done to determine the extent of the cartilaginous component of the fissure. (See also **footnotes 125 & 144.**)

surface of the lacrimal bone itself forms the lateral wall of the boney canal (see 17[5-7]) which drains the maxillary sinus complex. (See also the ventral nasal concha bone and footnote 145.)

The single septum of bone - vide supra under the introductory paragraph - that connects the inner aspect of the nasal surface to the inner aspect of the external surface of the lacrimal bone, completely divides the **lacrimal sinus** (*Sinus lacrimalis* **15**[16]) into **dorsal** (**15**[16`]) and **ventral** (**15**[16``]) compartments. The septum of bone joins the external lamina along the route of the (naso-)lacrimal canal (15[6]). The septum and the position of the (naso-)lacrimal canal, determines the dorsal border of the proper part of the maxillary sinus (16[26`]).

The ventral compartment of the lacrimal sinus lies ventral to the orbit and extends caudally into the lacrimal bulla. Rostrally, it communicates directly with the proper part of the maxillary sinus (Sinus maxillaris 16[26`]) and therefore with the maxillary sinus complex (16[27`]). (See also maxilla and palatine bones, as well 20[9] under the zygomatic bone.)

The dorsal compartment of the lacrimal sinus lies medial to the orbit and it may be subdivided by smaller septa. Caudally, it communicates with the frontal sinus and therefore - indirectly - with the ethmoidal meatuses. Medially and dorsally, it communicates with the dorsal conchal and nasal sinuses if the latter is present. (See also footnotes 27, 108 & 147.)

In some individuals, a **smaller sub-compartment** (**15**[16```]) communicates with the ethmoidal cells medial to the orbit *****[131].

Taking origin from the internal surface of the orbital part of the lacrimal bone, a **rostro-**

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131 Note that the dorsal component of the lacrimal sinus (15[16`]) as well as this sub-compartment (15[16```]) does not communicate with the maxillary sinus complex, but only with the frontal sinus complex.

ventral process (**15^{17}**) - seen only in lateral view after the maxillary sinus has been exposed - projects rostro-ventrally into the maxillary sinus. It forms the lateral aspect of an **infraorbital pillar** (**$15^{17`}$**)* [132] . The lacrimal component of the infraorbital pillar is also fused caudo-medially to the orbital process (19^{16}) of the palatine bone.

132 An **infraorbital pillar** ($15^{17`}$) is not listed in the *N.A.V.* The infraorbital pillar as found in the savannah buffalo is a laterally flattened but wide pillar of bone that has **palatine, lacrimal, maxillary and ethmoid components**. The pillar extends in a rostro-ventral direction from the orbital region to the caudal end of the ipsilateral superior dental arc. The pillar serves the purpose as biomechanical strut during mastication as follows **:** The lacrimal and ethmoid components of the pillar are connected to the deep aspects of the orbit, and from there they can relay infraorbital pillar pressures to the external lamina of the frontal bone in the region of the frontal fossa (1^{14}). That region of the skull is overtly strong. The maxillary and palatine components in turn connect the distal end of the pillar to the ipsilateral lingual side of the caudal maxillary dental alveoli. Without this support, the already arched osseus palate would flex too much dorsally during chewing, because the width of the palate between the last upper molar teeth is much wider than what the strength of the palatine bones can deal with. Detail of the components that contribute to the formation of the infraorbital pillar is as follows **:** The medial wall of the infraorbital pillar is formed by the lateral septum ($19^{6```}$) of the horizontal part of the palatine bone and by a smaller part of the perpendicular lamina (19^{13}) of the palatine bone that lies in front of the sphenopalatine foramen. Both these palatine components project dorsally beyond the dorsal level of the palate, where they are fused to each other. Retaining some characteristics of their dual origin, they form the **rostral** (19^{7}) **and caudal** (19^{8}) **palatine parts** that form the **medial wall of the infraorbital pillar**. The orbital process (19^{16})of the palatine bone has a minor contribution to the caudo-medial aspect of the infraorbital pillar. The **lateral wall of the infraorbital pillar** is formed by the rostro-ventral process (15^{17}) of the **lacrimal bone**. Ventro-laterally, a short dorsal process (16^{34}) of the infraorbital canal (16^{28}) - with its supporting ventral septum on the lingual side of the dental alveoli - adds a **maxillary part** to the infraorbital pillar. Fusion of the pillar to the maxillary part is at the lacrimomaxillary suture (15^{9}). Dorso-medially, the infraorbital pillar is fused to a part of the orbital plate ($11^{3`\mathbf{b}}$) of the ethmoid bone at a part of the palatoethmoidal suture (19^{9}), to yield the **ethmoidal component of the infraorbital pillar**. In some animals the ethmoid component to the pillar is much larger than in others. At the rostral border of the pillar, the palatolacrimal suture (19^{17}) is intimately ossified even in young animals. (See also **Discussion**, chapter four, point 1.)

16. THE MAXILLARY BONE
(*MAXILLA*)

(See figures **3.6, 3.7, 3.11, 3.25, 3.26, 3.32 - 3.34, 3.36, 3.37, 3.39 - 3.42, 3.44 - 3.46 & 3.49**.)

The maxillary bone (or maxilla) is the largest of the facial bones and consists of a body with palatine and alveolar processes. The body forms a major rostral part of the skull. Ventro-medially, the palatine process of the maxilla forms the middle part of the boney palate (13 [3]). Ventro-laterally, the alveolar process forms the **alveolar margin** (*Margo alveolaris* **16** [1]) of the maxillary bone. The alveolar process harbours all the maxillary cheek teeth. The general shape of the maxilla and its processes, resembles that of a three-sided pyramid, presenting three triangular surfaces of interest **:** The lateral or facial surface (16 [5]) is convex, the medial or nasal surface (16 [20]) is strongly concave and the ventral palatine or oral surface (see footnote 134) is nearly flat. The bases of the triangular surfaces of the maxilla lie caudally and the apices rostrally. The apical parts of the three surfaces are fused to the incisive bone to form the apex of the skull. The apical half and another dorsal third of the **body of the maxilla** (*Corpus maxillae* **16** [2]), consists of non-aerated bone. The rest of the body, and the palatine process, is aerated by a sinus complex. Thereby, each of the three surfaces in the basal half of the pyramidally shaped maxilla, not only have external surfaces, but also internal surfaces to consider.

<u>The triangular lateral or facial surface of the maxilla.</u>

The base or caudal border of the lateral surface is fused to the zygomatic bone ventrally and the lacrimal bone dorsally, at the zygomaticomaxillary (20 [5]) and the lacrimomaxillary sutures (15 [9]) (Sutura zygomaticomaxillaris / lacrimomaxillaris) respectively. (See the zygomatic and lacrimal bones.)

The dorsal border of the lateral surface is fused caudally to the nasal and rostrally to the incisive bones. The former articulation is at the nasomaxillary suture (Sutura nasomaxillaris 14 [1]). (See also nasal bone.) The latter articulation forms the dorsal and major part of the **maxilloincisive suture** (*Sutura maxilloincisiva* **16**[3]). (See also 18[7] , footnote 123 under nasal bone, and vide infra for a ventral part of the maxilloincisive suture.) In some animals the nasal and the incisive bones do not meet and therefore part of the dorsal maxillary border can be free. That free edge of the maxilla then forms the caudal part of the ventral border of the nasoincisive incisure (13[10]). (See also incisive and nasal bones.) The free part on the dorsal border of the maxilla can be about 10 mm long.

The ventral border of the lateral surface has caudal and rostral parts. The caudal part not only borders, but also masks, the alveolar process of the maxilla (16[1]). The rostral part is demarcated from the lateral border of the ventral surface (vide infra) along the **interalveolar margin** (*Margo interalveolaris* **16**[4]) or **diastema** (**16**[4`] ). (See also 21[15`] for the mandibular diastema.)

The triangular ventral surface of the maxilla **:**

The base or caudal border of the ventral surface is concave rostro-caudally, and it is fused to the horizontal part of the palatine bone at the palatomaxillary suture (19[5]) (Sutura palatomaxillaris). (See also palatine bone.)

Caudo-laterally, the ventral surface borders and masks the alveolar process of the maxilla (16[9]). The rostro-lateral margin of the ventral surface is formed by the diastema (16[4`]). The diastema is concave caudally and convex rostrally.

The medial border of the ventral surface is fused in the median plane to its counterpart of the other side (vide infra under 16[17]). Together, the antimeres of the ventral surface of the maxilla, forms the middle part of the osseus palate.

The triangular nasal surface of the maxilla **:**

Being strongly concave from medial to lateral, the base or caudal border of the nasal surface extends from ventro-medially to dorso-laterally. The caudal border can be divided into medial, lateral and central thirds. (See 16[21] to 16[21``] for three ridges that divides the nasal surface into four unequal parts.)

Medially, the caudal border is fused to the palatine bone, dorsally to the lacrimal bone and centrally to the ventral conchal bone at the palato-, lacrimo- and conchomaxillary sutures respectively. (See 15 [9] and 15 [13] for detail about the lacrimomaxillary suture.) The conchomaxillary (17 [2`]) and palatomaxillary (19 [5]) sutures are incomplete, leaving a large permanent fissure (17 [2]). This fissure is therefore formed by merging defects of both the conchomaxillary and palatomaxillary fissures * [133] between these three bones. (See footnotes 143 & 144 under ventral conchal bone.)

The dorsal and dorso-rostral borders of the nasal surface coincide with the respective borders of the lateral facial surface of the maxilla, and articulate with the nasal and incisive bones at the nasomaxillary and maxilloincisive sutures respectively. (See 14 [1] and 16 [3] as well as footnote 123.)

The medial border of the nasal surface is fused in the median plane mainly to its antimeric counterpart, but also to part of the vomer. The sutures involved are the median palatine and the vomeromaxillary (12 [4]) sutures. The latter suture only occurs more dorsally, incorporated into the nasal crest (16 [23]). The arrangement of these sutures and how the vomer articulates with the maxilla but not the palatine bone, is important to note in the savannah buffalo. (Vide infra under 16 [23] and see vomer.)

The facial surface of the body and the tooth bearing parts of the maxilla **:**

The lateral or **facial surface** (*Facies facialis* **16** [5]) of the maxilla forms the largest part of the facial surface of the skull (vide supra for borders of the triangular surface). It is formed by the external surface of the external lamina of the body that also includes the non-aerated dorsal third and the apical half of the body. It is convex from dorsal to ventral and bears a large **facial tuber** (*Tuber faciale* **16** [6]) at the level of the third or fourth maxillary cheek teeth ($P^{\underline{4}}$ or $M^{\underline{1}}$). A rounded low ridge extends caudally from the tuber to the infraorbital margin (20 [4]) in a steady dorsal curve. It is more pronounced in old animals to form - what should be

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133 The conchomaxillary and palatomaxillary fissures are not listed in the *N.A.V.* (See **footnote 143 &144**.)

regarded - as a **facial crest** (*Crista facialis* **16**[7]). (The facial crest is not illustrated - consult figure 3.7 for the best lateral view of an old bull. See also 20[8] for the zygomatic part of this crest.) Dorsally and rostrally to the ridge and the tuber, the lateral surface of the maxilla is concave. In young animals the part of the lateral surface ventral to the ridge is slightly convex. In old animals however, it is always concave. Boney changes can reshape and / or erode this part of the external lamina of the maxilla. Reshaping can be so severe that proximal parts of the roots of the molar teeth can be exposed in some individuals. (Technically, it means that the masseter muscle then also takes origin from the roots of those exposed molar teeth. Protrusion of the proximal end of a mandibular cheek tooth root was also observed in one case on the medial side of the mandible. See 21[31``] and figure 4.2.) The **infraorbital foramen** (*Foramen infraorbitale* **16**[8]) lies rostral to the tuber, 35 - 50 mm dorsal to the alveolar margin of the first premolar tooth ($P^{\underline{2}}$). It is the primary rostral opening of the infraorbital canal (13[32] and vide infra under 16[28]). In some animals, this opening may be accompanied by a secondary smaller opening, usually ventral to the primary one. The caudal part of the alveolar margin (16[1] , vide supra) projects ventrally beyond the level of the palate as part of the **alveolar process** (*Processus alveolaris* **16**[9]). The alveolar process contains the teeth's sockets or **dental alveoli** (*Alveoli dentales* **16**[10]) for the six cheek teeth. The dental alveoli are hidden from view by the alveolar margin (16[1]) of the lateral surface of the maxilla that lies over it. Despite that, vertical orientated **alveolar ridges** (*Juga alveolaria* **16**[11]) on the facial surface, may etch the true roots (Radix dentes) of the cheek teeth in old animals. Individual alveoli are arranged from rostral to caudal, separated from each other by **interalveolar septa** (*Septa interalveolaria* **16**[12]). The alveoli are arranged in a slight lateral curve. In old animals the curvature is more marked between the last premolar and the first molar ($P^{\underline{4}}$ and $M^{\underline{1}}$). In young animals that part of the maxillary body that contains the alveolar process for developing molar teeth, projects caudally beyond the caudal extend of the boney palate. (See 13[3] and 19[4] under the palatine bone.) It forms the blunt ending and rounded **maxillary tuber** (*Tuber maxillae* **16**[13]). The last molar tooth to erupt, whether $M^{\underline{2}}$ or $M^{\underline{3}}$, develops from within the tuber before it erupts. The size of the tuber is therefore dependant on the stage of development (of either $M^{\underline{2}}$ or $M^{\underline{3}}$) which again depends on the age of the animal. The size of the maxillary tuber also depends on how far eruption of each of these molars has proceeded. $M^{\underline{1}}$ develops rostral to the tuber, and therefore never really affects the size of the tuber. After $M^{\underline{3}}$ has erupted, and as the animal ages, the ventral part of the maxillary tuber diminishes in size, while the dorsal part may become fused to the lacrimal bulla (15^{7}). The **medial surface** (*Facies pterygopalatina* **16**^{14}) of the tuber borders the pterygopalatine fossa (13^{30}) laterally. Ventrally, the tuber of young animals is rounded. In older animals, the tuber becomes laterally flattened, and the caudo-ventral margin of the tuber is remodelled to end in a **sharp caudo-ventral ridge** (**16**$^{14`}$). In old animals (after all the molars have erupted and the sharp caudo-ventral ridge has formed), the tuber is marked ventrally by a **triangular concave area** (**16**$^{14``}$). The rostral border of the triangular area is form by the third molar ($M^{\underline{3}}$). The lateral and medial borders of the triangle are formed by two lines that joint the sharp ridge.

In older animals, the once large tuber is less obvious, because of the following **:**

Relative to the horizontal part of the palatine bone, the alveolar processes of the cheek teeth as a whole, move more rostrally as the animal ages. Therefore in older animals, that part of the tuber that still projects caudally past the caudal extent of the boney palate, becomes smaller and smaller. Other factors, apart from relative movement of the alveolar process, also play a role in this phenomenon. The total volume of the remaining embedded parts of teeth continuously diminishes with age. That is governed by continuous eruption and wear of teeth, including contact surface wear and mesial drift. The result of all these natural events is that the maxillary tuber becomes less obvious. (See discussion on the relative positional changes of the palatine bone relative to the maxilla in the paragraph following the paragraph in which 19^{24} is discussed.)

<u>The palatine process of the maxilla and its two surfaces</u> **:**

The **palatine process** (*Processus palatinus* **16**^{15}) projects medially from the ventral part of the body and alveolar process, as two horizontal layers. It is extensively aerated except the **apical part** (**16**$^{15`}$). The **dorsal layer** (**16**$^{15``}$) forms part of the medial or nasal surface (vide infra) of the maxilla, whereas the **ventral layer** (**16**$^{15```}$) forms the oral or palatine surface of the maxilla (see also 19[3])*[134] . The process contains the voluminous **maxillary part of the palatine sinus** (*Sinus palatinus* **16**[16]). (See also 19[6] for the palatine part of the palatine sinus and 16[27] for the connecting aperture that links the palatine sinus to the larger proper part of the maxillary sinus 16[26`] .) That part of the palatine sinus contained in the palatine process of the maxilla has medial, caudal, lateral and rostral borders **:**

The medial and caudal borders of the sinus are formed by **vertical septa** (**16**[16`]) which connect the dorsal (16[15``]) and the ventral (16[15```]) layers *[135] . The lateral border of the sinus is formed by **another septum** (**16**[16``]) but this septum is incomplete. It is fused against the lingual surfaces of the cheek teeth alveoli, dorsal to which the palatine sinus communicates freely with the proper part of the maxillary sinus (vide infra under 16[26`]). The medial septa of the left and the right-hand sides fuse along the median plane to each other at an intermaxillary suture *[136] to form the middle or **maxillary part of the median palatine suture** *(Sutura palatina mediana* **16**[17]). (See also palatine and incisive bones for caudal and rostral parts under 19[6`] and 18[5] respectively, as well as footnote 146.) The antimeric median septa (16[16`]) form a **double layered palatine septum** *(Septum sinuum palatinorum* **16**[18]) which separates the sinuses of the left and right maxillary bones *[137] . The suture forms a raised and prominent ridge on the nasal side (vide infra under 16[23]). If the maxilla is considered in a lateral view, the rostral extent of the maxillary part of the palatine sinus ends at the level where the palatine and apical parts of the maxilla meet. This level lies halfway between the first permanent cheek tooth (P^2) and the caudal end of the palatine fissure (13[7]). Thus, in young animals, developing first and second permanent premolars (P^2 and P^3), can both be seen in the rostral part of the sinus in median views of skulls. Rostral to the sinus, the apical

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134 The *N.A.V.* does not list an (oral) palatine surface to the palatine process of the maxilla, but it would be convenient to do so.

135 The vertical septa form as result of exaggerated sutures that form on the lines where the palatine process fuses with the surrounding bones that contribute to form the osseus palate.

136 The *N.A.V.* does not recognize an intermaxillary suture, but it would be convenient to do so.

137 The *N.A.V.* does not distinguish between the pars maxillaris and the pars palatina of the suture, the septum or the sinus of the palate. It would be convenient to do so.

part of the palatine process of the maxilla diverges away from the median plane. Thereby, in combination with the palatine processes (18 ^{4}) of the incisive bone, two para-median palatine fissures form (see 13 ^{7}). At the caudal end of the diverging apical parts of the maxilla, the palatine processes of the incisive bones are fused to the maxilla at a ventral part of the maxilloincisive suture (see 16 ^{3} for dorsal and major part of this suture)* [138] . These sutures are well ossified in old animals, but in younger animals - even as old as 2 years - the terminal ends of these processes of the incisive bone are still cartilaginous. In prepared skulls of young animals, these incisive parts boil away and therefore it may appear falsely as if the palatine fissures of the left and right-hand sides are confluent with each other.

The caudal septum (16 $^{16`}$) of the maxillary part of the palatine sinus is fused to a similar septum of the horizontal part of the palatine bone (19 $^{6``}$) at the palatomaxillary suture (19 ^{5}), to form a **double layered transverse septum** (**16** ^{19}). The septa of both components of the transverse septum are incomplete laterally, allowing free communication between the maxillary part of the palatine sinus and the palatine sinus of the palatine bone. (See also 19 ^{6} under the palatine bone.)

The nasal surface of the maxilla **:**

The medial or **nasal surface** (*Facies nasalis* **16** ^{20}) of the palatine process of the maxilla (vide supra for borders of the triangular surface) is concave from dorsal to ventral. The nasal surface is divided into four unequal parts by three longitudinal ridges. The three ridges are positioned dorsally, medially and intermediately. They all diverge caudally **:**

The dorsal ridge is the **conchal crest** (*Crista conchalis* **16** ^{21}) and it extends from the rostral nasal osseus opening (13 ^{9}) to the lacrimomaxillary suture (15 ^{9}). The rostral part of the ridge is free. Caudally, the ridge is fused to the process (17 ^{4}) of the ventral conchal bone that gives origin to the basal lamina (17 ^{8}) of the conchal scrolls. The conchal crest and the

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138 The *N.A.V.* does not distinguish between the different parts of the maxilloincisive suture (16 ^{3}). It would be convenient to do so because - at least in the prepared skull - it appears as three totally separate sutures.

basal lamina separates the middle and the ventral nasal meatuses (see 13[15 & 16]).

The **medial ridge** (**16**[21`]) (not illustrated) on the nasal surface of the maxilla, takes origin from the caudal end of the palatine fissure and extends caudally to join the medial palatine suture (16[17]). It joins the medial palatine suture at the level of the first premolar tooth (P^{2}), where it merges with the nasal crest (16[23], vide infra).

The **intermediate ridge** (**16**[21``]) (not illustrated) is rounded. In young animals it is inconspicuous.

The four parts of the nasal surface - divided by the above three ridges - have the following characteristics **:**

The surface dorsal to the conchal crest is slightly concave and it forms the dorsal part of the lateral nasal wall, facing medio-ventrally.

The surface between the conchal crest and the intermediate ridge is strongly concave. It overlies the palatine part of the maxillary sinus, and in young animals this surface can be very thin. It forms the ventral part of the lateral nasal wall and the lateral part of the floor of the nasal cavity. Caudally, this surface contains the **lacrimal groove** (*Sulcus lacrimalis* **16**[22]). The groove lies immediately ventral to the level of the conchal crest (16[21]). Caudally, the groove leads to the rostral opening of the boney (naso-)lacrimal canal (15[14``]) on the nasal side of the lacrimomaxillary suture. (See footnote 126.)

The surface between the intermediate and the medial ridge is also concave and forms the major and medial part of the floor of the nasal cavity. Its caudal part overlies the palatine part of the maxillary sinus (16[26], vide infra).

The surface area medial to the medial ridge forms a minor part of the floor of the nasal cavity (only rostrally). This surface area faces dorsally.

Both the intermaxillary (16[17] and see footnote 136) and the interpalatine (19[16`]) parts of the median palatine suture, is raised on the dorsal side of the palate to form a prominent ridge, the **nasal crest** (*Crista nasalis* **16**[23]). The vomeromaxillary suture (12[4]), is accommodated in the dorsal part of the intermaxillary part of the medial palatine suture only, and not in the interpalatine part too. It is important to note this arrangement of fusion between the vomer and the palate in the savannah buffalo. (See **Discussion**, chapter four, point 14.) The palatine part of the nasal crest is not as prominent as the maxillary part.

The oral surface of the maxilla **:**

The ventral palatine or oral surface of the palate - see footnote 134 and see Facies palatina 19[3] under the palatine bone - is slightly concave from medial to lateral. It forms the major and middle part of the roof of the oral cavity and boney palate.

The rostral opening (19[22]) of the major palatine canal (13[33]) usually opens onto the ventral surface of the horizontal part of the palatine bone. (See palatine bone.) It may however open on the palatomaxillary suture (19[5]) in which case an inconspicuous **palatine groove** *(Sulcus palatinus* **16**[24]) can then be seen near the caudal border of the ventral surface of the palatine part of the maxillary bone. The relative position of the palatomaxillary suture - when compared to the positions of the maxillary cheek teeth - varies according to age. (See paragraph following the paragraph in which 19[24] is discussed.)

The median palatine suture on the oral side is only slightly raised (vide supra). The rostral border of the oral surface of the maxilla, lateral to palatine fissure, is narrow and it is fused to the body of the incisive bone at a ventral part of the maxilloincisive suture (16[3]).

The maxillary cheek teeth **:**

In adults animals that have a full complement of teeth, three premolars and three molar teeth are contained on each side in the dental alveoli of the alveolar processes of the maxilla.
Drawing a line that would connect the cheek teeth, the interalveolar margin (16[4]) and the body of the incisive bones of both sides, would describe a laterally flattened arch. This arch forms the upper or **superior dental arc** (*Arcus dentalis superior* **16**[25]). The superior dental arc is incomplete rostrally. Neither are there any teeth in the region of the diastema, nor are there any upper incisive teeth in the incisive bone. The dental alveoli, and subsequently the

placement of the left and the right maxillary cheek teeth within this arch, are placed wider apart than those of the mandible. (See 21^{26} & $21^{26`}$.) The vestibulo-lingual axes of maxillary cheek teeth converge distally. (See **Glossary of terms** right at the end, and see measurement §52 under section D **: Craniometric data**. Also see figures 3.69 & 3.70.)

<u>The maxillary sinus, the infraorbital canal and the biomechanical support system for the maxillary cheek teeth</u> **:**

The maxilla contains the **maxillary sinus** (*Sinus maxillaris* **16** ^{26}) in the caudal half and ventral two thirds of the maxillary body (16^{2} , vide supra). The shape of the maxillary sinus corresponds largely with the outer shape of the maxilla. Therefore, the sinus is also roughly pyramidal in shape, with the apical part directed rostrally. It is bordered by the internal surfaces of internal laminae (1^{4}) of the nasal and oral surfaces of the maxilla, and by the external laminae of the facial surface of the maxilla (16^{5}), plus that of other facial bones (vide infra). The osseus delimitations of the maxillary sinus are therefore as follows **:**

- # Laterally, the external lamina of the facial surface of the maxillary body.
- # Dorso-medially, the body of the conchal bone (17^{1}) and the nasal surface of the palatine part of the maxilla (vide infra under 16^{27}).
- # Caudally, the aerated lacrimal bone. An internal part of the non-aerated zygomatic bone (20^{9}) also contributes to the caudal osseus border.
- # Ventrally, the oral surface of the palatine part of the maxilla as well as the roots of the cheek teeth alveoli.

The maxillary sinus is divided incompletely by the infraorbital "canal" (16^{28} , vide infra) - and a ventral supporting septum the canal has (vide infra under $16^{28`}$ ) - into lateral and medial compartments. The lateral compartment forms the lateral **proper part of the maxillary sinus** (**16** $^{26`}$). The medial compartment is the maxillary part of the palatine sinus (16^{16} , vide supra). Caudally, the proper part is continuous with the ventral compartment ($15^{16``}$) of the lacrimal sinus, medial and ventral to the orbit. (See also lacrimal bone.) The most rostral extent of the proper part of the maxillary sinus extends approximately to the level of the facial tuber (16 [6]). The ventral border of the sinus approaches the alveolar margin, following the advancement of the cheek teeth as they continue to erupt from their alveoli as the animal ages. The boney (naso-)lacrimal canal (15 [6]) lies at the level of the dorsal border of the proper part of the maxillary sinus. Medially, the proper part of the sinus is bordered partially by the infraorbital canal, dorsal to which it communicates with the palatine part of the sinus via the large **maxillopalatine aperture** (*Apertura maxillopalatina* **16** [27])* [139]. This aperture connects the complete palatine sinus of the maxillary and palatine bones, to the proper part of the maxillary sinus. The proper part of the maxillary sinus - which also communicates with the ventral compartment of the lacrimal sinus (15 [16``]) - as well as both parts of the palatine sinus (16 [16] and 19 [6]), form the **maxillary sinus complex** (**16** [27`]). The maxillary sinus complex drains via a membrane lined osseus canal (17 [5] & see footnotes 143 - 145 under the ventral conchal bone) to the middle nasal meatus (13 [15]).

The **infraorbital "canal"** (*Canalis infraorbitalis* **16** [28]) (also see 13 [32]) traverses the sinus parts of the maxilla from rostral to caudal. It is not a canal embedded in trabecular bone, but it is a semi-free pipe-like structure. It is usually straight, with a complete osseus wall of its own, having a continuous inner surface and lumen as well as a continuous outer surface along its whole length. Ventrally, along its whole length, a **supporting septum** (**16** [28`]) connects the outer wall of the canal to the **interradicular septa** (*Septa interradicularia* **16** [29]) of the lingual roots of the third premolar (either $DP^{\underline{4}}$ or $P^{\underline{4}}$) and all the molars ($M^{\underline{1}}$, $M^{\underline{2}}$ and $M^{\underline{3}}$). The canal and its supporting septum divide the maxillary sinus incompletely into lateral proper and medial palatine parts (vide supra). Various **small alveolar openings** (*Foramina alveolaria* **16** [30]) in the floor of the canal, continues as very **small alveolar canals** (*Canales alveolares* **16** [31]) in the supporting septum towards the true roots of the teeth. Rostrally, the inner lumen of the infraorbital canal open at the infraorbital foramen (16 [8]) on the facial surface (16 [5]) of the maxilla. In some skulls, a **minor alveolar canal** (*Canalis alveolaris* **16** [32]) may continue rostral to the infraorbital foramen, in the non-aerated apical part of the maxilla. This minor alveolar canal diminishes progressively in diameter, just to end

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139 The maxillopalatine aperture (Apertura maxillopalatina 16 [27]) is a splanchnological term as listed under that section in the *N.A.V.*, but it is a useful term to describe this osseus opening.

blindly - at least macroscopically - in the trabecula of the apex of the maxilla or incisive bone. The caudal opening of the infraorbital canal - at the **maxillary foramen** (*Foramen maxillare* **16**[33]) - opens into the pterygopalatine fossa (13[30]), medial to the dorsal part of the base of the maxillary tuber (16[13]).

Apart from the supporting septum of the infraorbital, it also has a **short dorsal process** (**16**[34]) near the maxillary foramen. This process contributes to the formation of the infraorbital pillar (15[17`]). (See footnote 132 under the lacrimal bone.) The short dorsal process - plus the lacrimal component (15[17]) of the infraorbital pillar - borders the ventral compartment of the lacrimal sinus medially.

In older animals the infraorbital canal (16[28]) is laterally flattened. Rostrally the wall of the infraorbital canal is thicker where it unites with the external lamina of the maxilla. The attachment of the infraorbital canal to the infraorbital pillar (via the short dorsal process) and to the teeth (via the ventral septum), renders a major support to the lingual side of the alveoli of the cheek teeth. (See footnote 132.)

Rarely, the rostral part of the infraorbital canal can be fused to the external lamina of the maxilla at the level of the caudal end of the facial tuber in which case the canal is then medially curved and not straight ***** [140] .

<u>Postnatal embryological development of teeth and the formation of associated temporary canals and foramina</u> **:**

Trabecular spongy bone (1[5`a]) surrounds the dental alveoli (16[10]) to form the interalveolar septa (16[12]) and the interradicular septa (16[29]) as described above. The type of spongy bone and the extent to which it is developed, differs in young and old animals. In old animals, maxillary trabecula is not as well developed as the equivalents of mandibular dental alveoli. However, in young animals, maxillary trabecula is better developed (more voluminous) especially before the development of the permanent teeth.

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140 The facial tuber (16[6]) is the major insertion point of the sternocephalic muscle. As this muscle is a strong flexor of the head, it may play a role in reshaping the maxilla - and therefore of the infraorbital canal - in the skulls of certain animals. (See also **footnote 191**.)

Enamel organs (**16** [35])* [141] - which produce the molars and the permanent premolars - displace the trabecula to form **"cavities"** (**16** [36]). It must be realized that these "cavities" are as seen in prepared skulls, and are actually filled completely by the enamel organs and their products at various stages of development. These "cavities" enlarge, to eventually obtain dimensions that are slightly larger than the permanent teeth they have to form. By that stage, trabecula has been totally displaced, as well as some compact bone. In the case of premolars, the "cavities" start to develop as small structures between the mesial and the distal roots. Or sometimes, in the case of the second mandibular premolar, it may start off more lingually or more mesially. The sequences of formation of permanent teeth are first the three molars (from the first to the third) and then the three premolars (from the second to the fourth permanent premolar). (See also **Applied Anatomical Aspects**.) Resorption of deciduous premolar roots, and subsequent discarding of the temporary tooth cup, form part of the process of creating the final dimensions of the "cavity" each enamel organ ultimately needs. A "cavity" so formed, is linked via a short canal that opens at a temporary foramen to form a **temporary gubernacular canal** or **gubernaculum dentis** (**16** [37])* [142] . A gubernacular canal forms for each permanent premolar that is to be formed, and it is always positioned lingual to the deciduous premolar that will be displaced. In the case of the maxillary premolars, a gubernacular canal opens on the maxillary part of the osseus palate. In the case of the mandibular premolars, the gubernacular canals open on the molar part (21 [14]) of the mandibular body (21 [2]) in which the premolars and molars are situated.

The gubernacular canals are temporary because they are only present during those months that precede the eruption of the premolars. Usually only two gubernacular canals

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141 The enamel organs (16 [35]) are listed in *Nomina Histologica* under Odontogenesis. Although the detail of tooth formation falls beyond the scope of this study, these structures had to be studied to comprehend the osteological detail seen in this study.

142 Neither the term gubernaculum dentis nor gubernacular canal (16 [37]), are *N.A.V.* terms. Even though the term does not even appear in the human list of anatomical terms or in the list of Veterinary Embryology terms, the term is a very suitable term taken from human literature on the subject of tooth development. In the case of the savannah buffalo, the enamel organs for the permanent premolars develop from the oral mucosa. By active resorption of bone, the enamel organ anlage first creates a cavity - but eventually pierces the maxilla and mandible - lingually to the deciduous premolar that is to be replaced. The enamel organ anlage progressively moves deeper into the spongy bone to obtain its final position between the mesial and distal roots. The enamel organ continuously enlarges, but the connection with the oral mucosa is maintained for a while. That connection causes the development and sustenance of gubernacular canals, and explains their temporary nature.

can be seen at a time in the premolar groupings of each quadrant. (See Table 3.4 under section E **: Applied Anatomical Aspects**). The reason why not three gubernacula can be seen simultaneously in each quadrant, but only two, is because by the time the gubernaculum for the last premolar is forming, that of the first has already disappeared again. Optimally, a maximum of eight gubernacula can be seen in skulls and mandibles of immature animals when temporary teeth are shed. (See **Applied Anatomical Aspects** of the teeth of the savannah buffalo under section E for detail on the eruption sequence of teeth.)

17. THE VENTRAL CONCHAL BONE
(*OS CONCHAE NASALIS VENTRALIS*)

(See figures **3.40 - 3.42**. Also see 3.9, 3.35, 3.36, 3.40 - 3.42.)

The ventral conchal bone consists of a body (17[1]), a rostral process (17[4]), a horizontally placed basal lamina (17[8]), and two medially placed scrolls (17[9]). The body and the rostral process lie almost in the sagittal plane and they form part of the lateral nasal wall. (See also ethmoid, maxillary and palatine bones for other parts.) The two scrolls together form a single ventral nasal concha that occupies a large part of the nasal cavity. The body and the scrolls can be porous, or only partially porous in some animals. In most animals, the body (17[1]), its process (17[4]) and the basal lamina (17[8]) consists of compact bone.

The **body** (**17**[1]) is of even thickness, and is essentially circular in outlines. It has medial and lateral surfaces. Topographically, the body is situated (caudo-)ventral to the pathway of the (naso-)lacrimal canal (15[6]), whereas the process of the ventral conchal bone is situated dorso-rostral to the rostral opening of that canal (15[14``]). The medial or nasal surface of the body is concave. The lateral surface of the body is convex and it forms part of the dorso-medial wall of the maxillary sinus and maxillopalatine aperture. (See 16[27] under the maxilla.)

Rostro-ventrally the body is incompletely fused to the nasal surfaces of the maxillary and palatine bones respectively, leaving a **large permanent fissure** (**17**[2]) between the three bones. This large fissure (17[2]) involves the palatomaxillary suture (19[5]), the **conchomaxillary suture** (Sutura conchomaxillaris **17**[2`]) and a rostral part of the **conchopalatine suture** (Sutura conchopalatina **17**[2``])* [143]. The body is fused ventrally to the nasal surface of the palatine bone. (See also palatine bone).

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143 The conchomaxillary suture (Sutura conchomaxillaris 17[2`]) and the conchopalatine sutures (Sutura conchopalatina 17[2``]) are not listed in the *N.A.V.* as also referred to under **footnote 133**. Rostrally, the conchopalatine suture ends in the large permanent fissure (17[2]). The caudal end of the conchopalatine suture ends in the larger permanent compound fissure (17[3]). (See also **footnote 144**.)

FIGURE 3.40 : OSTEOLOGY

THE RIGHT HALF OF A SKULL OF A MATURE BULL. SCROLLS OF THE DORSAL AND THE VENTRAL CONCHAE ARE REMOVED (MEDIAL VIEW)
NOTE : IN (a) THE BODY AND THE BASAL LAMINA OF THE VENTRAL CONCHAL BONE ARE IN SITU, AND IN (b) THEY ARE REMOVED

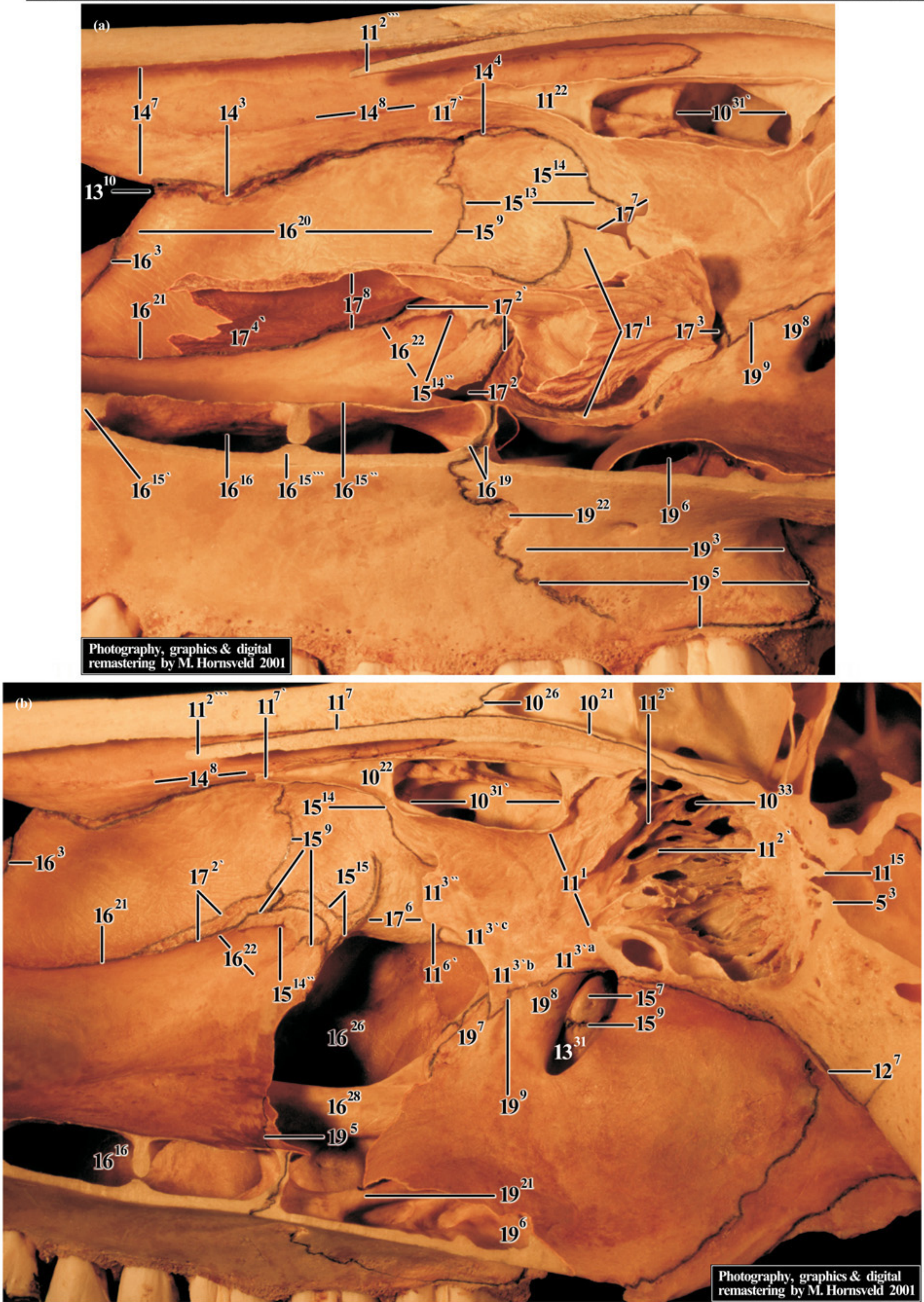
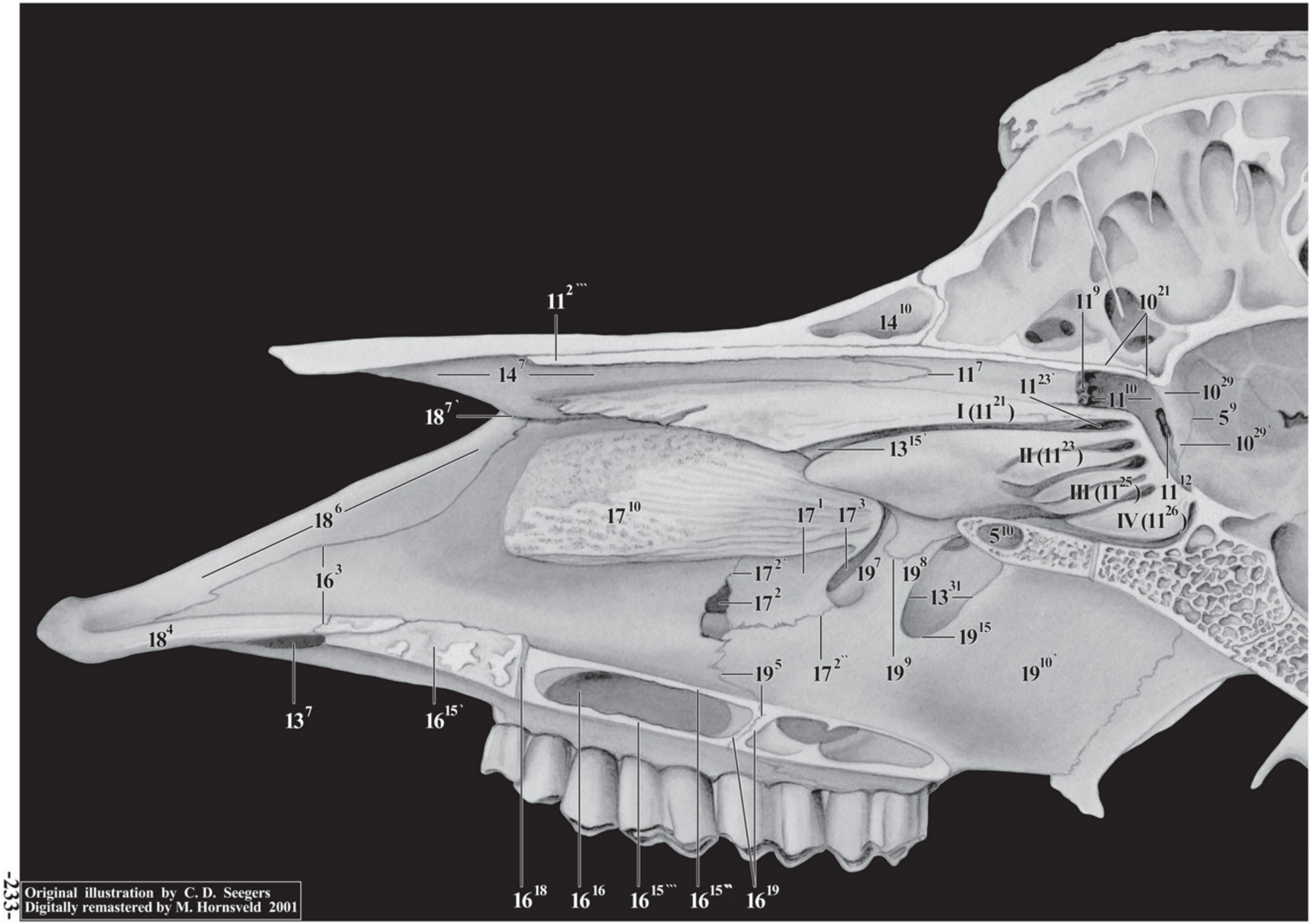


FIGURE 3.41 : OSTEOLOGY

VIEW SIX OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW). THE CONCHAE IN SITU



Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.41 : OSTEOLOGY

VIEW SIX OF THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW). THE CONCHAE IN SITU

FIGURE 3.42 : OSTEOLOGY

THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW). THE CELLULAE, BULLAE AND SINUSES OF THE CONCHAE ARE EXPOSED BY PARTIAL SCULPTURING

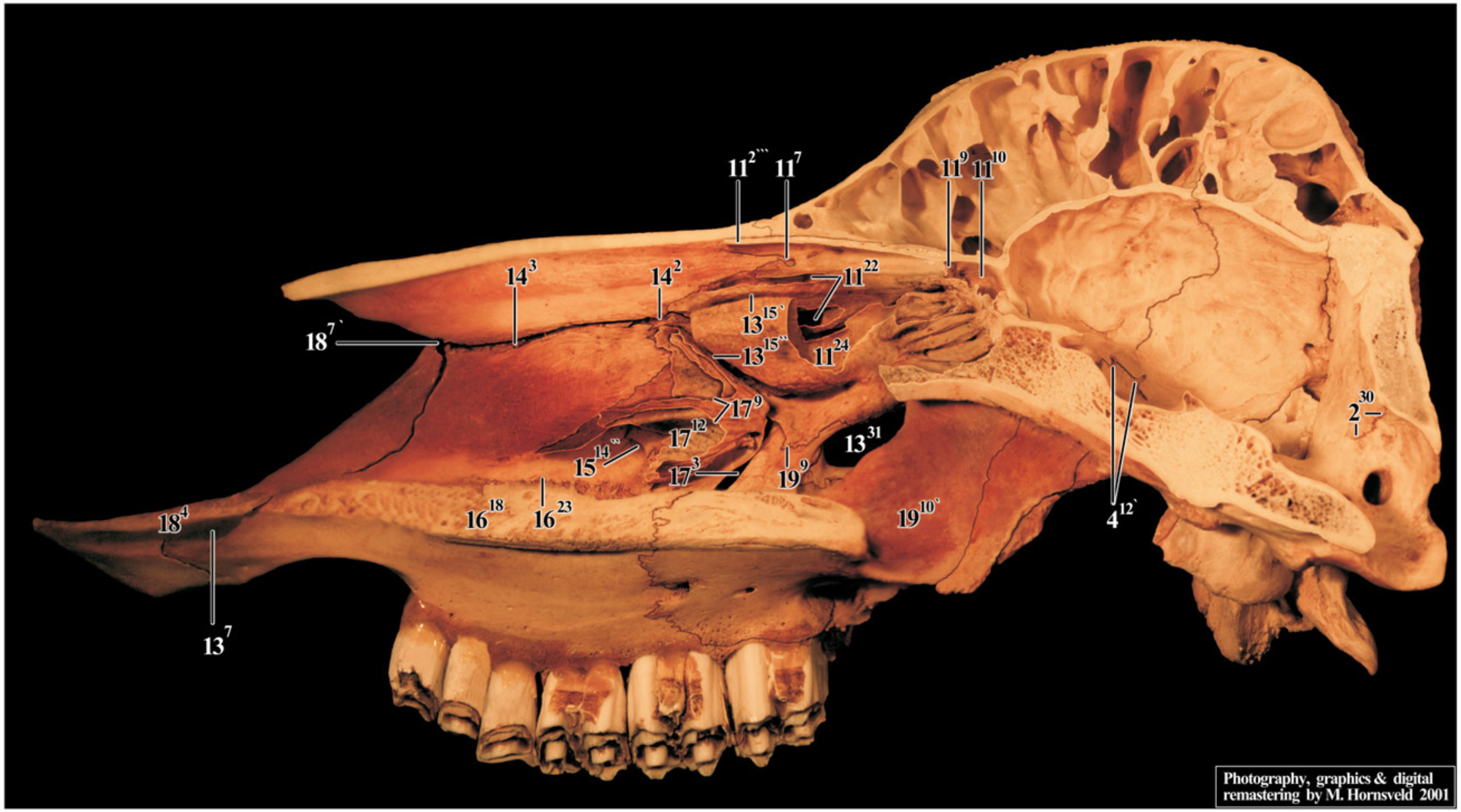


FIGURE 3.42 : OSTEOLOGY
THE RIGHT HALF OF A SKULL OF A MATURE BULL (MEDIAL VIEW).
THE CELLULAE, BULLAE AND SINUSES OF THE CONCHAE ARE EXPOSED BY PARTIAL SCULPTURING

The caudal border, and the caudal part of the dorsal border, is separated from the palatine, ethmoid and lacrimal bones by an even **larger permanent compound fissure** (**17**[3]). The larger compound fissure (17[3]) borders the caudal half and to some extend also the caudo-dorsal border of the body of the ventral conchal bone. This fissure involves a caudal part of the conchopalatine suture (17[2``]), the **concho-ethmoidal suture / fissure** (Sutura / Fissura concho-ethmoidalis **17**[3`]) and the lacrimoconchal (15[15]) sutures * [144]. (See also palatine, ethmoid and lacrimal bones.) In many animals studied, the conchopalatine suture (17[2``]) is incomplete or at most, poorly formed, which may affect the sizes of the fissures (17[2 & 3]) at both ends of that suture.

The **rostral process** (**17**[4]) is triangular with its **apex** (**17**[4`]) rostrally and the **base** (**17**[4``]) caudally. The apical part is fused to the conchal crest (16[21]) of the maxilla. The basal part of the process, as well as the rostro-dorsal part of the body, is fused laterally to the internal lamina of the lacrimal bone at the lacrimoconchal suture (15[15]). The caudal margin of the process is free and it forms the rostral part of a **boney canal** (**17**[5]). Neither the **osseus entrance to this canal** (**17**[6]) - on the side of the maxillary sinus - nor its **osseus opening towards the middle meatus** (**17**[7]), has been named yet * [145].

The **basal lamina** (**17**[8]) is a horizontal plate of bone that projects medially from the body and its process. Near the nasal septum the lamina divides into a **larger dorsal** and a **smaller ventral spiral lamella** (**17**[9]). The lamellae are coiled centripetally to form two

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144 See paragraph preceding **footnote 143** for comments on the large fissure (17[2]). The concho-ethmoidal suture / fissure (Sutura / Fissura concho-ethmoidalis 17[3`]) is not listed in the *N.A.V.* Of all the sutures and the fissures involved in the large and the larger compound fissures that border the body of the ventral conchal bone, the *N.A.V.* only lists the palatomaxillary (19[5]) and the lacrimoconchal (15[15]) sutures. It would be convenient to have all the sutures and fissures involved in these two fissures listed. Both the large (17[2]) and the larger compound (17[3]) fissures are permanent fissures and they are closed off by a layer of mucoperiosteum and a layer of nasal mucosa in the living animal. No cartilage seems present in these fissures. These membranous layers effectively separate the nasal cavity from the maxillary sinus. The absence of cartilage in the fissures was not confirmed microscopically.

145 The osseus components of the boney canal (17[5 / 6 / 7]) are unnamed. The canal is a laterally flattened canal that connects the dorsal part of the maxillary sinus - and therefore also of the maxillary sinus complex - to the middle nasal meatus. The caudal part of the canal is formed by a deep groove (11[6]) in the rostral border of the orbital lamina of the ethmoid bone (11[3``]), the rostral part by the body and the basal part of the process of the ventral conchal bone and the lateral part by the internal lamina (nasal surface) of the lacrimal bone (15[13]). The medial part of this boney canal is incomplete. However, in life animals, the medial part is completed by mucous membrane that lines the nasal cavity. The osseus part of the canal is approximately 15 - 20 mm long, approximately 3 mm wide and its rostro-caudal dimension can be as much as 15mm to 20 mm. The membranous opening of this osseus canal in the middle nasal meatus, is the **nasomaxillary opening** *(Apertura nasomaxillaris*).

longitudinal scrolls, arranged dorsal and ventral to the basal lamina respectively. Together they form the large **ventral nasal concha** (*Concha nasalis ventralis* **17** [10]). The scrolls are not attached to the walls of the nasal cavity or the nasal septum. The concha projects rostrally beyond its laminar attachment, and ends at a point just rostral to the nasoincisive incisure (13 [10]). Between the spirals and the basal lamina, as well as between consecutive peripherally situated coils, longitudinal recesses are formed. The dorsal and the ventral recesses communicate freely with the middle and the ventral nasal meatuses respectively. More centrally in each spiral, lamellae may fuse to form spaces. These spaces are subdivided by various transverse septae, dividing them into smaller **cells** (*Cellulae* **17** [11]) and larger compartments or **bullae** (*Bulla conchalis ventralis* **17** [12]). The position and the size of the cells and the bullae are inconstant. On average, there are approximately 8 compartments (cells and bullae) in the dorsal spiral and 6 in the ventral spiral.

18. THE INCISIVE BONE

(*OS INCISIVUM*)

(See figures **3.25, 3.32 - 3.34, 3.37, 3.41 & 3.42**. Also see 3.8, 3.9 & 3.11.)

The incisive bone consists of a rostral body (18[1]) with a large nasal process (18[6]) laterally and a small palatine process (18[4]) medially. Both processes project caudally. The body and processes of the incisive bone form the most rostral part of the face and palate to form the apex of the skull. The body and the nasal process also form the ventral and the lateral borders respectively of the rostral osseus nasal opening (see also 13[9 & 10]). In some animals, the nasal process is shorter than in others, and in those cases it does not form the complete ventral border of the nasoincisive incisure. (See paragraph following 18[7] and see footnote 123 under the nasal bone.)

The **body** (*Corpus ossis incisivi* **18**[1]) makes up the free transverse part of the incisive bone. The body is attached laterally and medially by the nasal and the palatine processes to the apical and palatine parts of the maxilla (vide infra). The body is dorso-ventrally flattened and lies in the same horizontal plane as the boney palate (13[3]). It presents dorsal and ventral surfaces and rostral and caudal margins. Laterally, the body is much thicker.

The rostral free margin of the body forms the **labial surface** (*Facies labialis* **18**[2]) which is convex from medial to lateral. This labial surface is continued laterally onto the facial surface of the nasal process, as well as the facial surface of the maxilla.

The caudal free margin of the body forms the **palatine surface** (*Facies palatina* **18**[3]). It is acutely concave from medial to lateral and it borders the para-median palatine fissure (13[7]) rostrally. (See also footnote 146.)

The dorsal or nasal surface of the body is concave from lateral to medial. It forms the floor of the nasal vestibulum and contributes in part to the ventral border of the rostral osseus nasal opening (13[9 & 10]).

The ventral or oral surface of the body is flat and forms the most rostral part of the roof of the boney palate. It is continuous with the oral (palatine) surface of the boney palate. The lateral border of the oral surface is continuous with the interalveolar margin (16[4]) of the maxilla. Together the bodies of the left and the right antimeres of the incisive bone form an even arch. (See the superior dental arc under 16[25]). In the live animal the ventral surface bears a soft tissue structure, the **dental pad** (*Pulvinus dentalis* **18**[3`]), as the incisive bone bears not incisive teeth.

The **palatine process** (*Processus palatinus* **18**[4]) projects caudally in a para-median position, tapering from lateral to medial. In prepared skulls of young animals, the whole process tapers gradually to terminate into a sharp point. In old animals, only the distal end of the process is acutely tapered. The palatine process borders the para-median palatine fissure medially and in young animals the antimeres border the “interincisive fissure” (13[8]) laterally. In older animals the ossification process of the palatine processes of the incisive bone is further advanced and the palatine processes extend further caudally (and more medially) than in immature animals. Distally (caudally), the median border of the palatine process of the incisive bone, is fused dorsally to the rostral extremity of the keel of the vomer at the vomeroincisive suture (12[5]). (See also vomer.) In old animals the disto-lateral part is fused for a short distance to the apical part (16[15`]) and palatine process (16[15]) of the maxilla at a ventral part of the maxilloincisive suture (16[3]). (See also the maxilla.) The left and right palatine process, as well as the antimeric incisive bodies articulate at the **interincisive suture** (*Sutura interincisiva* **18**[5]). In old animals, the suture ossifies over its whole length to form a complete osseus **rostral incisive part of the boney palate** (**18** $^{5`}$)* [146] . (See also 16 ^{17} for the maxillary part of the median palatine suture.) The most rostral points of the completely ossified interincisive suture, is the Prosthion*# or point **P**.

The distance between **P** and **P`** - on the medial edge of the ridge on the occipital condyle (2 $^{14``}$) - gives the maximum skull length. That measurement is more accurate than the 'condylobasal length'. The distance between **P** and **B** (on the ventral margin of the occipital foramen 2 ^{1}), gives the skull axis, **axis III**. (See FINAL COMMENT 11 in section D **: Craniometric data**, and compare standard measurement numbers 2 & 3, and additional measurement number §63.)

In dorsal view, the ossification of the interincisive suture rostral to the rostral end of the keel, may present a sutural or Wormian bone in some old individuals. (See footnote 28.)

The **nasal process** (*Processus nasalis* **18** ^{6}) of the incisive bone projects dorso-caudally from the lateral side of the body, also tapering distally into a sharp point. It presents a **dorsal free** (**18** $^{6`}$) and a ventral attached border. The nasal process has **lateral or facial** (**18** $^{6``}$) and **medial or nasal** (**18** $^{6```}$) surfaces. The ventral border is fused to the dorsal borders of the facial and nasal surfaces of the maxilla, at the dorsal part of the maxilloincisive suture (16 ^{3} , vide supra). In some animals the distal end of the process may or may not reach the nasal bone to articulate with it. When it does, its fusion to the nasal bone forms a short **nasoincisive suture** (*Sutura nasoincisiva* **18** ^{7}). A nasoincisive suture may be retained, to form a **nasoincisive fissure** (Fissura nasoincisiva **18** $^{7`}$*) (see footnote 123) which would be

146 The medial parts of the body and the palatine processes of the incisive bone of young animals are partially cartilaginous. This is especially so on the medial sides, where the antimeres articulate with each other in the median plane, at the interincisive suture (18 ^{5}). What can therefore be interpreted as an "interincisive fissure" (13 ^{8}), is actually due to cartilage of the incisive bone that have boiled away in the preparation of immature skulls. It would therefore be a misnomer to describe an "interincisive fissure" when the interincisive suture (18 ^{5}) actually does ossify completely, but just at a later stage. (See figure 3.32.) Because the palatine processes also fuse distally, to the maxilla, two separate para-median "palatine fissures" (13 ^{7}) are also formed. However, it is also debatable whether they are true fissures in the living animal. Dissections on "wet" specimens of animals of approximately 3 - 4 months old, showed that each "palatine fissure" is closed off completely by cartilage. It is not known whether that cartilage solely belongs to the tubular part of the vomero-nasal organ, or whether is it cartilage that actually forms that part of the palate. No histology was done to distinguish the one possibility from the other as is falls beyond the scope of this study. After passing through the cartilage filled "palatine fissures", the ducts of the antimeric vomero-nasal organs join and drain on the oral side - via the incisive duct - into the oral cavity. By implication, the "palatine surface" of the incisive bone (18 ^{3}) - facing the "palatine fissure" - would also be a total misgiving. Most of these aspects of the palatine- and interincisive fissures (13 ^{7} and 13 ^{8}) have also been discussed under those numbers in subsection 13 **: Introduction to the facial bones**.

a rostral continuation of a nasomaxillary fissure (14^3). In old bulls with both a nasomaxillary and a nasoincisive fissure, the latter part of the fissure would be the last to ossify. (See also footnote 123 and **Discussion**, chapter four, point 4.) The dorsal border of the nasal process of the incisive bone forms most if not all of the ventral margin of the nasoincisive incisure (13^{10}). If the nasal process does not reach the nasal bone - it may be as much as 10 mm shorter than the particular border of the maxilla - the maxilla then forms the ventral edge of the angle of the nasoincisive incisure (13^{10}). (Also see paragraph following 16^3 under the maxilla.) Subsequently, in those cases, no nasoincisive suture (18^7) is formed. This variation appears to be not gender related although the length of the nasoincisive suture appears to be longer in older individual animals. The lateral or facial surface of the nasal process forms the most rostral part of the face. The medial surface of the nasal process forms the most rostral part of the lateral nasal wall. The nasal process is approximately 90 mm long in young animals and approximately 140 mm long in old animals.

19. THE PALATINE BONE

(*OS PALATINUM*)

(See figures **3.26, 3.34, 3.35, 3.37, 3.39 - 3.42**. Also see 3.6 & 3.8.)

The palatine bone consists of horizontal (19 [2]) and perpendicular laminae (19 [10`]). The horizontal lamina forms the caudal palatine part of the boney palate and palatine sinus (13 [3] and 19 [6] respectively). As it is extensively aerated - similar to the palatine process of the maxilla - it has separate dorsal and ventral layers facing the nasal and the oral cavities respectively. The perpendicular lamina lies caudal to the horizontal part in a sagittal plane and can be considered as either laterally flattened or mono-lamellar. It forms the major part of the lateral wall of the boney choana (13 [12]) and a large part of the pterygopalatine fossa (13 [30]).

The **nasal surface** (*Facies nasalis* **19** [1]) of the dorsal **horizontal lamina** *(Lamina horizontalis* **19** [2]) is concave from medial to lateral. It forms the caudal part of the floor of the nasal cavity. The **palatine surface** (*Facies palatina* **19** [3]) of the ventral horizontal lamina faces the oral cavity. The internal surfaces of the dorsal and ventral horizontal lamina face the palatine sinus and each other. Caudally, the nasal and palatine surfaces are united with each other at the caudal **free margin** (*Margo liber* **19** [4]) of the palate, medial to a bulky para-median process (vide infra under 19 [10]). The dorsal and the ventral horizontal laminae form the caudal palatine part of the boney palate. (See also incisive bone and maxilla for the rostral and middle parts respectively.) Rostrally, both the nasal and the palatine surfaces are fused to the equivalent surfaces of the palatine process of the maxilla at the **palatomaxillary suture** (*Sutura palatomaxillaris* **19** [5]).

The two layers of the horizontal lamina of the palate are separated from each other by the voluminous palatine part of the **palatine sinus** *(Sinus palatinus* **19**[6])* [147] . The layers of the horizontal part of the palate are connected to each other by means of vertical septa as a result of the extensive aeration of the palate * [148] . These septa form the **median** (**19**[6`]), **rostral** (**19**[6``]) and **lateral** (**19**[6```]) borders of the sinus - and of the horizontal lamina - of the palatine bone.

Rostro-laterally however, parts of the rostral and the lateral septa do not unite with the nasal surface (19[1]) of the palate, as the nasal surface of the palate in that region is fused instead to the body of the ventral conchal bone at the conchopalatine suture (17[2``]). The complete conchopalatine as well as part of the palatomaxillary suture (19[5]) on the nasal surface (19[1]) of the palatine bone are however incomplete due to the two large fissures situated around the body of the ventral conchal bone. (See 17[2&3] as well as footnotes 143 & 144).

The medial septa (19[6`]) of the left and the right-hand sides fuse along the median plane at the **interpalatine part of the median palatine suture**. (See also 16[17] and footnote 136 for the intermaxillary part.) Similar to the intermaxillary part of that suture, the antimeric median septa also form a double layered palatine septum (16[18]). It divides the palatine sinus completely into left and right-hand sides. The median palatine suture is raised only on the nasal surface. (See Crista nasalis 16[23] under the maxillary bone.)

The rostral septum (19[6``]) is fused to a similar septum of the palatine process of the maxillary bone at the palatomaxillary suture (19[5]) to form a double layered transverse

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147 It would be convenient to constantly denote a *pars maxillaris* (16[16]) and a *pars palatina* (19[3]) for the palatine sinus, as well as the same two parts for the palatine suture and for the palatine septum. (See **footnotes 136 & 137**.) Without such distinctions, confusion can arise when one considers the maxillary sinus - which has proper and palatine parts - and the palate and its sinus. When one considers the boney palate per se (as an aerated osseus structure), then it has as a maxillary component (presently the palatine part) as well as the (proper) palatine part. It would also be convenient to distinguish in a distinct way between the external and the internal surfaces of the dorsal (nasal surface) and the ventral laminae (palatine surface) of the horizontal part of the palatine bone. It is suggested to denote the terms "**Facies antenasalis**" and "**Facies antepalatina**" to these faces of the nasal and palatine surfaces of the maxillary and palatine parts of the palate, to abridge these semantic problems. Similarly - in the case of the **lacrimal bone** - will terms such as "**ante-orbital**", "**antefacial**" and "**antenasal**", help to ease up the description of these surfaces for that bone.

148 The vertical septa form as result of the exaggerated suture formation that occurs on the lines where the palatine bone fuses with the palatine process of the maxilla.

septum (see 16 [19]). Both layers of the transverse septum are incomplete laterally * [149] .

The lateral septum (19 [6```]) is more extensive than the former two septa **:**

Laterally, it is fused mainly to the alveolar process of the maxilla. In the skull of one old animal studied, additional pneumatization of the dental alveoli between the second and the third molar teeth (M^2 and M^3) was seen to occur. Effectively - in that case - the interalveolar septum (16 [12]) between the molars was displaced. That means that the lateral septum of the palatine sinus, in the region ventral to the infraorbital pillar and ventral to the supporting septum (16 [28`]) of the infraorbital canal, can extend as far laterally as the lamina externa of the maxilla. Therefore the facial surface of the maxilla (rather, its internal or "antefacial" surface - see footnote 147) may then form the lateral border of the palatine sinus.

Unaffected by additional pneumatization - and as can only be seen from medially - the **'dorsal border'** of the **lateral septum** (19 [6```]), has **rostral** (**19** [7]) and **caudal** (**19** [8]) parts. Both parts extend dorsally beyond the dorsal level of the palate and the alveolar process of the maxilla. The medial surface of the rostral part is free and it forms part of the lateral wall of the palatine sinus. The medial surface of the caudal part is united with the smaller rostral part (19 [13]) of the perpendicular lamina that lies rostral to the sphenopalatine incisure (19 [15] , vide infra). The rostral and caudal parts (19 [7] & 19 [8]) form the medial wall of the infraorbital pillar (15 [17`]). (See footnote 132 under lacrimal bone.) Dorsally, these parts of the pillar - and therefore also included into it the lateral septum (19 [6```]) - is fused to a part of the orbital plate (11 [3`b]) of the ethmoid bone, at the **palatoethmoidal suture** (*Sutura palatoethmoidalis* **19** [9]). The rostral margin of the pillar is separated from the body of the ventral conchal bone by the conchopalatine part of the larger permanent compound fissure (17 [3]). (See also footnotes 143 & 144 under the ventral conchal bone.)

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[149] Because both the vertical septa are incomplete rostro-laterally, and because both are also separated from the nasal surface (19 [1]) in the same position, the rostral part of the palatine sinus can communicate dorso-laterally - between the body of the conchal bone and the infraorbital canal via the maxillopalatine aperture 16 [27] - with the lateral proper part of the maxillary sinus.

The caudal free margin (19^{4}) of the palate is bordered on either side - at least as it appears in ventral view - by a **bulky para-median process** (**19^{10}**). (Vide supra.) The process lies at the same horizontal level as the ventral surface of the osseus palate and it forms the ventral border of the **perpendicular lamina** *(Lamina perpendicularis* **$19^{10`}$**) of the palatine bone. Lateral to the process (19^{10}), a wide incision - which is more pronounced in young animals - separates the perpendicular lamina of the palatine bone from the maxillary tuber (16^{13}). The medial or **nasal surface** (*Facies nasalis* **19^{11}**) of the perpendicular lamina faces the nasal cavity, and it forms the lateral wall of the boney choana (13^{12}). The **maxillary surface** (*Facies maxillaris* **19^{12}**) of the perpendicular lamina faces laterally, towards the maxillary tuber (16^{13}), forming part of the medial wall of the pterygopalatine fossa (13^{30}). Dorso-rostrally, the perpendicular lamina also forms part of the medial wall of the maxillary foramen (16^{33}). Rostro-dorsally, the perpendicular lamina is incompletely divided into a **smaller rostral** (**19^{13}**) and a **larger caudal part** (**19^{14}**) by the **sphenopalatine incisure** (*Incisura sphenopalatina* **19^{15}**). The sphenopalatine incisure is the ventral part of the sphenopalatine foramen (13^{31}).

Rostro-laterally, the rostral part (19^{13}) is fused to the lateral septum of the horizontal part of the palatine bone ($19^{6```}$) to form part of the medial wall of the infraorbital pillar ($15^{17`}$). The rostral part ($19^{13}$) is fused dorsally to a part of the orbital plate ($11^{3`b}$) of the ethmoid bone at a part of the palatoethmoidal suture (19^{9}). (Also see footnote 132 under the lacrimal bone for a full description of the infraorbital pillar $15^{17`}$).

Caudo-dorsally, the rostral part (19^{13}) also gives rise to a slender **orbital process** (*Processus orbitalis* **19^{16}**) which projects dorsally. The distal part of this process forms a small part of the medial wall of the boney orbit (13^{21}). Caudally and rostrally, the process is fused to the orbital parts of the frontal and lacrimal bones respectively at the frontopalatine (10^{19}) and **palatolacrimal sutures** *(Sutura palatolacrimalis* **19^{17}**). The proximal part of the orbital process (19^{16}) is fused medially to a part of the orbital plate ($11^{3`b}$) of the ethmoid bone at a more lateral part of the palatoethmoidal suture (19[9]) to form the lateral part of the dorsal quadrant of the sphenopalatine foramen (13[31]). (Also see 11[3] under the ethmoid bone.) The sphenopalatine incisure (19[15], vide supra) forms the ventral three quarters of the sphenopalatine foramen. (Also see 13[31] under the Introduction to the bones of the face)*[150].

The larger caudal part (19[14]) of the perpendicular lamina is fused dorsally to the base of the skull, to various bones situated rostral to the body of the basisphenoid bone. Lateral, ventral and medial views reveal most of the following **:**

In lateral view, it can be seen that the lateral surface is fused dorsally to the wing of the presphenoid bone at the sphenopalatine suture (5[20]). (Also see footnote 49 under the presphenoid bone). Caudally it is fused to the pterygoid process of the basisphenoid bone at the basisphenoid part of the sphenopalatine suture (5[20`]). (See footnote 35 under the basisphenoid bone.) Dorso-caudally and caudo-ventrally it is fused over small areas to the body and the larger process (6[5]) of the pterygoid bone at the pterygopalatine suture (6[2]).

As revealed by a ventral view, the perpendicular lamina (19[10`]) of the palatine bone is fused as follows **:** Caudally, the medial surface is fused to the larger process (6[5]) of the pterygoid bone at a medial part of the sphenopalatine suture (5[20`]). The dorso-medial border is fused caudally to the vomer at the vomeropalatine suture (12[9]). Rostrally, the perpendicular lamina (19[10`]) of the palatine bone is fused to a part of the orbital plate (11[3`a]) of the ethmoid bone at a medial part of the palatoethmoidal suture (19[9], vide supra). The latter suture can best be evaluated if the skull is rotated towards a median view. Unless the palatoethmoidal suture (19[9]) is exposed by cutting bone away, this suture cannot be differentiated from the vomeropalatine and the vomero-ethmoidal sutures (12[9] and 12[10]), due to intimate fusion between the ethmoid plates, the wings of the vomer and the rostrum of the [prae-]sphenoid bone.

150 In the live animal, blood vessels and nerves pass from the pterygopalatine fossa via the sphenopalatine foramen (13[31]) to the nasal cavity and vice versa. The nasal side of the sphenopalatine foramen is closed off further by nasal mucosa.

The lateral maxillary surface (19[12]) of the caudal part of the perpendicular lamina (19[10`]) is rough and in old bulls it may show **uneven patterns** (**19**[18]) resembling a blood-vessel network. Next to the para-median process, the lateral surface bears an **oval raised area** (**19**[19]). It is better developed in older animals. The **caudal palatine opening** *(Foramen palatinum caudale* **19**[20]) of the **major palatine canal** (*Canalis palatinus major* **19**[21]) opens dorso-lateral to the raised area (19[19]). Rostrally, the canal opens on the oral surface of the horizontal lamina at the **major palatine foramen** (*Foramen palatinum majus* **19**[22]). This opening lies on or near the palatomaxillary suture (19[5]). The major palatine canal (19[21] and also see 13[33]) connects the pterygopalatine fossa to the oral cavity. The canal traverses the palatine sinus obliquely in a rostro-ventral direction. One to three **lesser palatine canals** (*Canales palatini minores* **19**[23]) may split from the main canal to open caudal to the main opening as the **minor palatine openings** (*Foramina palatina minora* **19**[24]). The larger and the smaller canals are supported by ventral lamellae that rest on the internal surface of the ventral horizontal lamina of the palatine bone. In young animals small sections on the free aspects of these canals can be incomplete.

In a ventral view of the osseus palate, the combined palatomaxillary sutures (19[5]) of the left and the right-hand sides, has a rostral curve. The position of the suture laterally - taking the molars as reference point - varies in animals of different ages **:**

Laterally it is fused to the lingual surface of the alveolar processes of the first molar ($M^{\underline{1}}$) at approximately 4 months of age, to the second molar ($M^{\underline{2}}$) in animals of approximately 2 years, and to the lingual surface of the third molar ($M^{\underline{3}}$) in old animals. The level of the rostral border of the suture (at the most apical part of the convex curve), is also not constant in animals of different ages. At approximately 4 months of age, a median point on the palatomaxillary suture lies on a line drawn between the third and the fourth deciduous premolars ($Dp^{\underline{3}}$ and $Dp^{\underline{4}}$). At approximately 2 years of age it lies between the last deciduous premolar ($Dp^{\underline{4}}$) and the first molar ($M^{\underline{1}}$). In old animals it lies on a line between the first and the second molars ($M^{\underline{1}}$ and $M^{\underline{2}}$). (See the point Palatino-orale (Po)*# under the section on the **Craniometric data**, and see measurement 62§.)

The change in the relative position of the palatomaxillary suture is due to relative rostral movement of the alveolar process of the maxillary bone relative to the position of the caudal osseus palate. (See also paragraph following 16[14``] under the maxillary bone.) The continued rostral movement of the dental alveoli of cheek teeth throughout life, is part of **normal mesial drift** (**19**[25]) of teeth. Increased contact surface wear between the distal parts of more mesially situated cheek teeth, would increase the magnitude of mesial drift of the more distally situated cheek teeth, especially that of the last molar. This is due to an additive effect caused by contact surface wear.

The caudal free margin of the boney palate between the bulky left and right para-median processes (19[10]), are concave, forming a semi-lunar horizontal arch. The arc demarcates the rostro-ventral border of the boney choana (13[12]). Because the keel of the vomer is not fused to the palatine bone, the choana is therefore incompletely divided. In some individuals the caudal free margin bears an inconspicuous or stubby **unpaired caudal nasal process** (*Spina nasalis caudalis* **19**[26]) in the median plane.

20. THE ZYGOMATIC BONE
(*OS ZYGOMATICUM*)

(See figures **3.26, 3.27, 3.31 - 3.34 & 3.39**. Also see 3.7 & 3.11.)

The zygomatic bone forms the rostral part of the **zygomatic arch** (*Arcus zygomaticus* **20**[1]). (See 7[18] and 10[6] for the temporal and frontal contributions to the zygomatic arch.) The zygomatic bone consists of a body and two processes. The exposed surfaces of the zygomatic bone forms part of the boney orbit (13[21]) and face, as well as a part of the maxillary sinus wall, despite the fact that it is not a typically aerated bone.

The **body** (**20**[1`])* [151] has lateral and orbital surfaces, which in young animals, are arranged approximately 90 degrees to each other (vide infra under 20[8] for the situation in old animals). The lateral or **facial surface** (*Facies lateralis* **20**[2]) forms the caudo-lateral part of the face. The **orbital surface** *(Facies orbitalis* **20**[3]) forms the latero-ventral part of the boney orbit (13[21]). The two surfaces meet at the **infraorbital margin** (*Margo infraorbitalis* **20**[4]). (See also 15[10] .) The supraorbital margin (10[8]) and the infraorbital margins together, form the orbital margin (see 13[20]) at the **orbital entrance** (*Aditus orbitae* **20**[4`]) to the boney orbit (13[21]). Medially, the body of the zygomatic bone is fused to the orbital and facial parts of the lacrimal bone at the lacrimozygomatic suture (15[2]). Rostrally and latero-ventrally the facial part of the body is fused to the maxilla at the **zygomaticomaxillary suture** (*Sutura zygomaticomaxillaris* **20**[5]). The body of the zygomatic bone has a temporal and a frontal process **:**

The **temporal process** (*Processus temporalis* **20**[6]) projects caudally and is fused to the ventral aspect of the zygomatic process of the temporal bone at the temporozygomatic suture (7[19]). Together they form the caudal part of the zygomatic arch. The medial surface of the temporal process (20[6]) faces the lacrimal bulla (15[7]).

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151 The *N.A.V.* does not list a separate body (20[1`]) for the zygomatic bone. An Arcus zygomaticus is listed under the Cranial bones (see 1[8]), as well as under the zygomatic bone (20[1]). It would be convenient to distinguish the processes of the zygomatic bone from a zygomatic body. The zygomatic body can be distinguished as the rostral part of the whole arch.

The **frontal process** (*Processus frontalis* **20^{7}**) is based partially on the body and partially on the temporal process of the zygomatic bone. It projects dorsally and is fused to the zygomatic process of the frontal bone (10^{6}) at the **frontozygomatic suture** (*Sutura frontozygomatica* **$20^{7`}$**). The zygomatic component of this part of the face, essentially forms the ventral half of the lateral angle of the boney orbit (13^{21}). The rostro-caudal dimension of the lateral osseus wall of the boney orbit (also contributed to by the frontal bone), approximately has a four-fold increase in a rostral direction as the animal ages. In young animals it is approximately 10 mm wide, and in old animals it can be up to 40 mm wide. It is more prominent in old animals especially old bulls. This accentuates the protruding infraorbital margin of old animals laterally. (See measurement §51 under the **Craniometric data**.) The frontozygomatic suture ($20^{7`}$) starts to ossify in animals of about 2 years. In some old animals, small remnants of the suture may remain un-ossified on the medial side only.

The lateral facial surface (20^{2}) of the zygomatic body is divided by a **boney ridge** (**20^{8}**). In young animals, the ridge divides the facial surface of the zygomatic body into lateral and ventral surfaces. In older animals, the ridge becomes more prominent, and it divides the zygomatic contribution to the face into **dorsal** (**$20^{8`}$**) and **ventral** (**$20^{8``}$**) parts. The ridge is continued caudally onto the temporal process (20^{6}), and rostrally onto the facial surface of the maxilla. The boney ridge (20^{8}) forms the zygomatic component of the facial crest of old animals. (See 16^{7} under the maxilla.) The dorsal part ($20^{8`}$) of the lateral facial surface is small and nonspecific. The ventral part ($20^{8``}$) of the facial surface of the zygomatic bone is concave from dorsal to ventral. In old animals it is even more concave, and its size increases at the expense of the dorsal part ($20^{8`}$). The extent to which the ventral part ($20^{8``}$) becomes ever more concave with age, is related to that part of the maxilla that also lies ventral to the facial crest. In old bulls, the ventral part ($20^{8``}$) of the facial surface, eventually lies opposite - and just ventral to - the orbital surface of the zygomatic bone (20^{3}). This accentuates the protruding infraorbital margin of old animals ventrally. (See FINAL COMMENT 13 under section D **: Craniometric data**.) At least one **foramen** (**$20^{8```}$**) opens on the concave ventral part (20[8``]) of the zygomatic bone. The foramen leads to a system of branching nutrient canals (2[7````]) that serves the zygomatic bone.

The body of the zygomatic bone is not aerated in the typical way where diploë between internal and external laminae are displaced. However, **an internal or "antefacial" surface of its rostral end** (**20**[9]) forms the caudal border of the lateral or proper part of the maxillary sinus (16[26]), just lateral to the ventral compartment of the lacrimal sinus (15[16``]). (See paragraph following (16[26]) under the maxilla and footnote 147 under the palatine bone.)

21. THE MANDIBLE

(*MANDIBULA*)

(See figures **3.43 - 3.49**. Also see figure **4.2** under **Discussion**, and see 3.10 & 3.11.)

The mandible is the longest bone of the face, measuring approximately 220 mm in young animals and up to 400 mm in old animals. Except for the most rostral part, the mandible is laterally flattened and each part of the antimeres lies in a near sagittal plane. The mandible is divided into caudal and rostral components. The caudal component is the **mandibular ramus** (*Ramus mandibulae* **21** [1]). The general longitudinal orientation of the ramus itself is nearly vertically placed. Caudally, each mandibular half articulates ipsilaterally with the squamous part of the temporal bone of the skull. The rostral component of the mandible forms the main part or **body of the mandible** (*Corpus mandibulae* **21** [2]). The antimeric bodies of the mandibular halves, converge rostrally. They meet and articulate with each other at an acute angle at the **intermandibular suture** (*Sutura intermandibularis* **21** [3]). (See also 21 [28] .) Both components of the mandible consist mainly of compact bone (1 [3`]). The dental alveoli or sockets (16 [10] ) that contain the teeth, consists of spongy bone of trabecular and lamellar types (1 [5`a] & 2 [31]).

<u>The ramus of the mandible</u> **:**

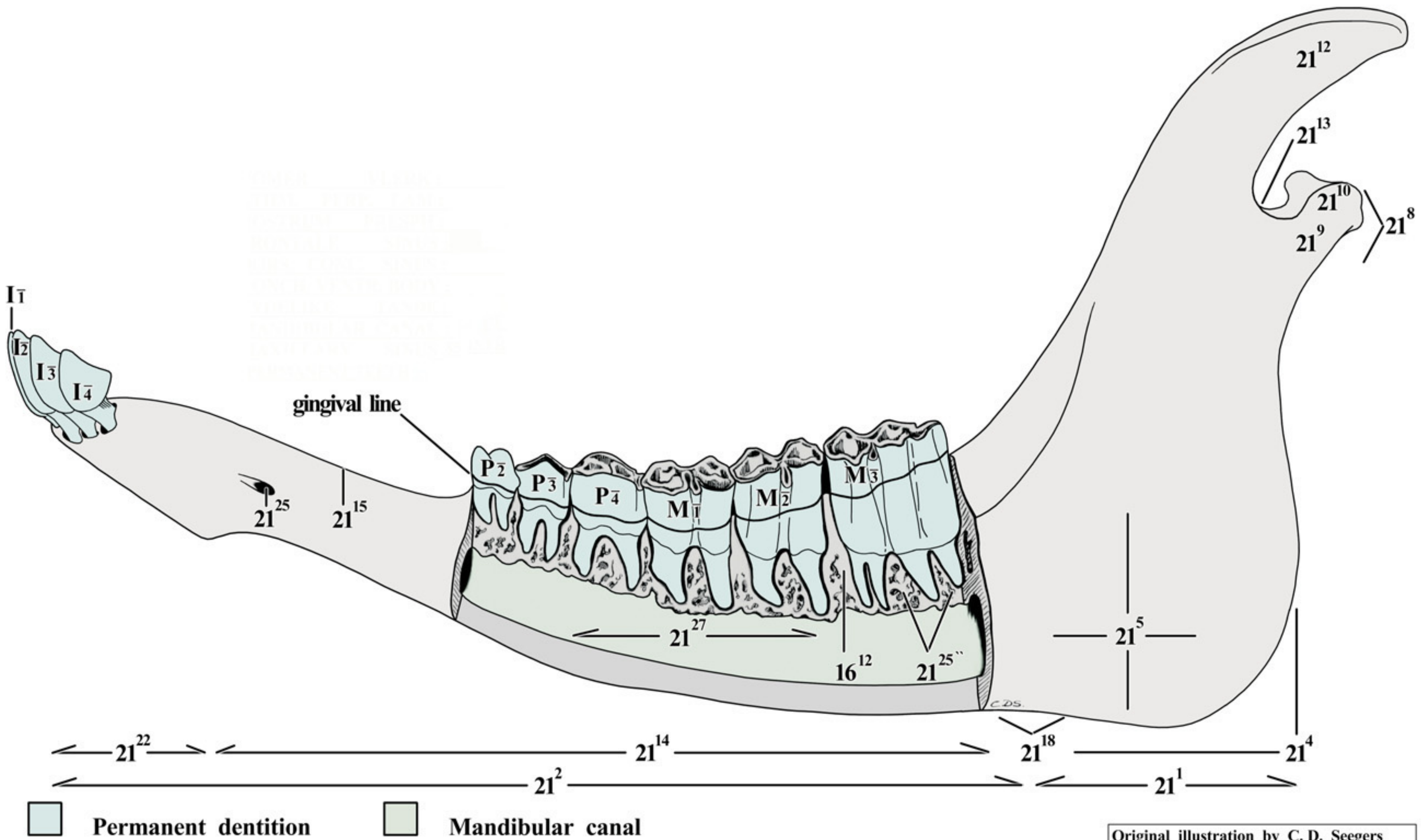
The ramus (21 [1]) has rostral and caudal margins, as well as lateral and medial surfaces. The caudal margin is concave dorsally and convex ventrally. The convexity of the latter part of this margin continues onto the ventral margin of the mandibular body (21 [2]) to form the **mandibular angle** (*Angulus mandubulae* **21** [4]). The rostral margin of the ramus is convex dorsally, but concave where it is continued onto the dorsal margin of the mandibular body. The lateral and the medial surfaces of the ramus are biconcave. The lateral concavity forms the **masseteric fossa** (*Fossa masseterica* **21** [5]) and is well demarcated especially in old individuals. The medial concavity forms the **pterygoid fossa** (*Fossa pterygoidea* **21** [6]), the borders of which are not clearly demarcated. The pterygoid fossa is marked by an **oblique shallow groove** (**21** [6`]) that crosses the fossa from rostro-ventrally to caudo-dorsally. In one

LINE DRAWING OF THE MANDIBLE OF AN OLD BULL (LATERAL VIEW)

FIGURE 3.43 : OSTEOLOGY

FIGURE 3.43 : OSTEOLOGY

LINE DRAWING OF THE MANDIBLE OF AN OLD BULL (LATERAL VIEW)

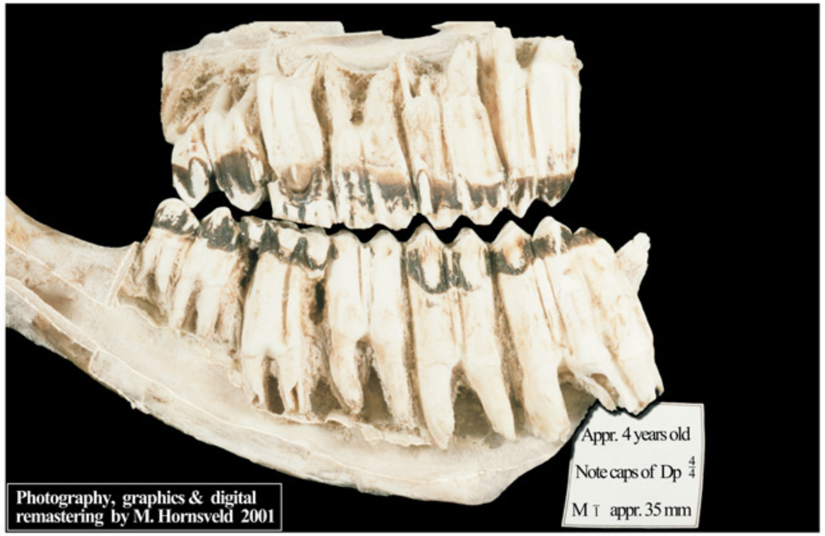


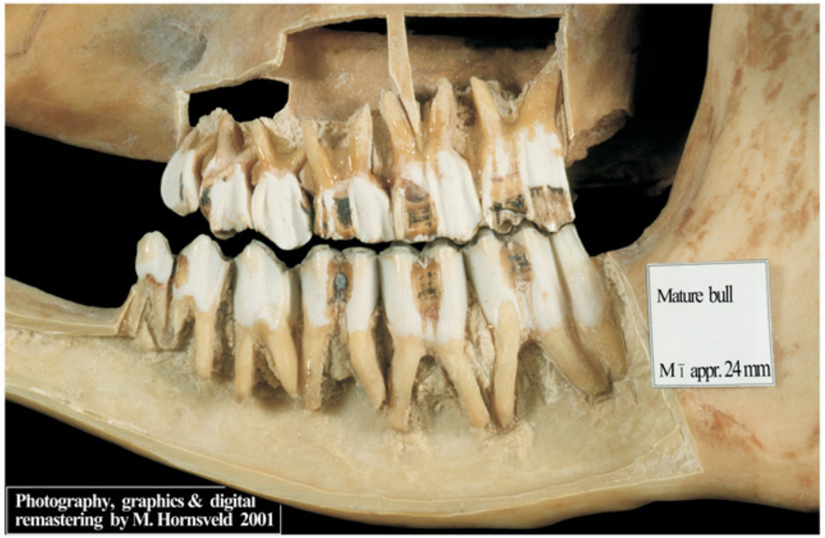
Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

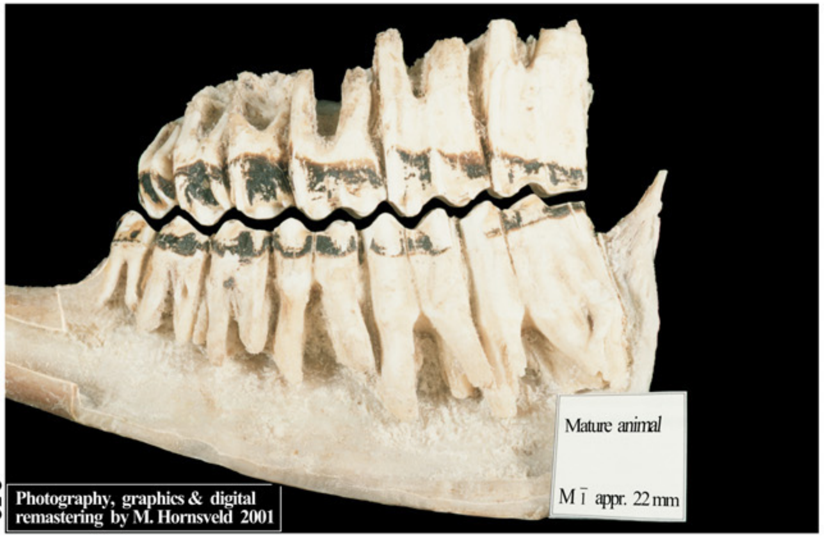
FIGURE 3.44 : OSTEOLOGY

OCCLUSAL PATTERN OF CHEEK TEETH (LEFT LATERAL VIEW)

FIGURE 3.44 : OSTEOLOGY
OCCLUSAL PATTERN OF CHEEK TEETH (LEFT LATERAL VIEW)







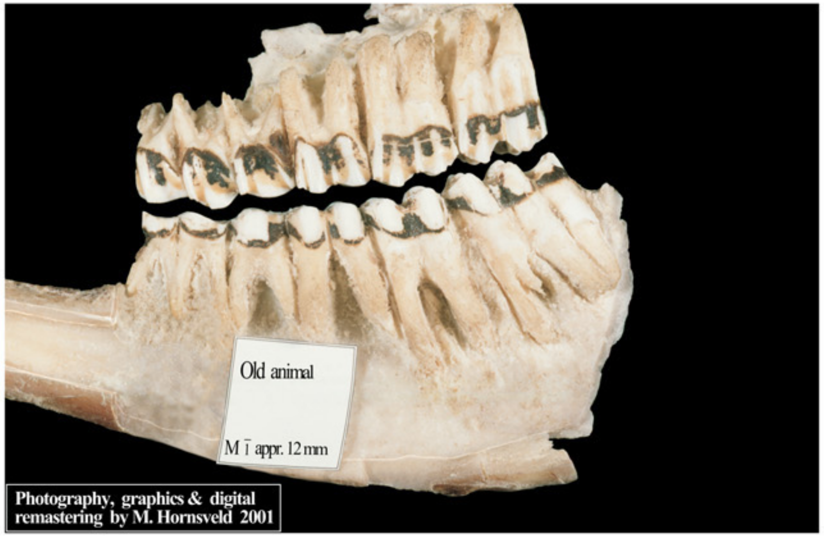
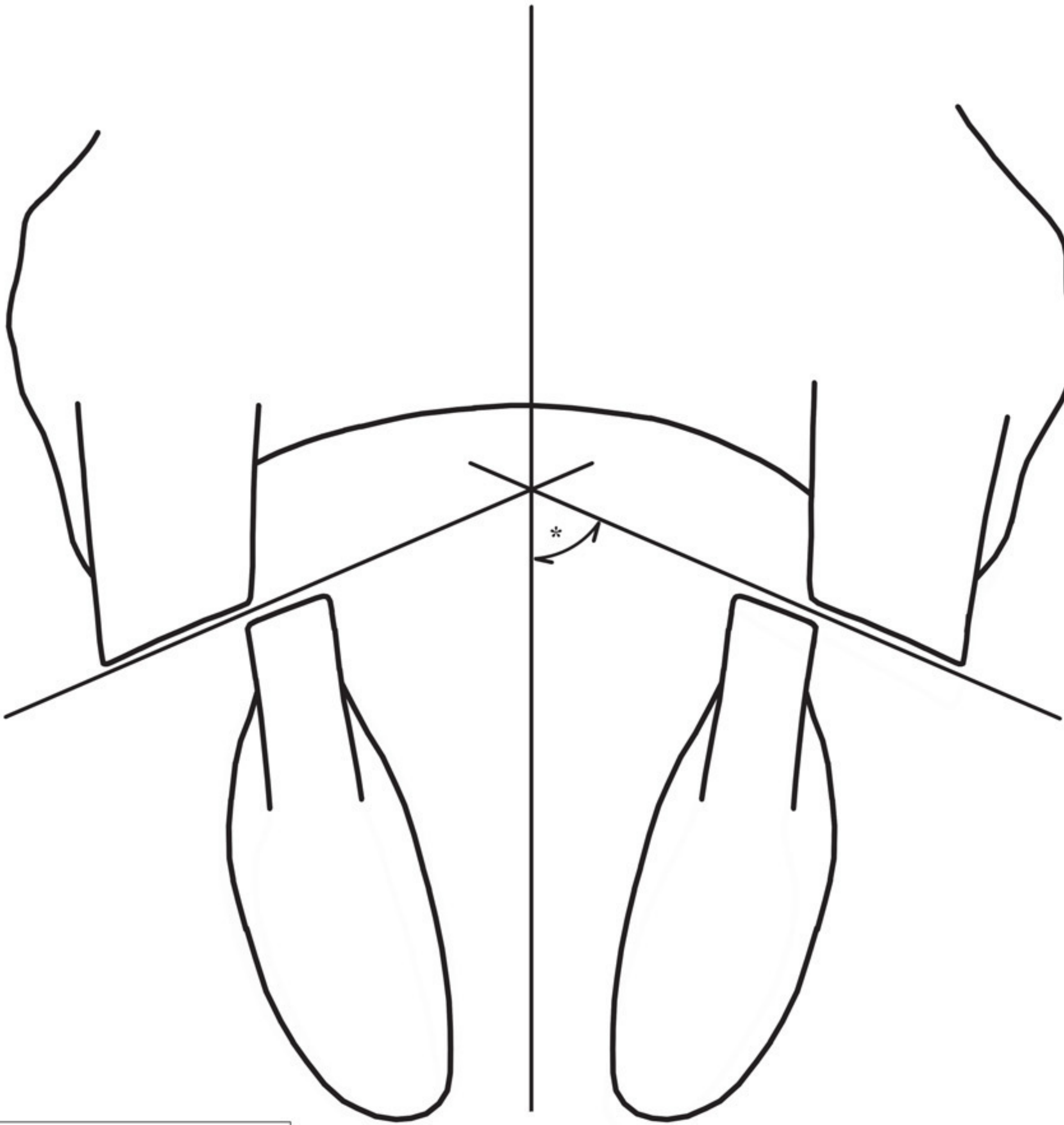


FIGURE 3.45 : OSTEOLOGY

ANISOGNATHIC DENTITION : CROSS SECTION THROUGH THE DENTAL ARCHES (FACIAL REGION - SCHEMATIC)



Original illustration by C. D. Seegers
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* See measurement §53 under Craniometric Data

FIGURE 3.46 : OSTEOLOGY

THE SUPERIOR DENTAL ARCH OF A MATURE COW WITH THE OCCLUSION SURFACES OF THE INFERIOR ARC TEETH SUPERIMPOSED IN CENTRAL OCCLUSION (VENTRAL VIEW)

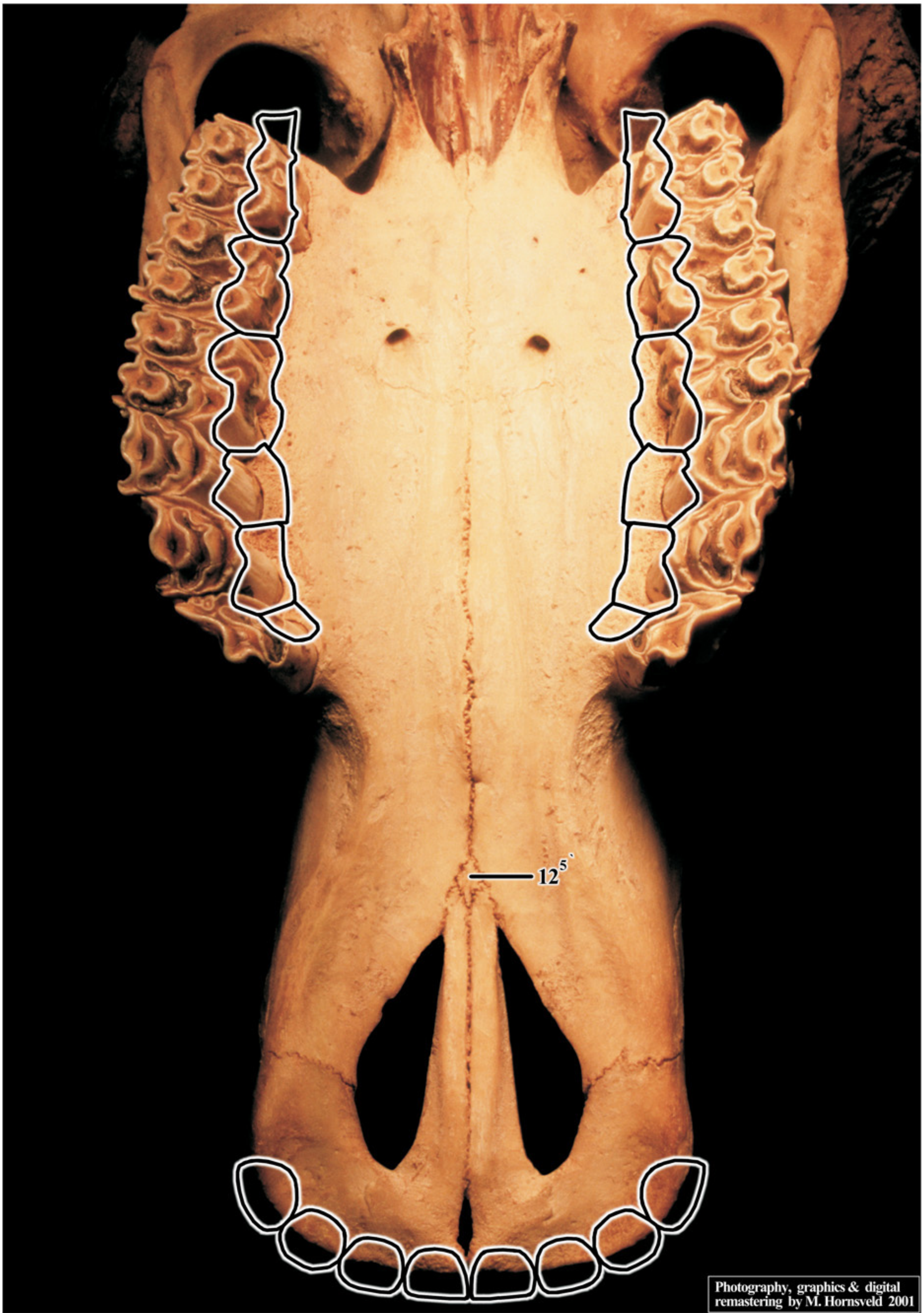


FIGURE 3.47 : OSTEOLOGY

THE INFERIOR DENTAL ARC OF AN OLD BULL (DORSAL VIEW)

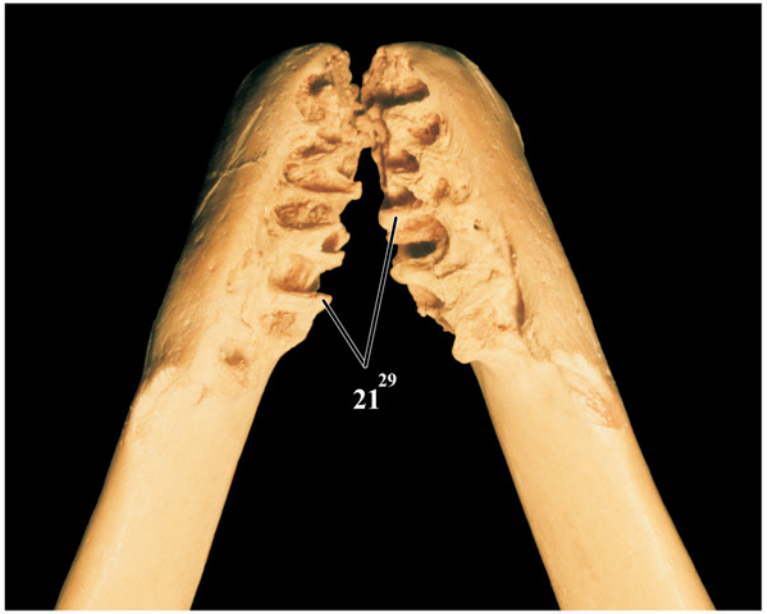
FIGURE 3.48 : OSTEOLOGY

THE OSSEUS COMPONENTS OF THE INTERMANDIBULAR JOINT OF A MATURE COW (LINGUAL AND VESTIBULAR VIEWS)

FIGURE 3.48 : OSTEOLOGY
THE OSSEUS COMPONENTS OF THE INTERMANDIBULAR JOINT OF A MATURE COW (LINGUAL AND VESTIBULAR VIEWS)

LINGUAL VIEW OF DISARTICULATED INTERMANDIBULAR SYNCHONDROSIS (THE INCISORS HAVE BEEN REMOVED)

VESTIBULAR VIEW OF DISARTICULATED INTERMANDIBULAR SYNCHONDROSIS (THE INCISORS HAVE BEEN REMOVED)



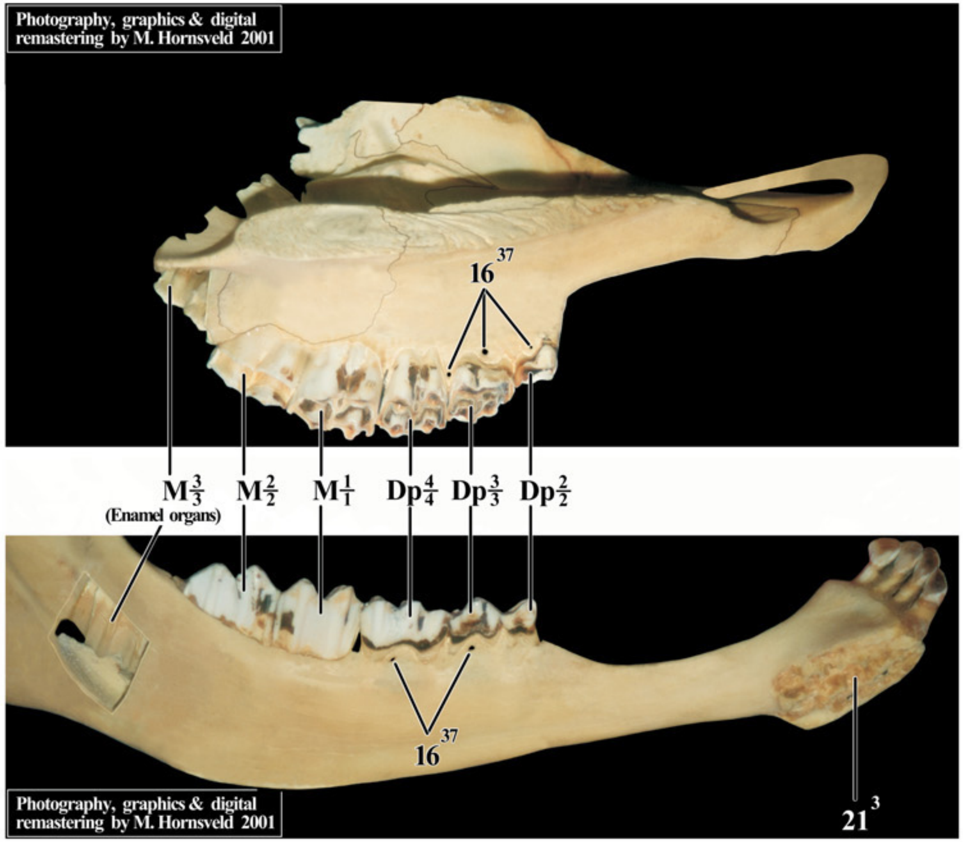
Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.49 : OSTEOLOGY

GUBERNACULA IN SUPERIOR AND INFERIOR DENTAL ARCHES (LINGUAL VIEWS OF LEFT ARCHES)

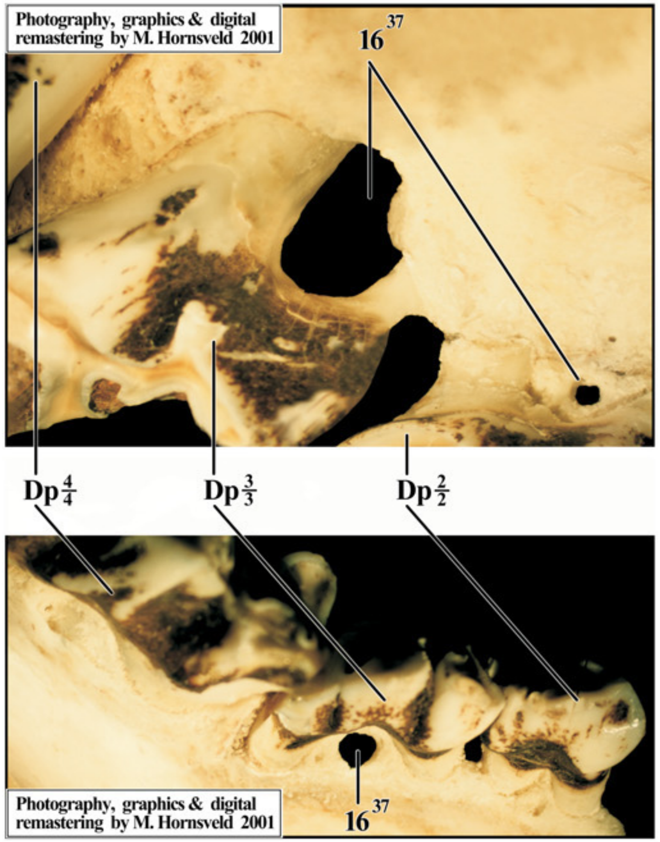
FIGURE 3.49 : OSTEOLOGY
GUBERNACULA IN SUPERIOR AND INFERIOR DENTAL ARCHES (LINGUAL VIEWS OF LEFT ARCHES)

GUBERNACULA OF SUPERIOR ARCH IN
A HEIFER OF APPROXIMATELY 16 MONTHS OF AGE



GUBERNACULA OF INFERIOR ARCH IN
A HEIFER OF APPROXIMATELY 16 MONTHS OF AGE

GUBERNACULA OF SUPERIOR ARCH IN
A CALF OF APPROXIMATELY 4 MONTHS OF AGE



GUBERNACULA OF INFERIOR ARCH IN
A CALF OF APPROXIMATELY 4 MONTHS OF AGE

case, an **additional smaller groove** (**21**[6``]) was also seen bilaterally. (See figure 4.2.) Just dorsal to the caudo-dorsal end of the oblique shallow groove, the pterygoid fossa is marked by the **mandibular foramen** (*Foramen mandibulae* **21**[7]). Dorsally, the ramus bears a rostral coronoid (21[12] , vide infra) and a caudal condylar process (21[8]), that end free **:**

The **condylar process** *(Processus condylaris* **21**[8]) has a **neck** (*Collum mandibulae* **21**[9]) from where the condyl expands laterally and medially. The expanded condyle forms the **"head" of the mandible** (*Caput mandibulae* **21**[10]) which has a larger rostral and a smaller caudal facet for articulation. The **larger facet** (**21**[10`]) faces dorsally, is concave from side to side, and slightly convex from rostral to caudal. It articulates at the temporomandibular joint (7[23]) - which is a synovial joint of the saddle type (*Articulatio sellaris* **21**[10``]) - via a disc (7[23`]), with the articular tubercle. (See 7[21] under the squamous part of the temporal bone.) The **smaller facet** (**21**[10```]) faces caudally and can be either flat or concave. It is positioned more medially on the condyle, and is better circumscribed in older individuals. It articulates with the retro-articular process (7[22]) of the temporal bone. (See also 21[30] below.)

The medial side of the condyle of the mandible is more bulky than the lateral part. Medially, near the articulation surface, it presents a rough, ill-defined area. This area can be slightly elevated or depressed, to form the **pterygoid pit** (*Fovea pterygoidea* **21**[11])* **[152]** .

The **coronoid process** (*Processus coronoideus* **21**[12]) projects dorsally beyond the level of the condyle, curving dorso-caudally. The convex rostral border of the coronoid process is sharply edged. The caudal border of the coronoid process is concave and is separated from the neck of the condyle (21[9]) by the **mandibular incisure** (*Incisura mandibulae* **21**[13]).

The body of the mandible and the inferior dental arc **:**

The body (21[2]) of the mandible is subdivided into and caudal molar and rostral incisive parts

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152 The pterygoid pit (21[11]) renders implantation not only to the lateral pterygoid muscle, but also to one of two insertions of an additional masticatory muscle. The additional muscle takes origin from the pterygoid crest. It is suggested to name this muscle the **Musculus pterygoideus accessorius**. The second insertion of the accessory pterygoid muscle, is on the articular disc (7[23`]). However, the myology of the muscles of mastication of the savannah buffalo falls outside the scope of this thesis. (Also see **footnote 191**.)

(21[14] & 21[22] - vide infra). They share the same lateral and medial surfaces, and their dorsal and ventral margins are continuous **:**

The caudal **molar part** (*Pars molaris* **21**[14]) of the mandibular body is further subdivided into rostral and caudal parts **:**

The rostral part is devoid of teeth, and its dorsal border forms the **interalveolar margin** (*Margo interalveolaris* **21**[15]) or **diastema** (**21**[15`] ) of the mandible. (See also 16[4`] for the maxillary diastema.) The diastema is marked by a sharp edge, which curves medially.

The dorsal margin of the caudal part forms the **alveolar margin** (*Margo alveolaris* **21**[16]). This region of the caudal part of the mandibular body contains the alveoli for the cheek teeth. In lateral view - disregarding the presence and position of the cheek teeth for the moment - the alveolar margin itself has a slight ventral curve. The alveolar margin lies approximately parallel to the gingival line. (See figures 3.65 - 3.70.)

At the junction of the body (21[2]) and the ramus (21[1]) of the mandible, the **ventral margin** (*Margo ventralis* **21**[17]) of the body presents a wide but shallow **vascular incision** (*Incisura vasorum facialium* **21**[18]). Rostral to the ill defined vascular incision - which lies just rostral to the mandibular angel (21[4]) - the ventral margin of the body is slightly convex. The lateral and medial surfaces of the body of the mandible forms the **buccal** and the **lingual surfaces** *(Facies buccalis / Facies lingualis* **21**[19 / 20]) respectively. No clear **mylohyoid line** (*Linea mylohyoidea* **21**[21]) could be seen on the lingual surfaces of any of the mandibles used in this study.

The **incisive part** *(Pars incisiva* **21**[22]) of the mandibular body, contains the alveoli for the incisors and it is dorso-ventrally flattened. The dorsal or lingual surface (21[20]) of the incisive part is to some extent concave. The ventral or **labial surface** (*Facies labialis* **21**[23]) of the incisive part faces the lips and is convex. The alveolar margin of the incisive antimeres considered together as one, curves rostrally to form the **alveolar**

arch (*Arcus alveolaris* **21**[24]). The **mental foramen** (*Foramen mentale* **21**[25]) opens at the junction between the buccal and the labial surfaces of the molar and the incisive parts respectively (vide infra). Often, much smaller secondary foramina open dorsal to the mental foramen to form **lateral mental foramina** (*Foramina mentalia lateralia* **21**[25`]).

The **dental alveoli for the mandibular cheek teeth** (**21**[25``]) are similar to the alveoli of the maxillary cheek teeth (see 16[10]), except that the open and closed ends, lie in opposite directions. (See 16[10] as well as the paragraph that precedes 16[35].) The substance of the dental alveoli is formed by trabecular (1[5`a]) spongy bone that also forms the interalveolar (16[12]) and interradicular septa (16[29]). In old animals the spongy bone of the mandible tends to be more of the lamellar type (2[31]) and is voluminous. The **dental alveoli for the incisor teeth** (**21**[25```]) are similarly composed of trabecular spongy bone (1[5`a]) but are differently arranged because the crowns of incisors are different, and because each incisor only has a single embedded root.

The enamel-covered crowns and the roots of the four incisors of each side, are very similar in morphology to each other. They lie next to each other in a near horizontal plane and their vestibulo-lingual axes diverge distally, in a radiating fashion. (See **Glossary of terms**, and see measurement §17 for the mandible under section D **: Craniometric data**. See figure 3.70.) The alveoli around the proximally embedded parts are also continuously remodelled as the incisors - like the molars - continue to erupt.

The morphology of the mandibular premolars and molars are similar to that of the maxillary premolars and molars. The sizes of the three premolars and the three molars in the upper and lower arcades, all increase slightly from rostral to caudal in each of the four quadrants. (See DENTAL CHARTS under section E **: Applied Anatomical aspects**.) Contrary to the diverging axes of the incisors, the vestibulo-lingual axes of mandibular cheek teeth converge distally. That is similar to these axes of the maxillary cheek teeth. Similarly too, the alveoli of the mandibular cheek teeth are also arranged in a slight lateral curve. (See **Glossary of terms** right at the end and see measurement §52 & 16§ for the cheek teeth under section D **: Craniometric data**. See figures 3.69 & 3.70.)

A line connecting the interalveolar and alveolar margins of both mandibular sides, would describe a laterally flattened arc. This arc, with all the mandibular incisors and cheek teeth, forms the lower or **inferior dental arc** (*Arcus dentalis inferior* **21** [26]). It is incomplete due to the absence of teeth in the diastema (21 [15`] ). The inferior arch is not as wide as the superior arc (see 16 [25] under the maxillary bone) and the dentition of the savannah buffalo is therefore **anisognathic** (**21** [26`]).

<u>The mandibular canal, the biomechanical aspects of the mandible, and the articulation of the mandible as a whole with the skull</u> **:**

The **mandibular canal** (*Canalis mandibulae* **21** [27]) extends between the mandibular foramen (21 [7]) caudally and the mental foramen (21 [25]) rostrally. The mandibular canal and the surrounding alveolar spongy bone - in combination with the physical structure of compact bone of the ramus and of the body - all have a biomechanical role to play in the rigidness of the mandible as a whole.

The caudal part of the mandibular canal traverses the ramus in a rostro-ventral direction. However, the position of the canal - as it traverses the molar part of the body - is parallel to the ventral margin but ventral to the proximal ends of the embedded roots of the cheek teeth. The roof of the canal is perforated by multiple small alveolar openings (Foramina alveolaria 16 [30]) which lead towards the roots of the cheek teeth via small alveolar canals (Canales alveolares 16 [31]). In young animals, the mandibular canal and its contents are dorso-ventrally compressed by the developing permanent teeth, and by their roots. Rostral and caudal to the compressed part, the canal is approximately 8 - 10 mm in diameter. In older animals - where the teeth have already advanced out of their alveoli - the canal becomes laterally flattened yet spacious. The molar part of the mandibular canal - ventral to the cheek teeth alveoli - can then measure approximately 29 mm x 12 mm in diameter, and 140 -160 mm long. The thickness of the lateral and medial walls (of compact bone) that overlays the dental alveoli of the mandibular cheek teeth, measures approximately 4 - 6 mm. Ventral to the canal, the thickness of the compact layer of bone is approximately 10 - 15 mm. Near the mental foramen the mandibular canal is much smaller in diameter and often divides into two or three branches. The short lateral branch - which can be double - opens obliquely onto the buccal surface near the mental foramen, as lateral mental foramina (21 [25`]). Other branches of the mandibular canal, which go on rostrally, continue into the incisive part of the mandible. These branches form minor alveolar canals (Canalis alveolaris 16 [32]) that end at the roots of the mandibular incisors.

The intermandibular suture (21 [3]) between the incisive parts of the bodies is a firm **synchondrotic joint** (*Synchondrosis intermandibularis* **21** [28]) in young animals (see also 1 [19]). Later in life, it appears to change either via a symphysis type of articulation (see also 22 [10]) or even a syndesmosis (22 [6]) to end only very rarely in some animals as a partial synostosis (1 [19`])* **[153]** .

The firmness of the intermandibular joint is augmented by the physical characteristics of the adjoining surfaces. Five or six **finger-like projections** (**21** [29]) of different sizes, interdigitate intricately with each other over the median plane. Functionally therefore - due to the firmness of the intermandibular joint - the two temporomandibular joints behave like a **condylar joint** (*Articulatio condylaris* **21** [30]). The interposed articular discs (7 [23`]) - making each temporomandibular joint congruent - are largely responsible for this mechanism. The physical shape of the discs as well as the mandibular and temporal components of the joints, allow limited lateral movement of the mandible relative to the skull* **[154]** .

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153 No histology was done on the intermandibular joint (21 [3]) to distinguish its synchondrotic nature (21 [28]) from degrees of synostosis (1 [19`]) via degrees of syndesmosis, or direct ossification of cartilage.

154 Pending experimental and mathematical proof, the biomechanical strength of the mandible of savannah buffalo is estimated to be very high. That strength is caused by the architectural layout of the structural components. The rigidity of the buffalo's mandible could be appreciated after the joints were studied, and after overlying bone was sculptured away in more than 18 specimens to expose the dental alveoli. The actual behaviour of healthy temporomandibular joints and the effect on the wear of teeth, could also be estimated after all those specimens were studied. Considering all anatomical aspects, including the superior and inferior arches as functional units, with the mesial drift (19 [25]) of upper and lower cheek teeth, the whole system appears to play an important role in the proper wear of teeth at occlusal and contact surfaces. (See **next footnote**.)

The mandibular cheek teeth remain in proper occlusion with maxillary cheek teeth. Without having markers on the mandible to relate the dental alveoli to, it can only be assumed that mesial drift (19 [25]) of mandibular cheek teeth, occurs in synchrony with mesial drift of maxillary cheek teeth * [155] .

Postnatal embryological development of teeth, the formation of associated temporary canals and foramina, and embryological remnants that can be seen in the mandible **:**

Temporary gubernacular canals (16 [37]) develop in the same way for permanent premolars of the mandible, as they do for the maxillary premolars. (See 16 [35 - 37] , as it also describes the postnatal development of mandibular teeth, and not only that of maxillary teeth. Also see footnote 142 for further comments.) No gubernacular canals for incisors develop.

A small defect of ossification is seen on the lingual surface of the mandible of young animals of approximately three to four months of age. This defect of ossification is located on the medial side of the mandible, rostro-dorsal to the pterygoid fossa, in the region where the ramus join the body. In calves of that age, the defect measures approximately 9 x 5 x 3 mm in size. The defect appears to be an **embryological remnant of Meckel's cartilage** (**21** [31]). In some old animals, evidence of the defect can be seen as an ossified "scar" - or just a **"mark"** (**21** [31`]) - on the lingual surface of the mandible. (See figure 4.2 a & b.) Because this mark does not form on a suture, it cannot actually be regarded as a sutural bone. For the same reason, it should also not be considered as a Wormian bone. (See footnote 28.)

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155 Contact surface wear at the distal ends of mandibular cheek teeth is clearly evident in the dentition of savannah buffalo. This occurs due to the very nature of the converging vestibulo-lingual axes of these teeth and how they are embedded in the dental alveoli. Therefore, mesial drift of individual mandibular cheek teeth appears to occur just as it does in maxillary cheek teeth. It also appears as if mesial drift of the dental alveoli of the mandibular cheek teeth - as a unit - undergoes mesial drift just like the cheek tooth tables of the maxilla (as described under the palatine bone - 19 [25]). However, an increase in the length of the mandibular ramus - between the temporomandibular joint and the caudal end of the molar part of the body - and how it can contribute to this phenomenon, is unknown. If the remnant of Meckel's cartilage can be used as a landmark, it appears as if the region between the remnant and the last cheek tooth contributes mostly to longitudinal growth of the mandible during that time in the life of the animal that the molars develop. Apart from that, the intermandibular joint (21 [3]) is the only suture of the mandible where bone can be added from for longitudinal growth. The length of the mandible nearly doubles during the lifespan of an animal. The absolute distance of mesial drift of mandibular cheek teeth, can therefore be expected to be relatively more than that of maxillary teeth. Although the study on the dentition of the savannah buffalo formed part of this study, the detail of how teeth form, erupt and wear, falls beyond the scope of this thesis. Regarding the dentition overall, the end result is good and the longevity of the animal is favourable, when the upper and lower cheek tooth rows remain matched.

A **false mark** (**21** [31``]) was seen in one case (unilaterally only) due to the proximal (apical) end of the distal root of the last molar that protruded through the compact bone on the lingual side of the mandible. (See figure 4.2 c.) It is not always easy to distinguish marks (or false marks) from periosteal bone reaction due to the effect of the origin of the medial pterygoid muscle on the edges of the pterygoid fossa (21 [6]).

22. THE HYOID BONE

(*APPARATUS HYOIDEUS*) [*OS HYOIDEUM*]

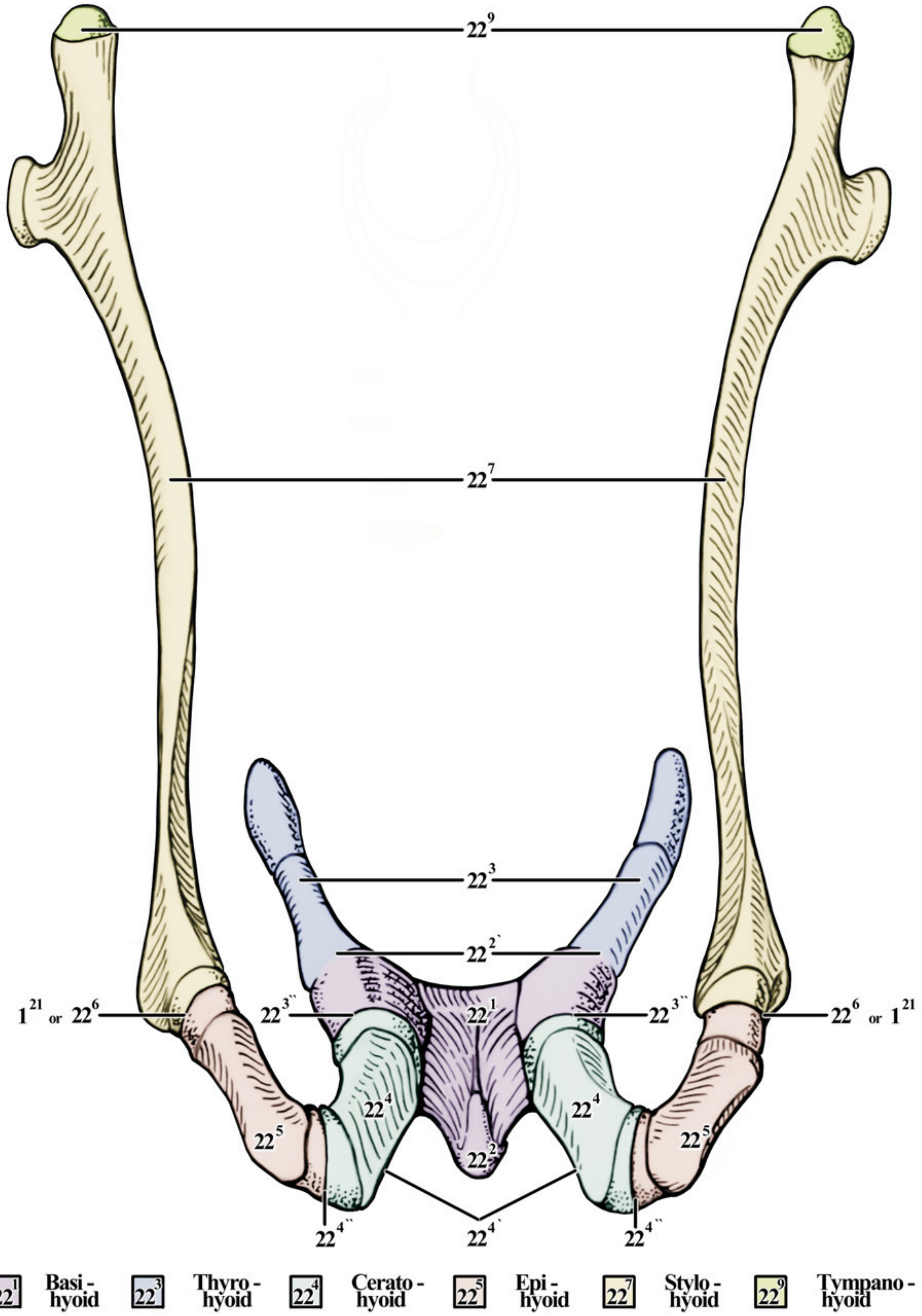
(See figures **3.50 & 3.51**. Also see 3.10.)

The [hyoid bone] is an outdated term, but it is a very convenient term to use when considering all the components of the hyoid apparatus in a non-functional way. The hyoid bone differs from other facial bones in a number of ways. First, it differs regarding the number of constituent parts, and how they are arranged, as there are both paired and unpaired components. Although the constituent parts have to be described individually, all the bones of the hyoid should rather be considered as part of a functional unit, and not as individual bones. Finally, the basic external and internal morphology of hyoid components, also differ from that of skulls bones. These differences include aspects such as the types of articulations found between the bones as well as the osseus types of bone from which they are made up. These morphological aspects may even vary between hyoid bones.

The hyoid bone consists of one unpaired and five paired components. Functionally, these eleven bones essentially form a swing, or a compound pendulum of bones. The unpaired component is the basihyoid bone, and for descriptive purposes, is regarded as the **base and proximal reference point** of the hyoid apparatus. The paired components of the hyoid bone are the stylohyoid, epihyoid, ceratohyoid, thyrohyoid and the tympanohyoid parts. The tympanohyoid differs from the other bones of the hyoid in that it is purely fibro-cartilaginous. Excluding the stylohyoid - which is laterally flattened - the other bones of the hyoid are mostly rodlike in shape with thin, not-so-compact, cortices (1[3`] Substantia compacta). The ratio of the cortex to spongy bone (1[5]) - except the stylohyoid again - is nearly the reverse of what is found in other skull bones. In many respects therefore, the individual bones of the hyoid resemble the structure of long bones of the appendicular skeleton. Also, it appears as if the way in which they ossify - based on visual interpretation of cut surfaces - resembles endochondral ossification. That is despite a developed "periosteum" (vide infra). The bones of the hyoid differ from long bones because they do not have true "epiphysis", and no secondary ossification centres develop at either end.

FIGURE 3.50 : OSTEOLOGY

LINE DRAWING OF THE HYOID APPARATUS (ROSTRAL VIEW)

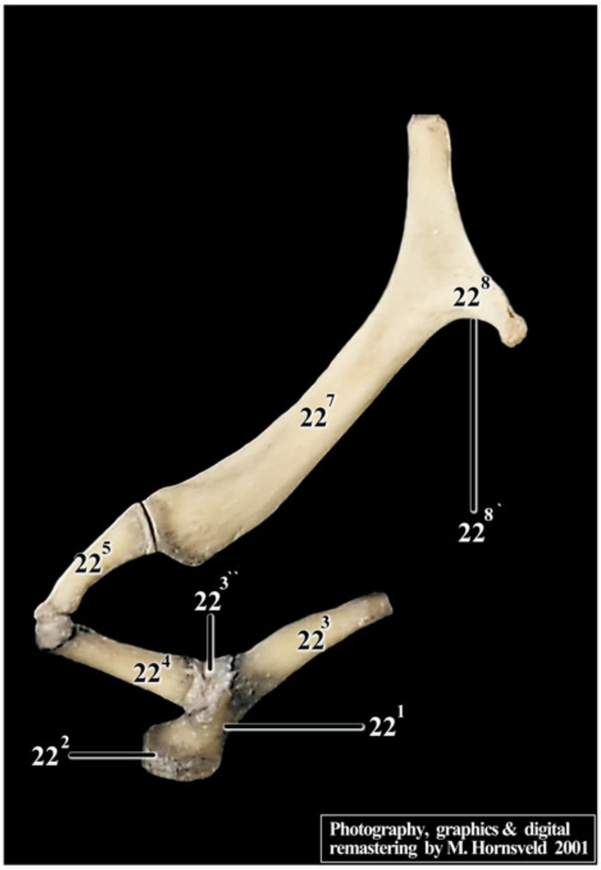


Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.51 : OSTEOLOGY

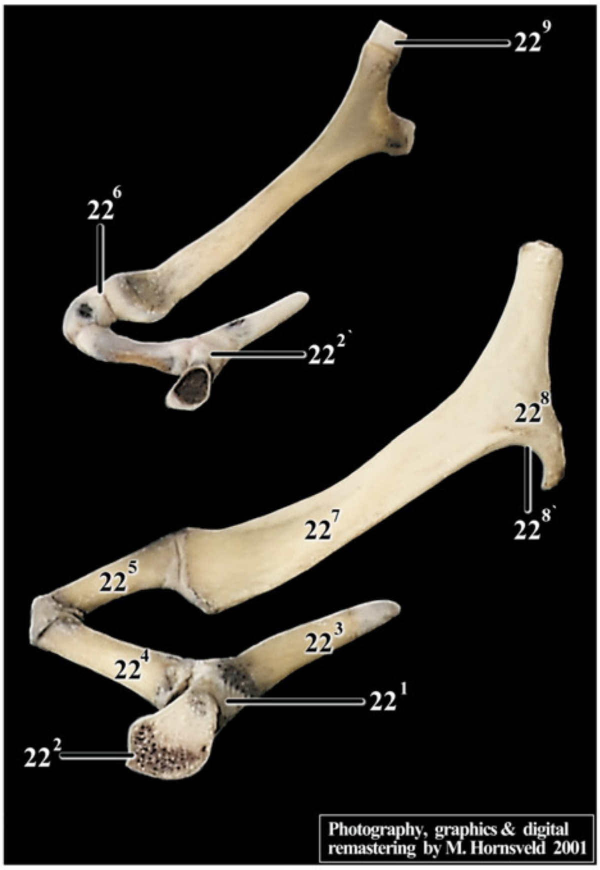
INDIVIDUAL COMPONENTS OF THE HYOID APPARATUS (VARIOUS VIEWS)

LATERAL VIEW OF HYOID APPARATUSSES OF AN OLD ANIMAL



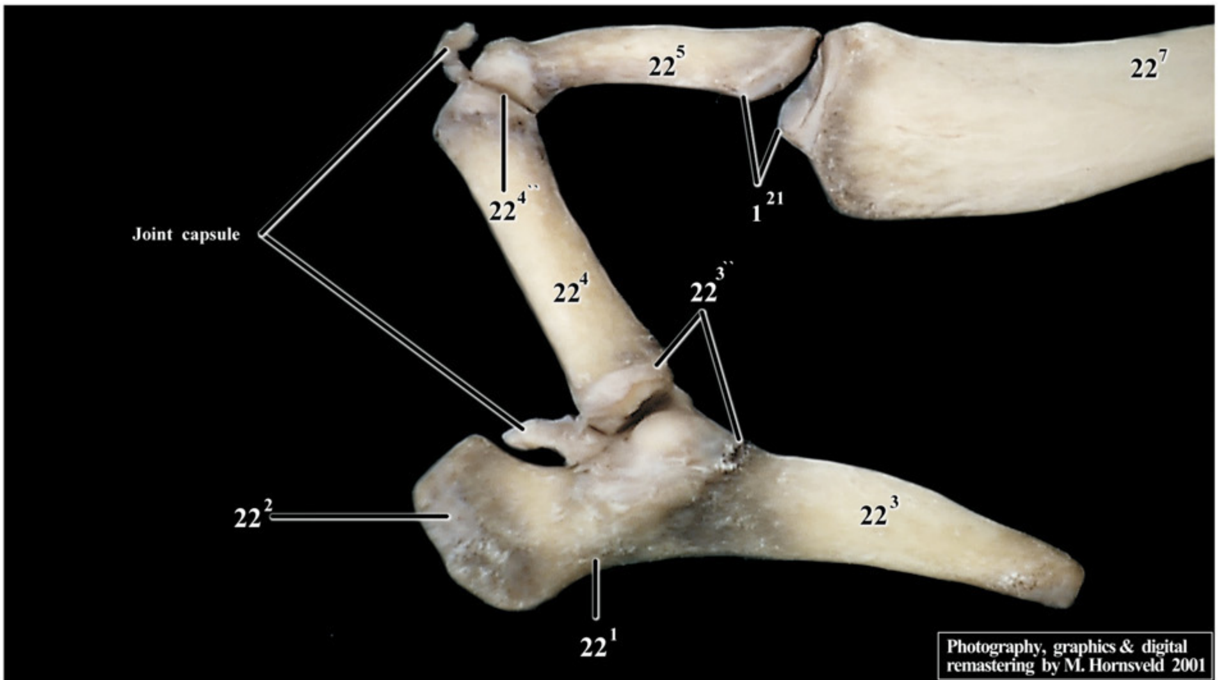
Photography, graphics & digital remastering by M. Hornsveld 2001

MEDIAL VIEWS OF HYOID APPARATUSSES OF A YOUNG AND A MATURE ANIMAL (above and below respectively)



Photography, graphics & digital remastering by M. Hornsveld 2001

OBLIQUE VIEW OF PART OF HYOID APPARATUS WITH SYNOVIAL JOINTS PARTIALLY EXPOSED



Photography, graphics & digital remastering by M. Hornsveld 2001

It is also convenient then, to use the term “diaphysial” parts - as another term of long bones - when reference is made to the mid sections of hyoid bones. The “diaphysial” parts are rich in red bone marrow (1[5``] Medulla ossium rubra) in young animals. Once again, the stylohyoid is different as it is always filled with yellow fat (1[5```]), and strangely enough, also lacks any spongy bone. The proximal and distal “epiphyseal” ends of hyoid bones - including the stylohyoid - remains cartilaginous till late maturity. The periosteum, around all the components of the hyoid bone, is markedly fibrous and well developed. It is so well developed in young animals, that the periosteum is much thicker than the cortices themselves. In very old animals, the periosteum is thin, and the “diaphysial” sections - between the cartilaginous “epiphyseal ends” - are completely ossified. The tympanohyoid however remains completely un-ossified.

<u>The unpaired body of the hyoid bone and the thyrohyoid</u> **:**

The **hyoid body** (*Basihyoideum* **22**[1]) - taken as base and as proximal reference point for the whole hyoid - is a curved bone that lies transversely across the median plane. The convexity of the curve faces rostrally. In the median plane, the rostral border of the basihyoid carries a stubby, laterally flattened, **lingual process** (*Processus lingualis* **22**[2]), that projects rostro-ventrally. The distal end of the process is convex and always cartilaginous. The body is fused on either side by means of large **basihyoid-thyrohyoid synchondrosis** (**22**[2`])*[156] to the **thyrohyoid bones** (*Thyrohyoideum* **22**[3]). Together, the body and the paired thyrohyoid bones describe a half circle that lies in a near horizontal plane *[157] . The caudal end of the thyrohyoid bone articulates by means of an ordinary fibrous joint (1[15]) with the **thyroid cartilage of the larynx** (**22**[3`]). The basihyoid-thyrohyoid synchondrosis of each side, has a convex protuberance dorsally. The convexity of the protuberance is such that it forms a synovial joint (1[21]) of an **ellipsoidal type** (**22**[3``])*[158] for articulation with the proximal end

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156 A basihyoid-thyrohyoid synchondrosis (22[2`]) is not listed in the *N.A.V.* It would be convenient to do so.

157 The topographical position of the hyoid apparatus and its constituent components, is taken as it is suspended in the skull in the datum plane. The datum plane is predefined by the longitudinal axis of the skull and the dorsum of the nose. (See **Glossary of terms** and **General Introduction**.)

158 The *N.A.V.* does not list a term for the ellipsoidal synovial joint (22[3``]) between the basihyoideum and the proximal end of the ceratohyoid bone (22[4]). It would be convenient to annotate this joint.

of the ceratohyoid bone (22[4] , vide infra). The synchondrotic joints between the body of the hyoid bone and the thyrohyoid bones, ossify in late adulthood to form synostoses.

The ceratohyoid bone **:**

The proximal end of the **ceratohyoid bone** (*Ceratohyoideum* **22**[4]) articulates at the ellipsoidal synovial joint (22[3``]) with the protuberance on the basihyoid-thyrohyoid synchondrosis (22[2`] , vide supra). From that articulation, the ceratohyoid projects in a rostro-dorsal direction. The ceratohyoid bone is equal in length to the thyrohyoid bone (22[3] ). It is a sturdy bone that has a medial **longitudinal ridge** (**22**[4`]). In young individuals, the distal end of the ceratohyoid articulates by means of a loose fibrous joint (1[15]) to the proximal end of the epihyoid bone (22[5] , vide infra). In old animals however, this joint reverts from a fibrous joint into a **true synovial joint** (**22**[4``]). (Also see 1[21] and vide infra under footnote 159.)

The epihyoid bone **:**

The proximal end of the **epihyoid bone** (*Epihyoideum* **22**[5]) articulates either via a loose fibrous joint (in young animals) or via a true synovial joint (in older animals) with the ceratohyoid as discussed above. Curving dorso-caudally, the epihyoid is a short bone that is approximately half the length of the ceratohyoid bone. It is slightly flattened laterally. Distally it articulates by means of a **dense fibrous joint** (*Syndesmosis* **22**[6]) with the proximal end of the stylohyoid bone. It appears as if in old animals, this joint may also revert into a synovial joint * [159] .

159 The *N.A.V.* does not list a synovial joint between the ceratohyoid and the epihyoid bones. It appears to be constant in all old savannah buffalo. The presence of the other synovial joint between the epihyoid and the stylohyoid, could not be verified irrevocably as a constant finding because the statistical number of hyoid apparatuses studied, was too low. (See **Materials and Methods**.) It would be convenient to annotate and list at least the synovial joint between the ceratohyoid and the epihyoid. These synovial joints develop from within the loose fibrous connective tissue of the joints. It appears as if both synovial joints only starts to develop after maturity and later in adulthood. However, the ages at which the joints start to develop, could not be determined for the savannah buffalo. Explicit descriptions of synovial joints at these articulations of the hyoid apparatus, could not be found in the literature of other domestic or non-domestic animals. What is seen here, might therefore be unique for the savannah buffalo. The embryological development of contributions from the second and third clasps (or branchial arches) of the primordial splanchnocranium, remains to be studied on the savannah buffalo. Ideally, such a study should be done on a comparative basis that includes all five the other species of wild Bovinae of the Southern African sub-region. No histology was done, as it falls beyond the scope of this study. (See **Discussion**, point 19.)

The stylohyoid bone **:**

The proximal end of the **stylohyoid bone** (*Stylohyoideum* **22**[7]) articulates at the syndesmosis (22[6]) with the epihyoid (22[5], vide supra). The stylohyoid is an elongated bone that is directed dorso-caudally. The bone is laterally flattened and it is approximately seven times longer than the epihyoid bone. The distal end of the stylohyoid is “fused” to the cartilaginous tympanohyoid bone (22[9], vide infra). Near the distal end, the stylohyoid bone has a prominent **stylohyoid angle** *(Angulus stylohyoideus* **22**[8]) which is a caudo-ventrally directed free process. The base of the process-like stylohyoid angle (22[8]), can be as wide as the stylohyoid bone itself, and its distal end is convex and cartilaginous. However, in old animals, the distal end becomes ossified too. The **ventral border** (**22**[8`]) of the stylohyoid angle - where it joins the distal end of the stylohyoid bone - can become markedly concave in some older animals. The cortex of the stylohyoid consists of a compact type of bone. The cortex surrounds a medullary cavity that is lacking spongy bone, but is filled with yellow fat (1[5```]) in the living animal.

The tympanohyoid bone **:**

The proximal part of the **tympanohyoid** (*Tympanohyoideum* **22**[9]) is progressively incorporated into the distal part of the stylohyoid bone by direct ossification. The tympanohyoid thereby becomes very short in old animals. No suture between the tympanohyoid and the stylohyoid can be seen. In both young and old animals, the tympanohyoid is purely fibro-cartilaginous in nature. The tympanohyoid attaches the distal end of the stylohyoid bone (22[7]) to the styloid process (7[45]) of the temporal bone. The tympanohyoid itself - by virtue of its fibro-cartilaginous composition - therefore forms the **symphysis** (*Symphysis* **22**[10]). This symphysis of the hyoid apparatus never ossifies, even in very old animals.

The greatest amount of intrinsic movement between the bones of the hyoid apparatus, occurs at the synovial joint between the body and the ceratohyoid bone at the ellipsoidal synovial joint. Articulation with the temporal bone via the symphysis (22[10]) is free, and it allows a rostro-caudal pendulum-like movement of the hyoid apparatus as a whole.

CHAPTER THREE

RESULTS

SECTION B : THE SKULL AS A WHOLE

(See figures **3.52 - 3.54**. Also see figure 3.2.)

INTRODUCTION **:**

The **Osteology of the Skull** is discussed in detail under 22 subheadings under section A. Individually, all the **Cranial bones** are discussed in the first thirteen subheadings, and the **Facial bones** in the remaining nine. Subheadings 1 & 13 are preambles to the cranial and the facial bones that make up the [neuro-]cranium and [viscero-]cranium respectively. The **Skull Cavities** are discussed in section C that follows this section. Section D deals with the **Craniometric data** and section E with the **Applied Anatomical Aspects**. Outstanding points of possible ontogenetic developmental differences - as well as of clear-cut differences or concepts in the osteology of the skull of the savannah buffalo - are considered under 23 **Discussion** points in chapter four. Although this section needs only very brief attention, the sections on **Skull Cavities**, **Craniometric data**, **Applied anatomical aspects**, and the **Discussion**, should be read with this section. All these sections evaluate '**The Skull as a Whole**'.

OVERVIEW OF THE SKULL AS A WHOLE **:**

The skull as a whole includes the cranial bones, the facial bones, the cranial-, nasal- conchal-, paranasal- and tympanic cavities, the mandible, the hyoid apparatus and the various joints, fusions and articulations that form between bones. The external configurations of all these bones, give the unique external morphology of the skull and mandible of the savannah buffalo.

The skull is essentially pyramidal in shape. Internal configurations of these bones determine the morphology of the cranial, nasal and oral cavities. The differences between the external morphology and the internal configurations of the cranial and the nasal cavities, give an

FIGURE 3.52 : THE SKULL AS A WHOLE

THE SYNCHONDROSES AT THE BASE OF THE SKULL OF A YOUNG CALF (DORSAL VIEW)

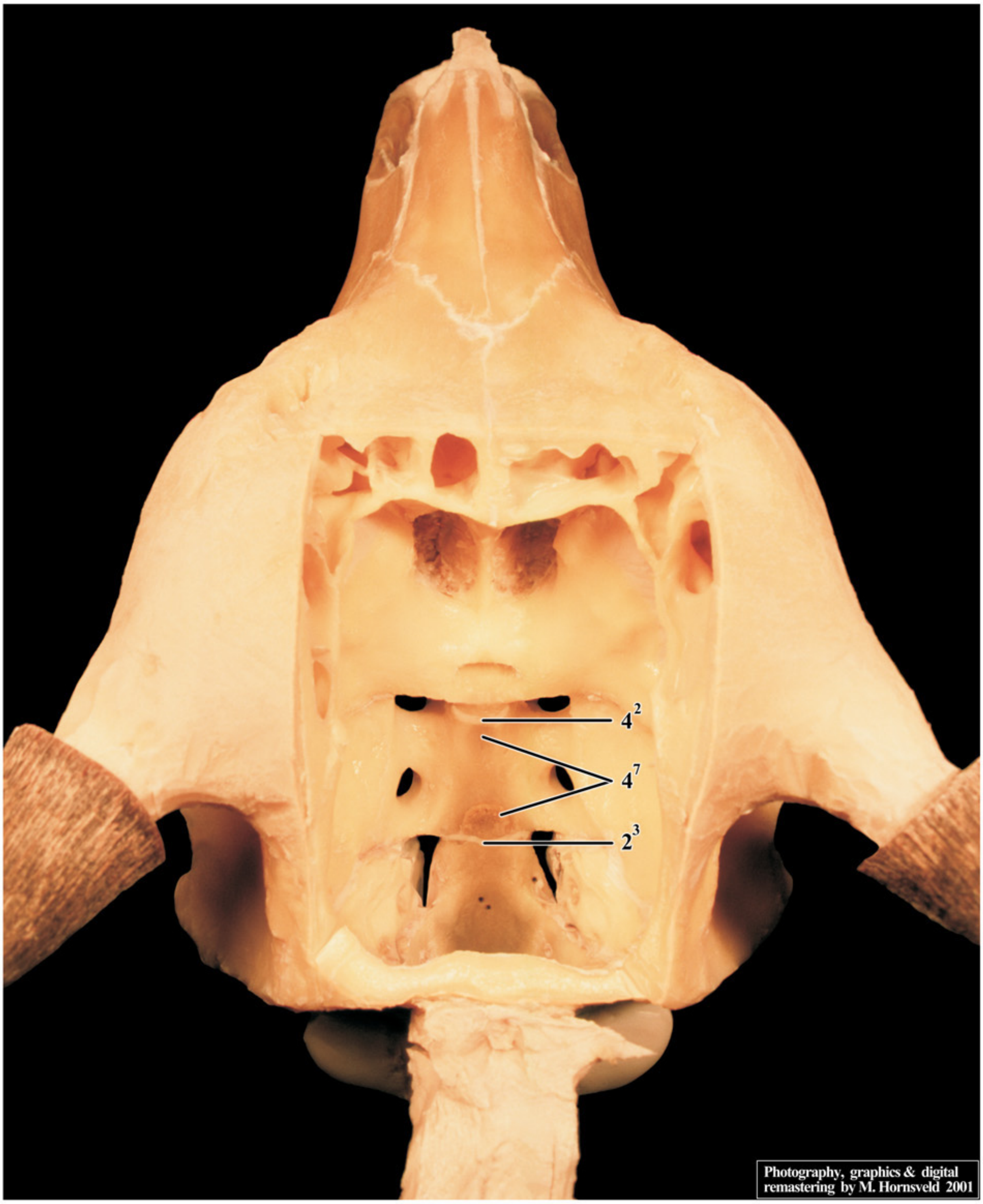


FIGURE 3.53 : THE SKULL AS A WHOLE

THE SYNCHONDROSES AT THE BASE OF THE SKULL OF AN IMMATURE ANIMAL (MEDIAL VIEW)

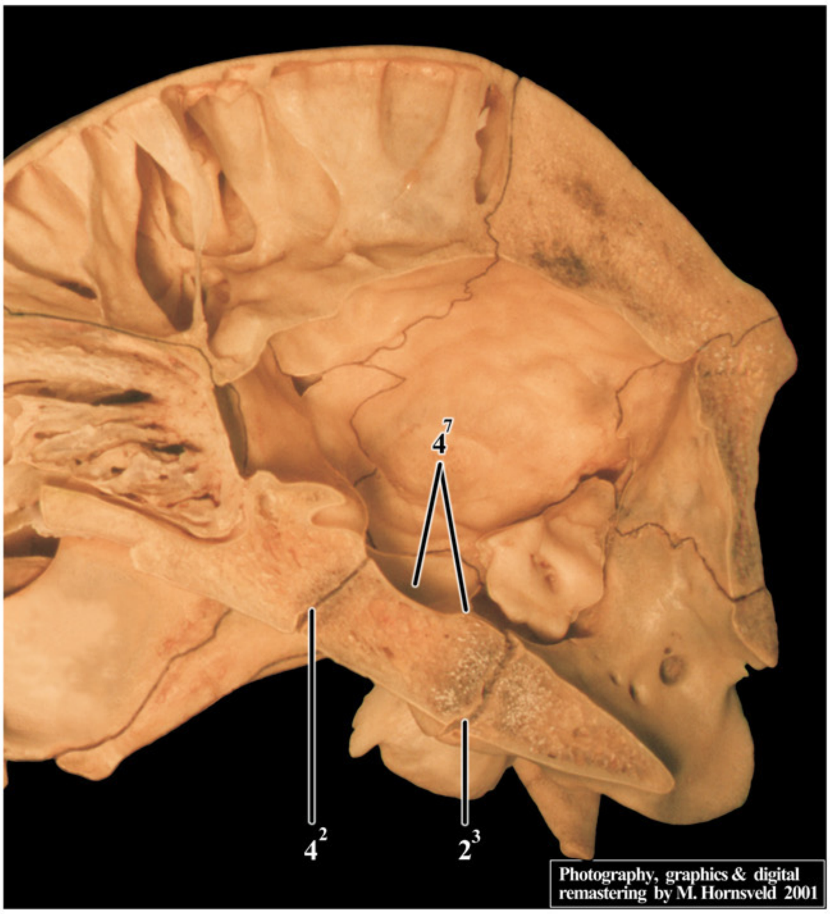


FIGURE 3.54 : THE SKULL AS A WHOLE

THE BASE OF THE SKULL OF AN OLD BULL (DORSAL VIEW)

FIGURE 3.54 : THE SKULL AS A WHOLE
THE BASE OF THE SKULL OF AN OLD BULL (DORSAL VIEW)

indication as to the size of the paranasal, conchal and tympanic cavities. Growth of the animal to acquire its eventual body-shape and size, is a fulfilment of genetic and environmental factors. To determine all that, falls beyond the scope of this study. But, growth ultimately determines the eventual size and shape of the bones of the head.

Ossification of the spheno-occipital and intersphenoidal synchondrosis (2 [3] and 4 [2] respectively) at the base of the skull are complete. (See figures 3.52 - 3.54.) The Turkish saddle (4 [7]) as a whole is annotated, and it shows the relative changes that take place in the hypophysial fossa (4 [4]) and the dorsum sellae (4 [5]) as animals age. In the illustration of the old bull, the hypophysial fossa is deep and the dorsum sellae is prominent. In that particular skull, the dorsum sellae also presents a dorsal groove and clear caudal clinoidal processes (4 [6]). The temporal meatus (7 [88]) and the condylar canal (2 [11]) are also indicated in the illustration of the old bull as they typically become voluminous in old animals. (Also see figure 3.2.)

Circumstantial evidence and a review of the literature indicate the following **:**

(1) The dimensions of the cranial cavity per se are determined more by the brain than by any other factors of the skull. The outer dimension on the other hand, shows excessive increases of parts of the [neuro-]cranium. These changes occur during the growth period of the animal. These increases are disproportionate to the volume of the cranial cavity and can best be seen in the skulls of old bulls. The enlarged outer dimensions of the [neuro-]cranial part of the skull (as seen in older animals), also satisfies the increased needs for muscle attachment at the head-neck junction.

(2) The final dimensions of the nasal cavity are determined by the external configuration of the facial bones that are in proportion to the [neuro-]cranium, to body size in general, and to the degree of aeration that occurred in the cranial and the facial bones. The [viscero-]cranium accommodates a set of teeth that are in proportion to the volume, type and quality of food that has to be taken in by this

animal. Masticatory muscles of matching size, takes origin from both the [neuro-]- and the [viscero-]cranium to insert on the mandible.

(3) The cornual process is induced by factors in the skin from which the epidermal horn takes origin from. Apart from genetic factors, the reciprocal interactions between the boney cornual process and the horn - which eventually culminates in "horn size" - are caused or influenced by hormones, and by the life span of the animal. The excessive and continuous enlargement of the base of the cornual process, and subsequently also of the Calvaria, distorts the outer dimensions of the [neuro-]cranium beyond what is induced for by the brain. The reason for the excessive development of the cornual process and the horn, falls beyond the scope of this study.

Minute detail of all the above aspects are considered in the text and in the **Discussion**. Because a study on the embryological development of the skull falls beyond the scope of this study, the skull as a whole can only partially be considered from a possible ontogenetic developmental point of view. The gross macroscopic appearance can however be fully appreciated. To what degree the ontogenetic development of the skull of the savannah buffalo is in par with the norm - as set by the bovine, other domestic animals and the human - is taken up in the **Discussion**. The peculiarities of the fissures, sutures, and fontanelles that are found in the skull of the savannah buffalo, forms part of the detail description and is taken up in the **Discussion** too.

CHAPTER THREE

RESULTS

SECTION C : THE SKULL CAVITIES

(See figures **3.55 & 3.56**.)

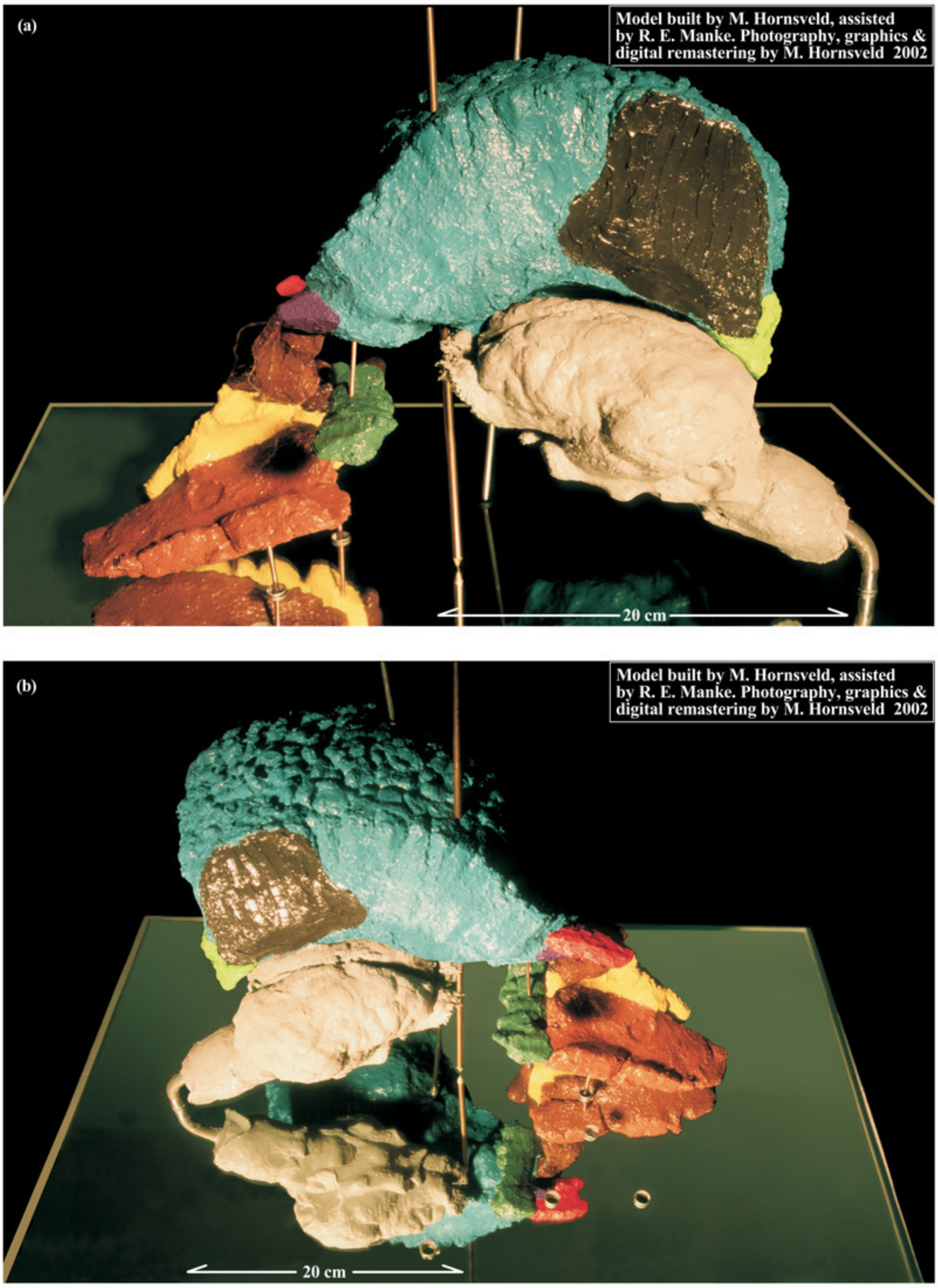
The " cranial cavity "

" Cavum cranii "

The internal layer of the bones that contribute to form the floor, lateral walls and roof of the "cranial cavity", have been discussed under the relevant bones of the cranium, as summarized in subheading 1. Also, those osseus boundaries which demarcate the borders between the rostral, the middle and the caudal compartments of the cranial cavity - as well as the ethmoidal fossae - have been discussed in detail under the relevant bones. (See for instance 5[12`] , 10[29] & 11[10] .) The cribiform plate of the ethmoid bone separates the cranial cavity from the nasal cavities. The "cranial cavity" harbour or contain the brain, the meninges and all the blood vessels associated with the brain. The membranous dura mater enhances the visual subdivisions of the cranial cavity in the living animal - as seen after removal of the brain - by being connected to various osseus prominences. The "cranial cavity" - filled up with the brain - is therefore not a true "cavity" but actually a semantic error that is allowed for descriptive purposes.

FIGURE 3.55 : SKULL CAVITIES

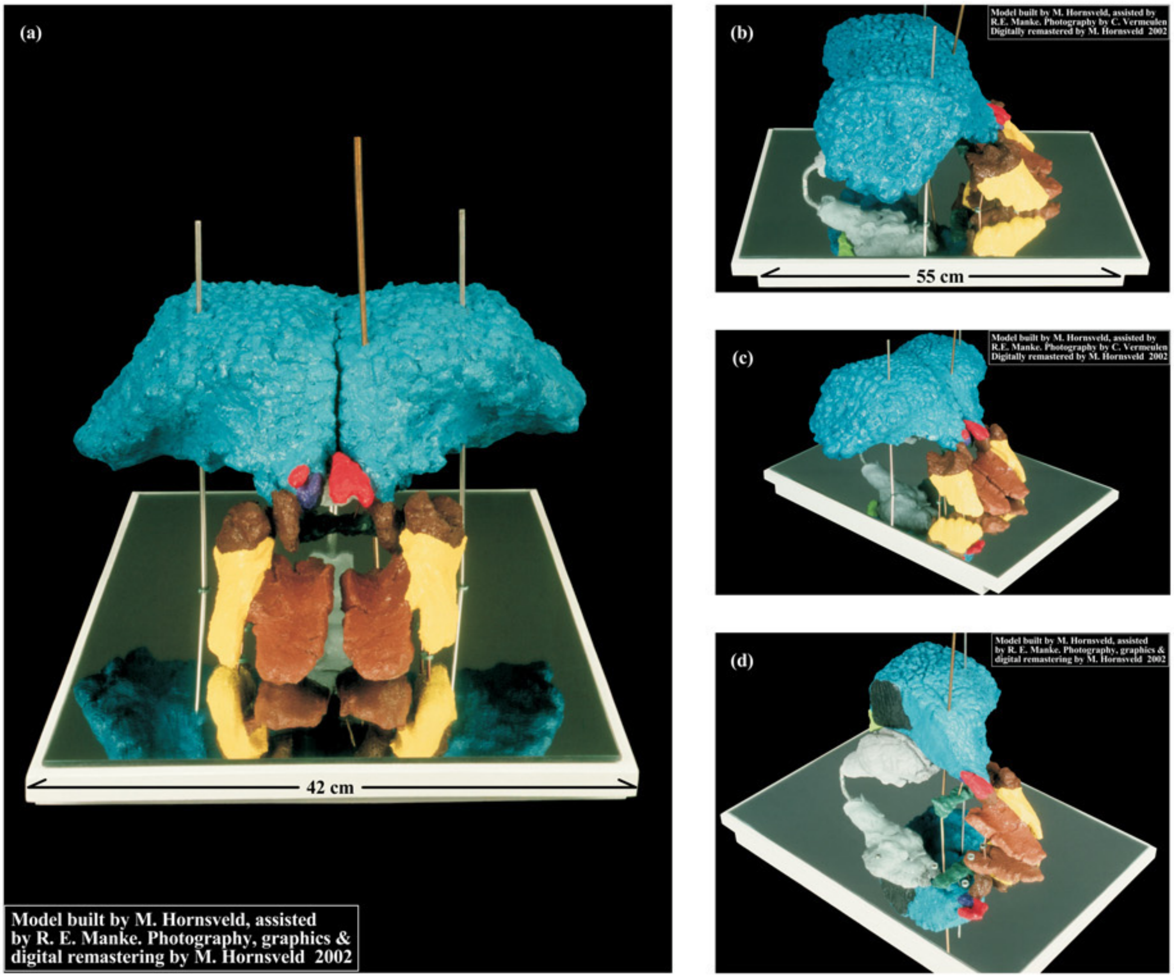
ENDOCAST OF THE CRANIAL CAVITY IN (a) LEFT AND (b) RIGHT VIEWS WITH MIRROR REFLECTIONS



Cranial cavity
Communication between left and right frontal sinus complexes
Occipital part
Frontal & Parietal parts
Nasal part
Dorsal conchal part
Sphenoidal part
Maxillary sinus
Palatine sinus
Lacrimal parts

FIGURE 3.56 : SKULL CAVITIES

ENDOCASTS OF THE OSSEUS BORDERS OF THE PARANASAL CAVITIES IN (a) ROSTRAL (b) LATERAL AND (c & d) ROSTRO-LATERAL VIEWS WITH MIRROR REFLECTIONS



Cranial cavity	Communication between left and right frontal sinus complexes	Occipital part	Frontal & Parietal parts				
Nasal part	Dorsal conchal part	Sphenoidal part	Maxillary sinus	Palatine sinus	Lacrimal parts		

The nasal and oral cavities

Cavum nasi & Cavum oris

The nasal and oral cavities are true cavities contained within the skull. In the live animal, the volume of the oral cavity is much smaller than the perception one gets when looking at the teeth and the external osseus borders of the facial part of the skull and the mandible. This is due to all the soft tissue structures associated with this part of the gastrointestinal tract. The size of the oral cavity varies between a potential space, to a voluminous space when the mouth is opened. In the living animal, the inner dimensions of the divided nasal cavity, is also much smaller than can be judged from the size of the face. This is so because the nasal conchae take up most of the space. Apart from the osseus structures, the nasal mucosa reduces the size of the nasal cavity even further. The detail of the internal osseus borders of the nasal cavity has been discussed under the relevant bones that make up the face (under subheadings 14 - 20). The nasal cavity is separated from the cranial cavity by the cribiform plates of the ethmoid bone and from the oral cavity by the boney palate. The osseus borders of the nasal cavity - and how the left and right antimeres are separated from each by the nasal septum - have been discussed under the bones of the face (subheading 13) and elsewhere (especially the ethmoid bone and vomer). The nasal cavity antimeres communicate ipsilaterally with the paranasal sinuses.

Paranasal cavities

Sinus paranasales / Bulla conchalis ventralis

The paranasal sinuses are paired structures that are air filled cavities within particular bones of the skull. Because of facts concerning the living animal, the paranasal sinuses are considered part of the Splanchnology of the head region, and specifically as extensions of the nasal cavity. However, the osseus borders and communications between components of the paranasal sinuses, as well as their connections to the nasal cavity, reflect the situation in the living animal closely. Further detail of these connections have to be confirmed by a separate study on the Splanchnology. In the live animal, the internal surfaces of the sinuses are lined with a mucous secreting respiratory epithelium. Where fissures disrupt the continuity between bones that form the inner osseus walls of the nasal cavity, a mucoperiosteum and a layer of nasal mucosa, would conceal the defects on the sinus and nasal sides respectively. No histology was done however to confirm that, as it falls beyond the scope of this study. The paranasal sinuses are subdivided into two functional compartments that are based on their separate communication to different parts of the nasal cavity. True communication of the maxillary sinus complex to the nasal cavity, is via a boney canal (see 17 [5]) and its nasomaxillary aperture, to the middle nasal meatus. (See footnote 145.) The apertures at both ends of that boney canal are delineated by nasal mucosa and therefore also forms part of a study on the Splanchnology. Communications of the frontal sinus complexes are via various openings into the ethmoidal meatuses (see under 11[4]). The osteological detail of these communications have been described under the relevant sections under the osteology and are discussed further in chapter four. (See **Discussion**.) The dorsal nasal concha communicates with the frontal sinus. The ventral conchal bone encloses bullae and cellulae. Based on circumstantial evidence supplied by the osteological detail, it is believed by this author that these spaces of the conchal bone are isolated spaces that do not communicate with the nasal cavity nor with the paranasal sinuses. The continuous enlargement of the air containing cavities in the skull depends not only on growth of the skull but also on continued displacement of the diploë.

The tympanic cavity

Cavum tympanii

The tympanic cavity (7 [41]) is part of the middle ear cavity. An additional cavity (7 [41``b]) was found in some skulls in the ventral part of the semi-tubular part of the tympanic part of the temporal bone. Such cavities communicate with the tympanic cavity, and by that they can effectively enlarge the resonating capacity of the middle ear. (See footnote 68.)

CHAPTER THREE

RESULTS

SECTION D : CRANIOMETRIC DATA

(See figures **3.57 - 3.71**.)

INTRODUCTION :

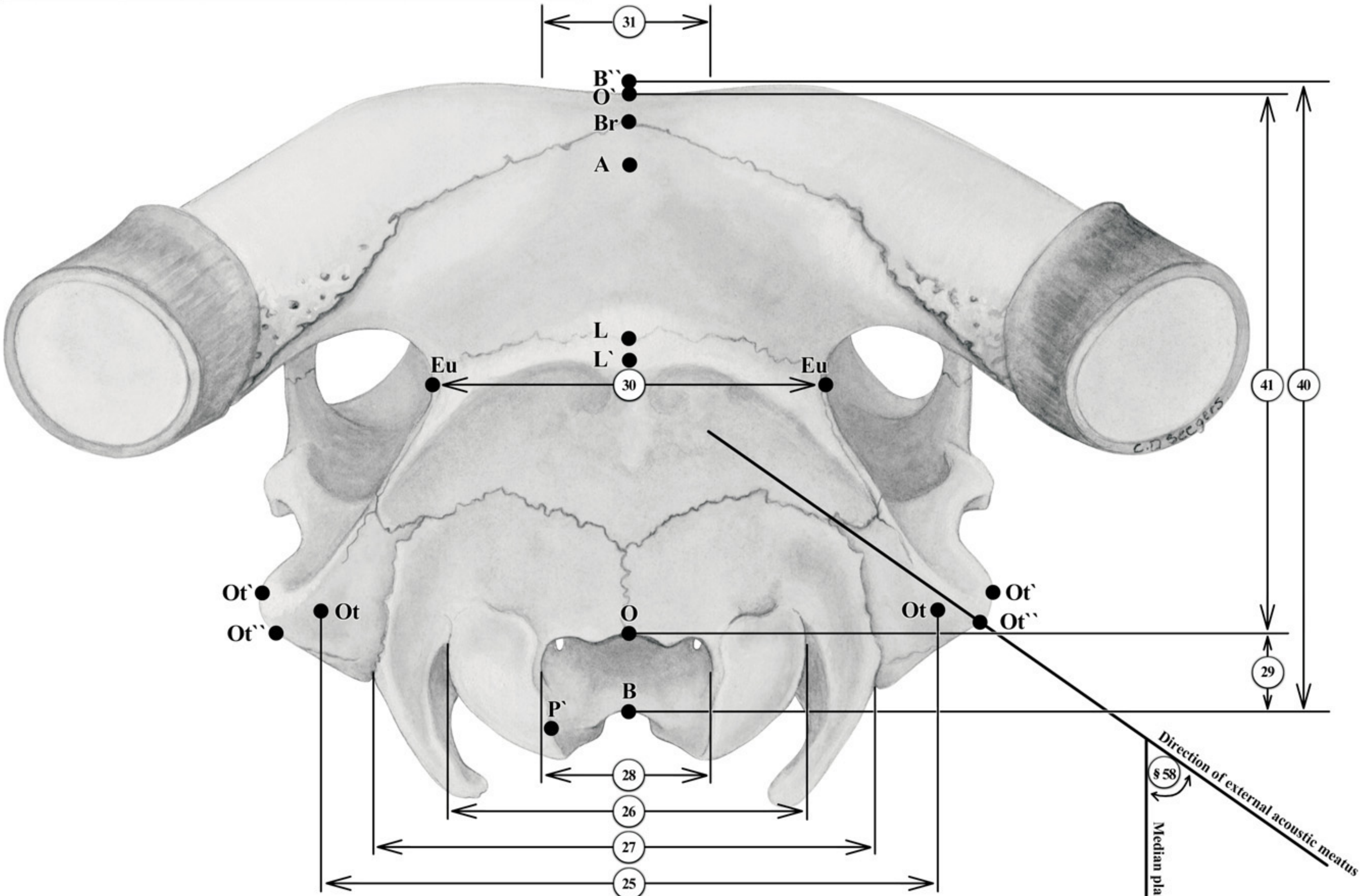
The craniometric data of skulls of two immature animals, two older animals and one trophy-sized savannah buffalo bull were analysed for this section. These skulls are representative samples of the skulls used in this study on the osteology. The data of these skulls should give readers that are not familiar with this animal, a good idea of the size of the skulls of this species. The relative and absolute growth of different parts of the skull (as described in section A) is not always that easy to comprehend. However, having the data of younger as well as of older skulls - and of both genders - analysed simultaneously, helps one to understand relative growth at least to some extent. The comparative way in which this section on the **Craniometric data** is approached, also helps to elucidate points of sexual dimorphism.

The ages and the age determination for the skulls used in this section are relevant. Based on the eruption and wear of the teeth - and on the ossification of the sutures - gives the following ages for the different skulls **:** The skull of the trophy-sized bull could have been between 15 and 20 years of age. The older cow resembles animals of approximately 10 - 15 years of age. The immature bullock represents male animals of approximately 2 years of age, and the heifer typifies females of approximately 16 months. The hyoid apparatuses used in this section spans the age group from three-month-old calves to old bulls. Unfortunately, no hyoid bone specimens of the immature bullock or heifer were available. Neither was the mandible available of the trophy sized bull.

Tables 3.1 - 3.3 reflect the results of the data collected and indexes calculated (vide infra).

FIGURE 3.57 : CRANIOMETRIC DATA

CAUDAL VIEW OF THE SKULL OF A HEIFER OF APPROXIMATELY 16 MONTHS



Original illustration by C. D. Seegers
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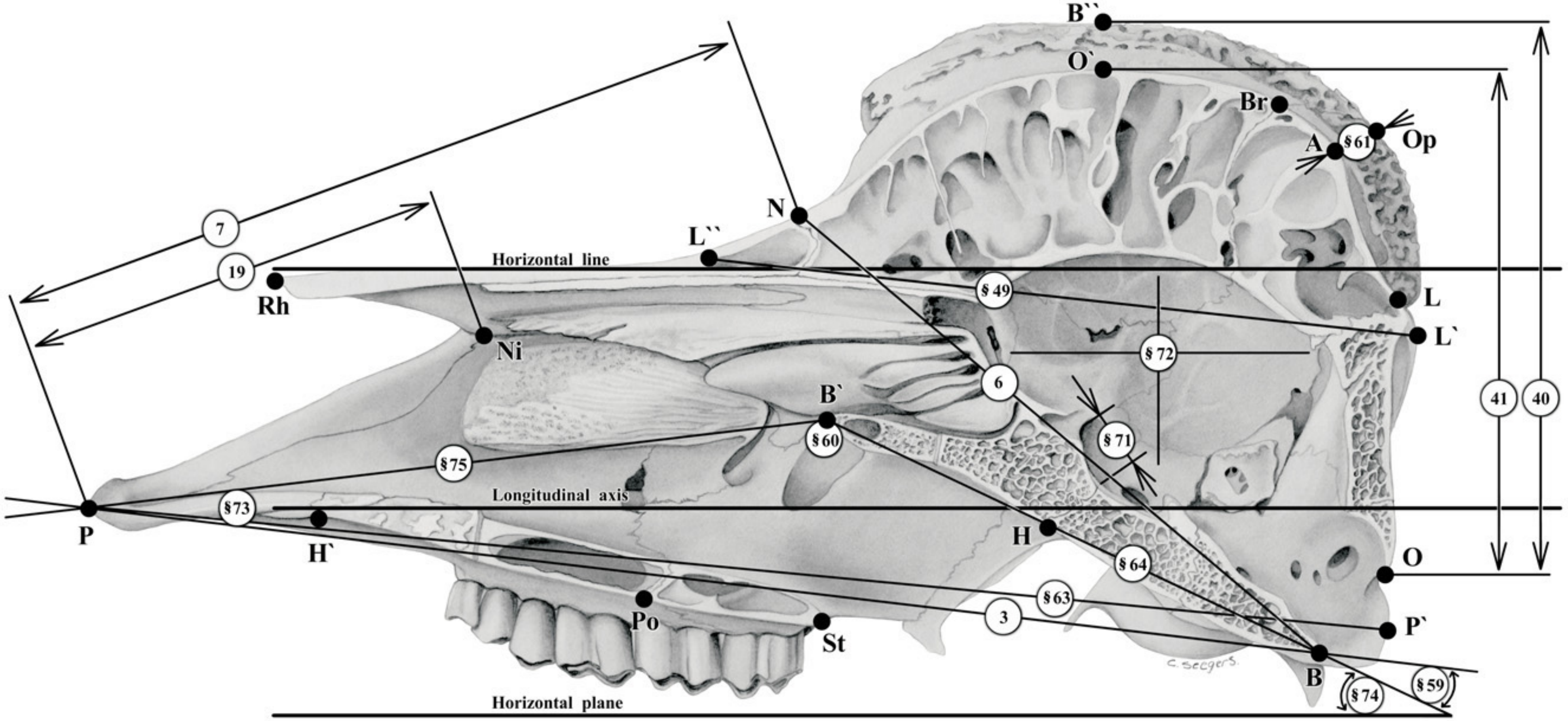
FIGURE 3.57 : CRANIOMETRIC DATA
CAUDAL VIEW OF THE SKULL OF A HEIFER OF APPROXIMATELY 16 MONTHS

FIGURE 3.58 : CRANIOMETRIC DATA

MEDIAL VIEW OF THE SKULL OF A MATURE BULL



Original illustration by C. D. Seegers
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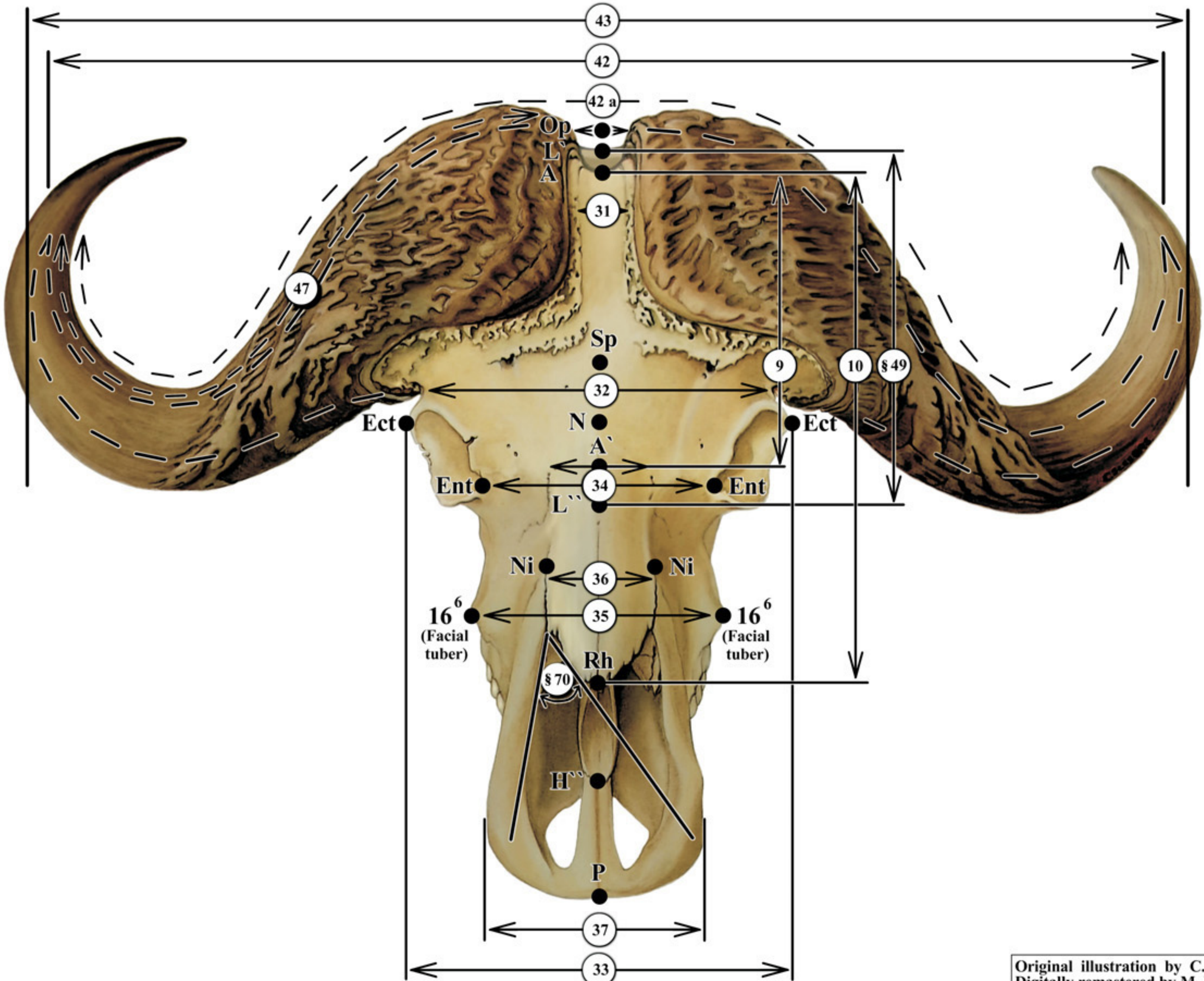
FIGURE 3.58 : CRANIOMETRIC DATA
MEDIAL VIEW OF THE SKULL OF A MATURE BULL

FIGURE 3.59 : CRANIOMETRIC DATA

DORSAL VIEW OF THE SKULL OF A MATURE BULL

FIGURE 3.59 : CRANIOMETRIC DATA
DORSAL VIEW OF THE SKULL OF A MATURE BULL



Original illustration by C. D. Seegers
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FIGURE 3.60 : CRANIOMETRIC DATA

THE VOMER (SEMI-SCHEMATIC)

THE VOMER (SEMI-SCHEMATIC)

FIGURE 3.60 : CRANIOMETRIC DATA

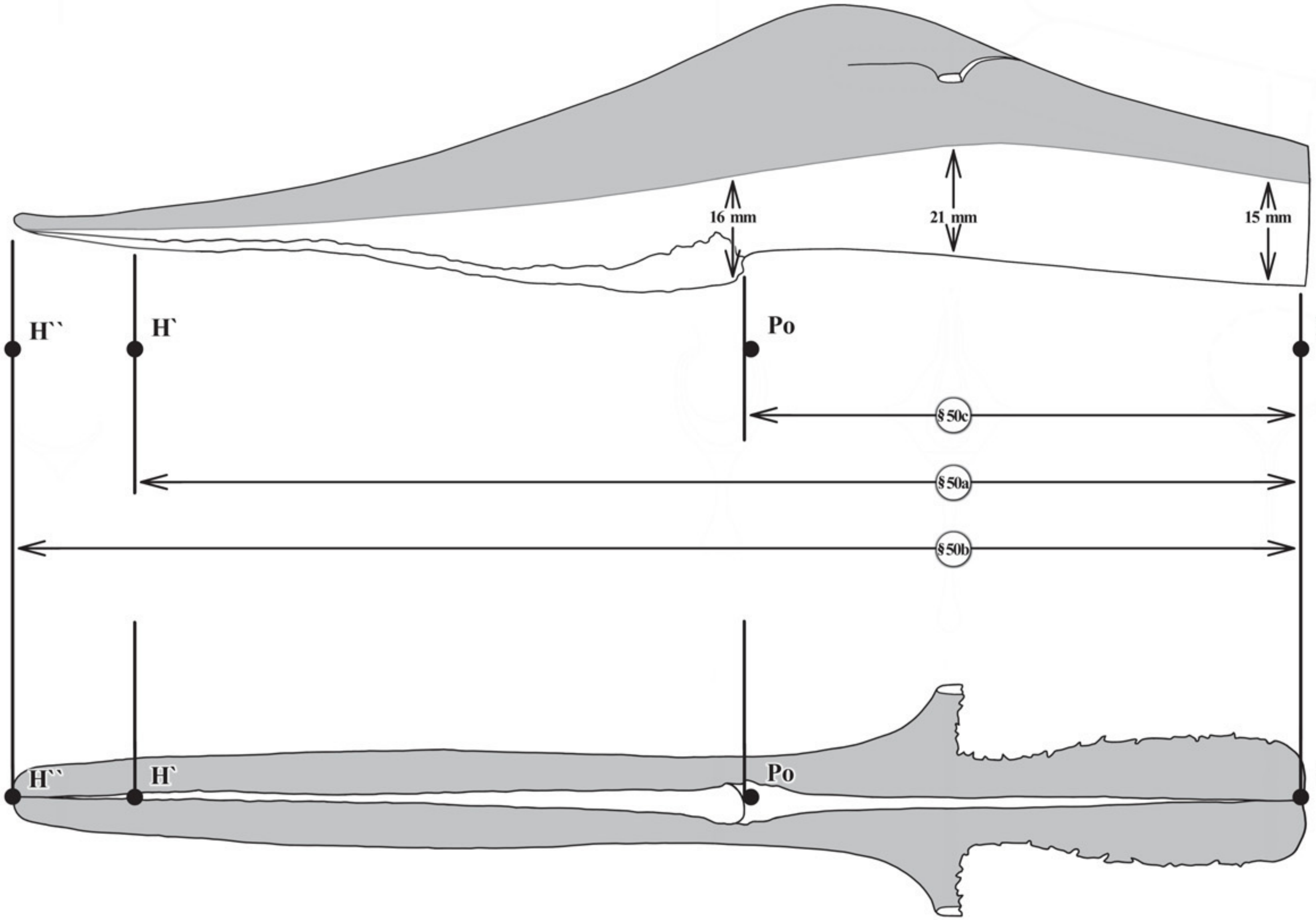

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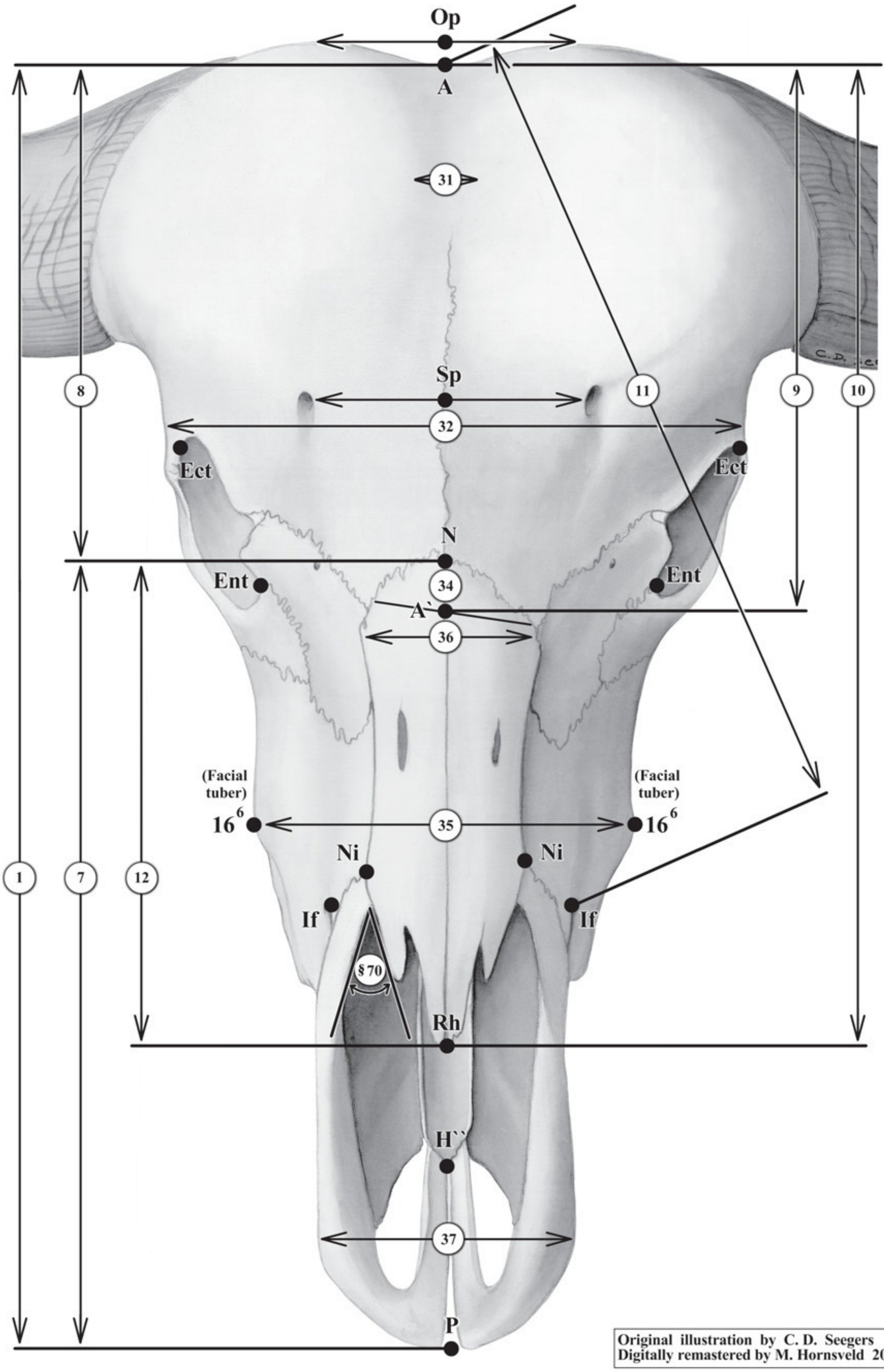
FIGURE 3.61 : CRANIOMETRIC DATA

DORSAL VIEW OF THE SKULL OF AN IMMATURE COW



Original illustration by C. D. Seegers
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FIGURE 3.62 : CRANIOMETRIC DATA

LATERAL VIEW OF THE SKULL OF AN IMMATURE COW

FIGURE 3.62 : CRANIOMETRIC DATA
LATERAL VIEW OF THE SKULL OF AN IMMATURE COW

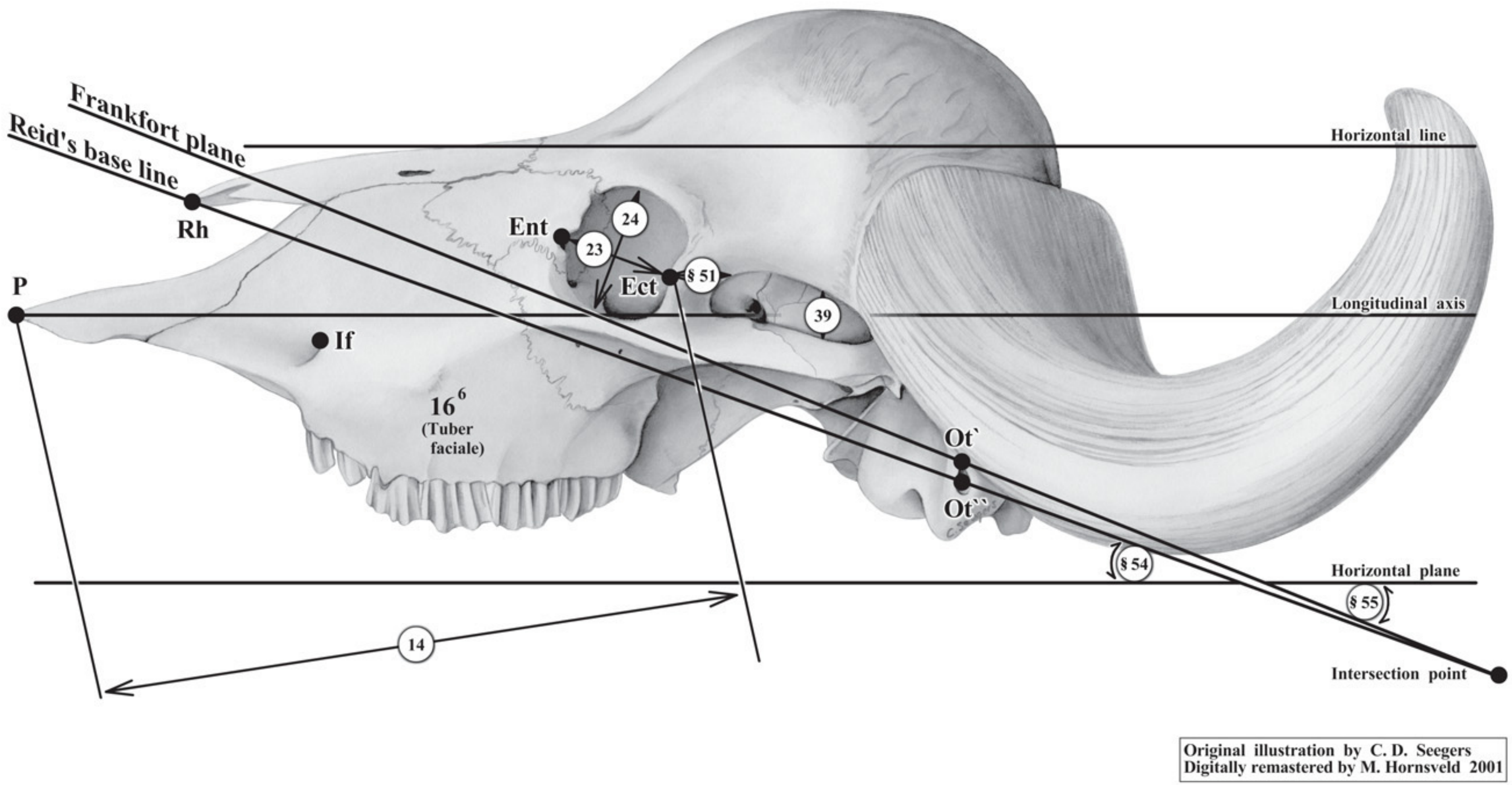
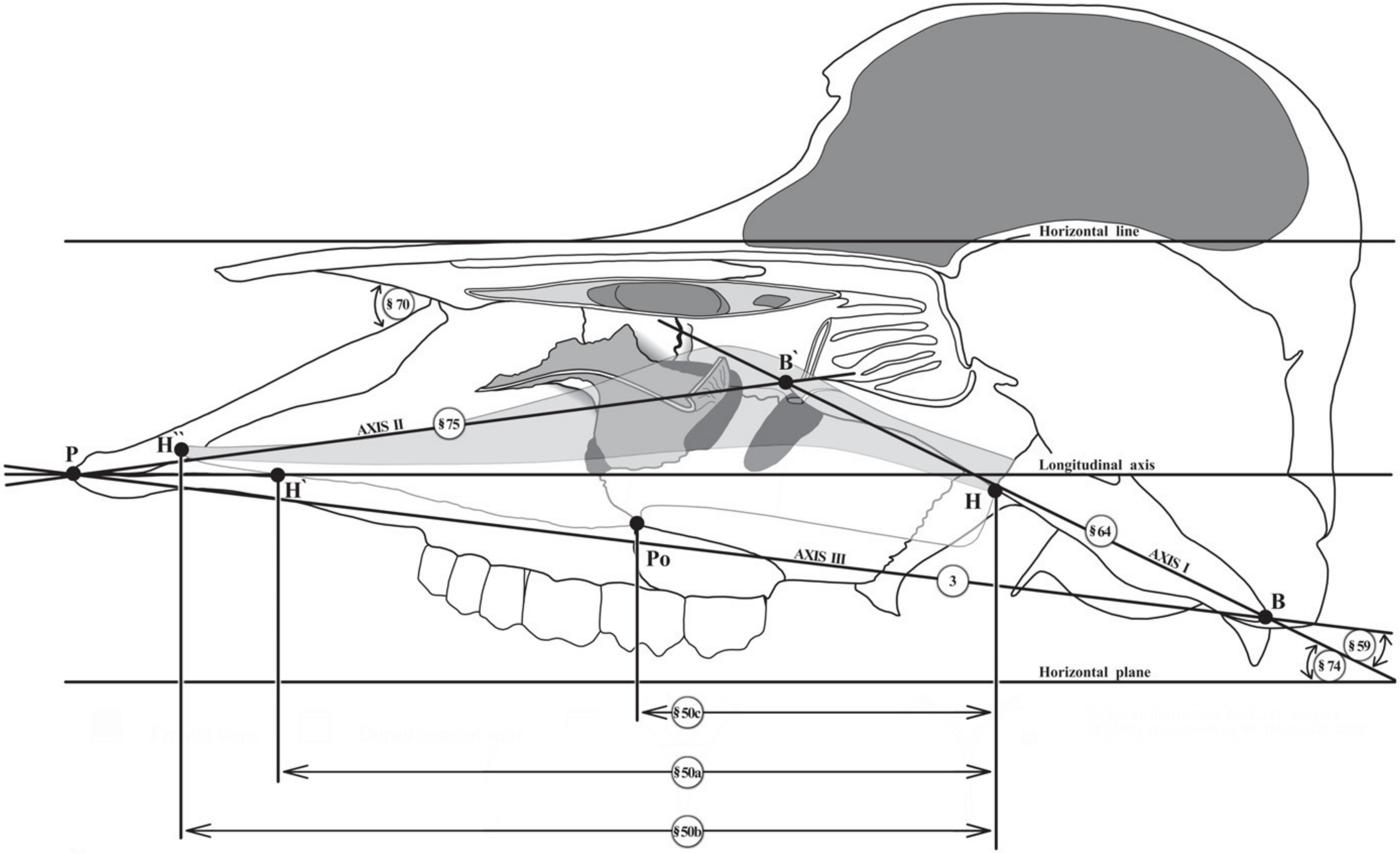


FIGURE 3.63 : CRANIOMETRIC DATA

LINE DRAWING OF THE RIGHT HALF OF A SKULL OF A MATURE BULL : MEDIAL VIEW OF AXIS I - III AND ANGLES FORMED.
THE VENTRAL NASAL CONCHA IS PARTIALLY REMOVED. OUTLINES OF THE VOMER IS SUPERIMPOSED OVER THE ILLUSTRATION (SEMI-SCHEMATIC)

FIGURE 3.63 : CRANIOMETRIC DATA
LINE DRAWING OF THE RIGHT HALF OF A SKULL OF A MATURE BULL : MEDIAL VIEW OF AXIS I - III AND ANGLES FORMED.
THE VENTRAL NASAL CONCHA IS PARTIALLY REMOVED.
OUTLINES OF THE VOMER IS SUPERIMPOSED OVER THE ILLUSTRATION (SEMI-SCHEMATIC)



Frontal sinus | Dorsal conchal sinus | Body of ventral concha | Vomer wings

Original illustration by C. D. Seegers
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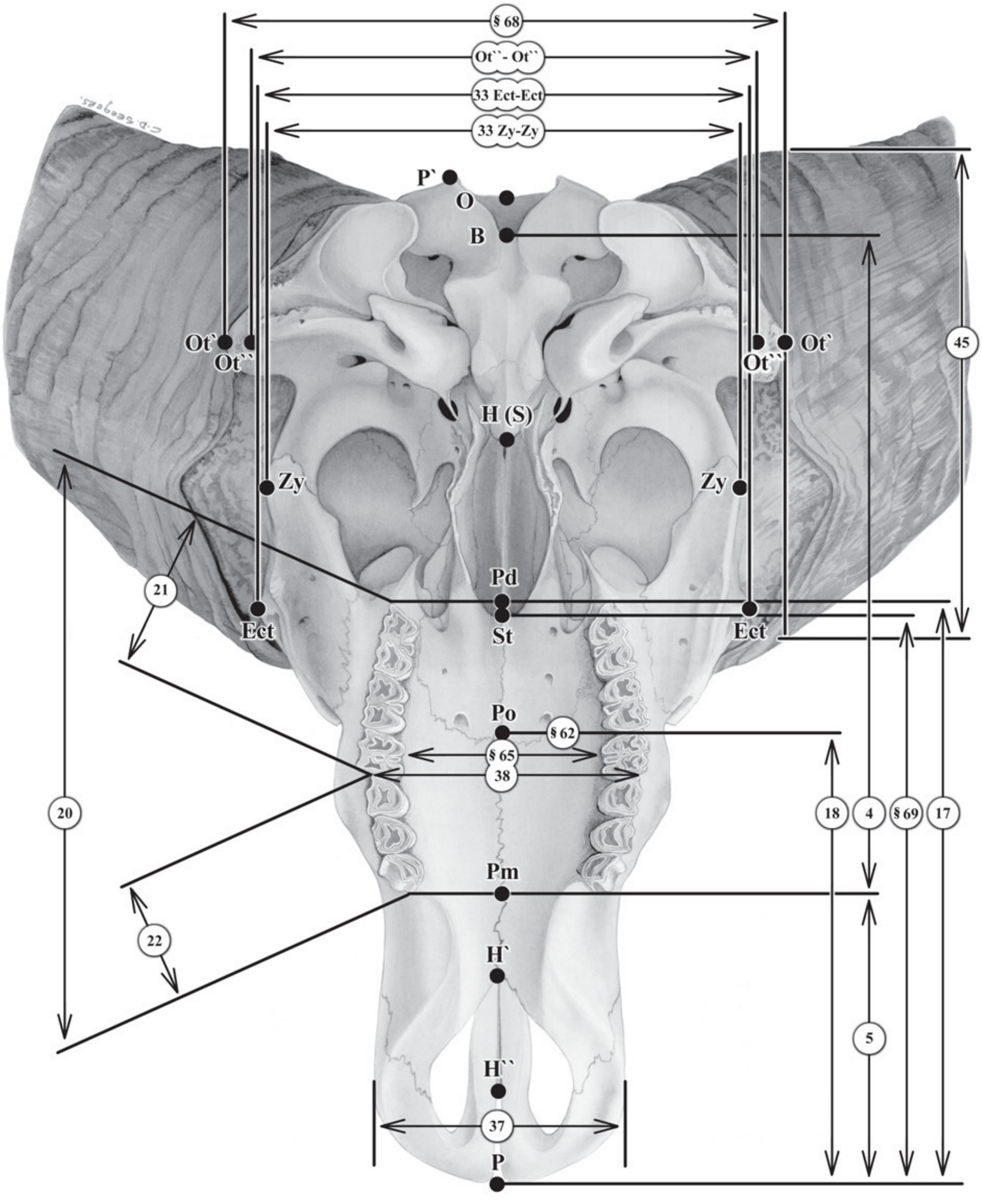
FIGURE 3.64 : CRANIOMETRIC DATA

VENTRAL VIEW OF THE SKULL OF A MATURE BULL



Original illustration by C. D. Seegers
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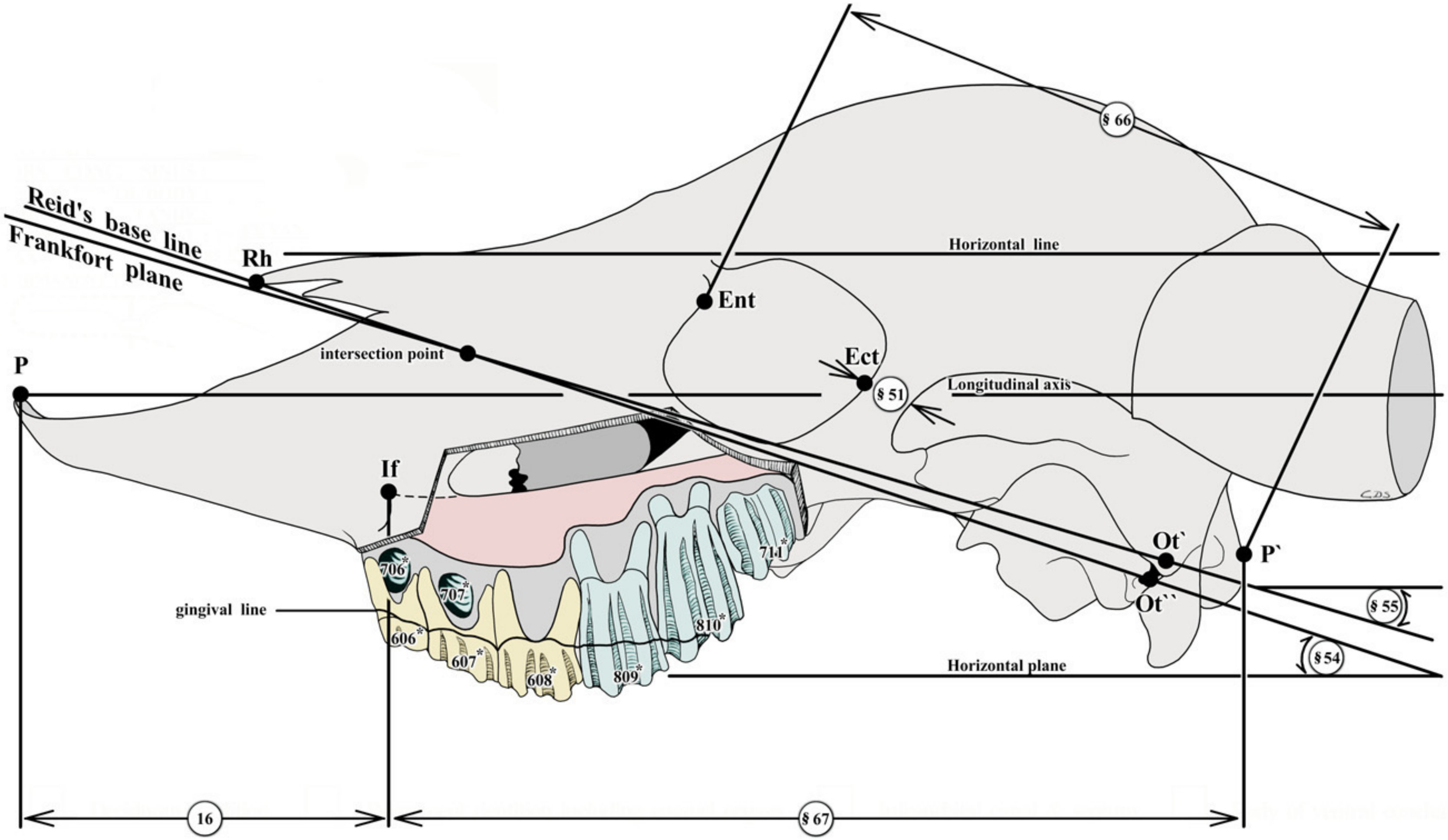
FIGURE 3.65 : CRANIOMETRIC DATA

LATERAL VIEW OF THE SKULL OF A HEIFER OF APPROXIMATELY 16 MONTHS
THE CORNUAL PROCESS IS CUT. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY.
PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)



Deciduous dentition | Permanent dentition including enamel organs | Infraorbital canal & septum | Body of ventral concha

* See Table 3.4 under Applied Anatomy

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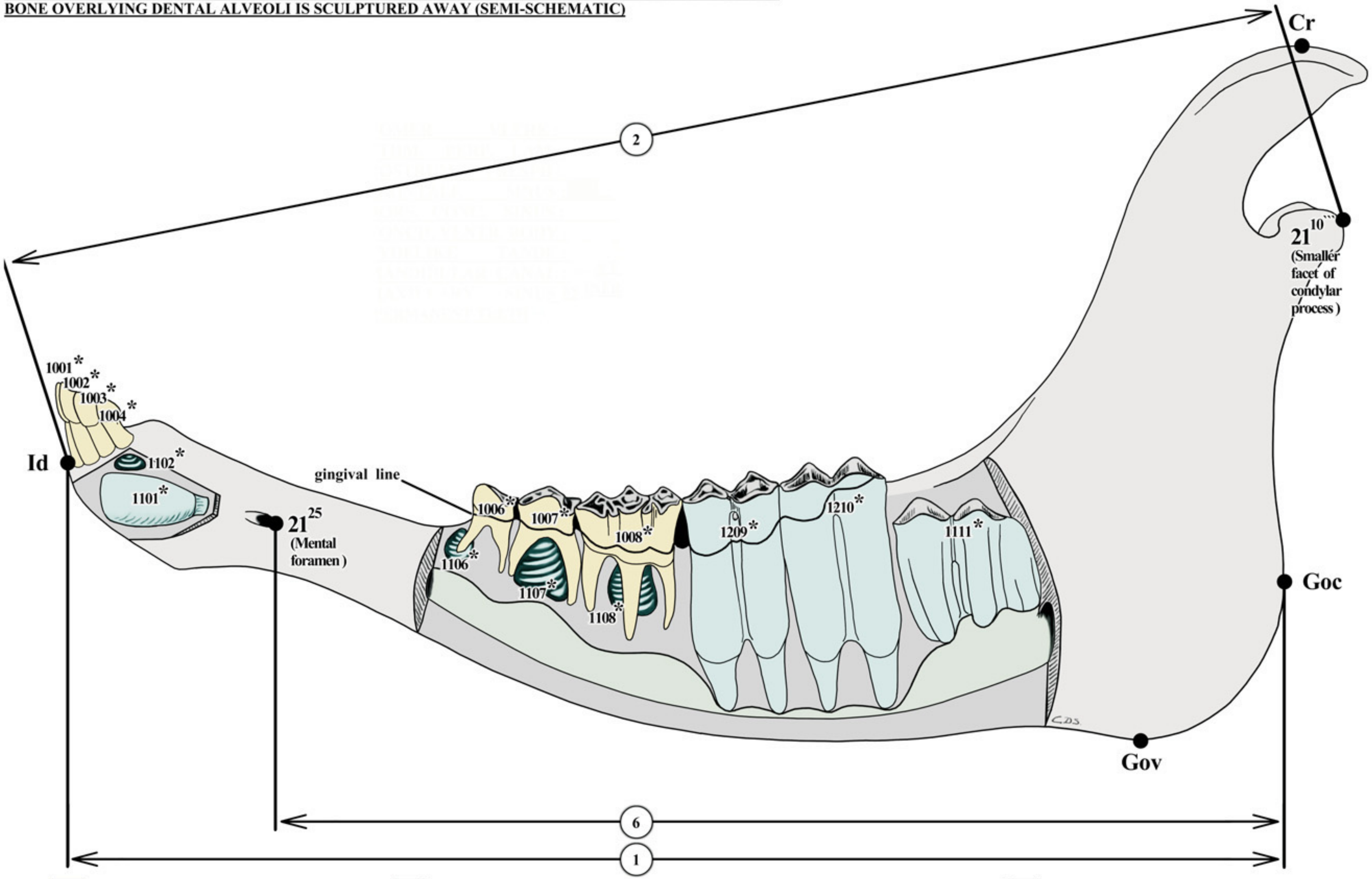
FIGURE 3.65 : CRANIOMETRIC DATA
LATERAL VIEW OF THE SKULL OF A HEIFER OF APPROXIMATELY 16 MONTHS
THE CORNUAL PROCESS IS CUT. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY.
PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)

FIGURE 3.66 : CRANIOMETRIC DATA

LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF A HEIFER OF APPROXIMATELY 16 MONTHS.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)



Deciduous dentition

Permanent dentition including enamel organs

Mandibular canal

* See Table 3.4 under Applied Anatomy

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FIGURE 3.66 : CRANIOMETRIC DATA
LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF A HEIFER OF APPROXIMATELY 16 MONTHS.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)

FIGURE 3.67 : CRANIOMETRIC DATA

LATERAL VIEW OF THE SKULL OF A BULLOCK OF APPROXIMATELY 2 - 2½ YEARS. THE CORNUAL PROCESS IS CUT AT THE LEVEL OF THE ZYGOMATIC ARCH. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY. PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)

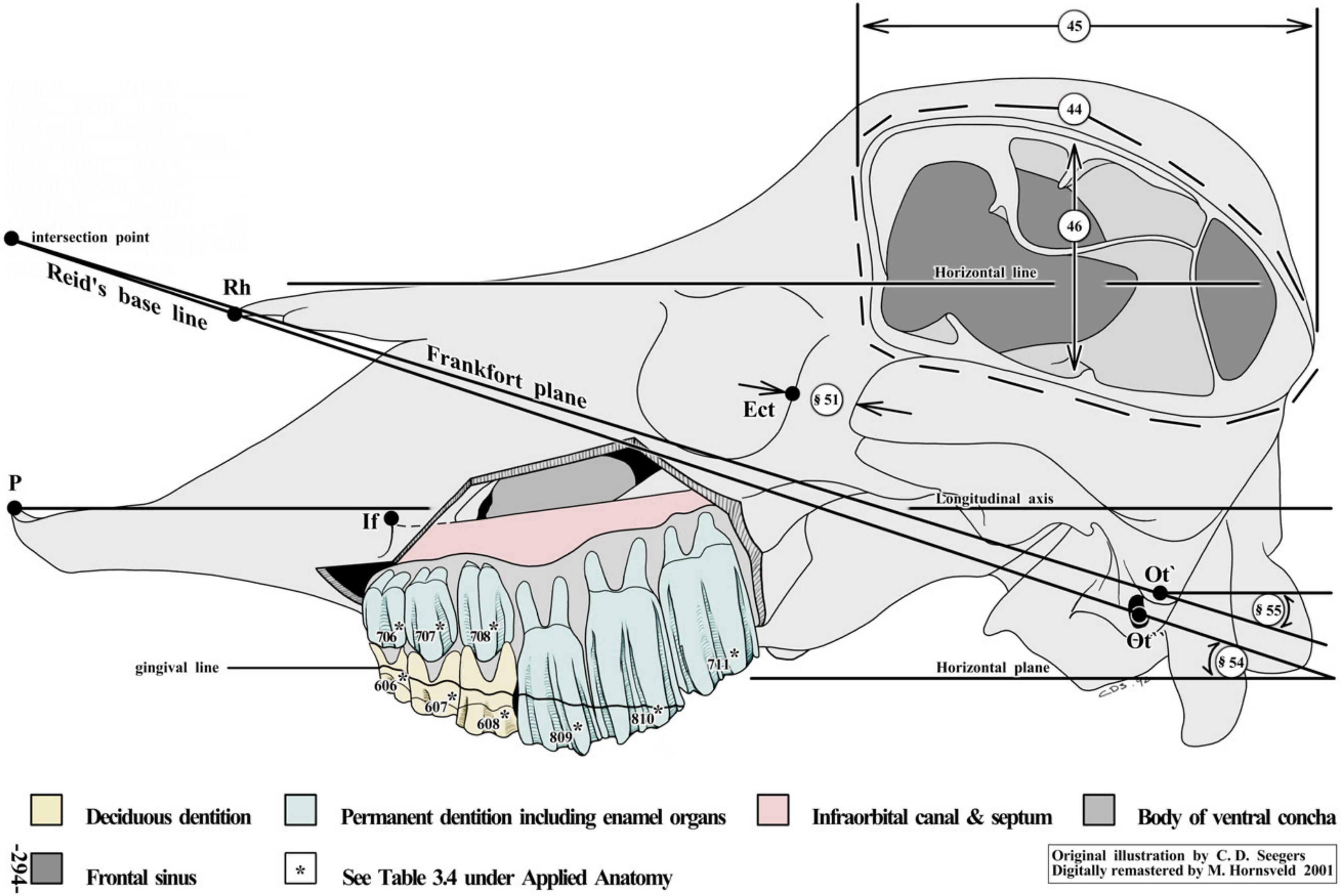
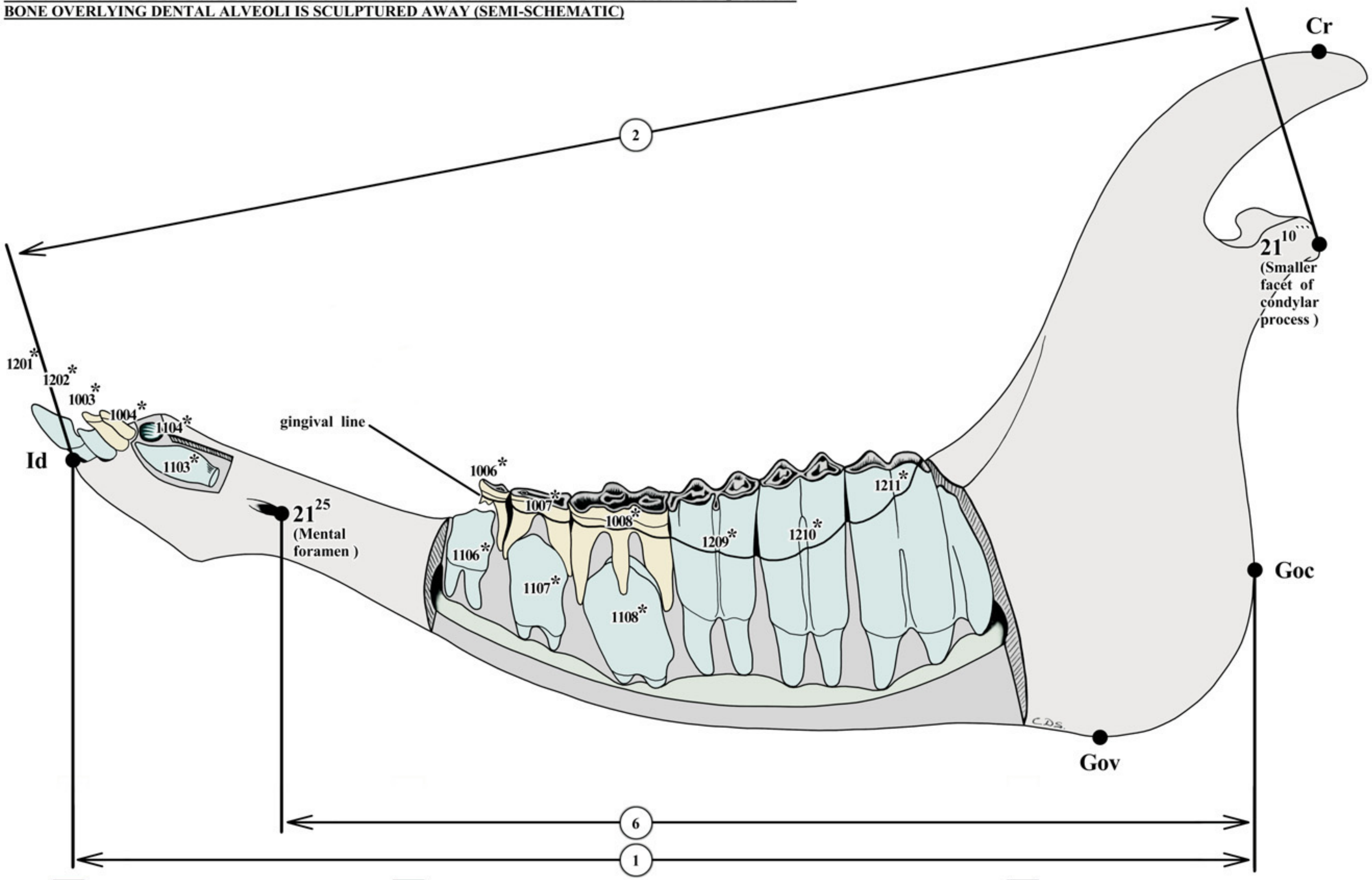


FIGURE 3.67 : CRANIOMETRIC DATA
LATERAL VIEW OF THE SKULL OF A BULLOCK OF APPROXIMATELY 2 - 2½ YEARS. THE CORNUAL PROCESS IS CUT AT THE LEVEL OF THE ZYGOMATIC ARCH. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY. PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)

FIGURE 3.68 : CRANIOMETRIC DATA

LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF A BULLOCK OF APPROXIMATELY 2 - $2\frac{1}{2}$ YEARS.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)

FIGURE 3.68 : CRANIOMETRIC DATA
LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF A BULLOCK OF APPROXIMATELY 2 - $2\frac{1}{2}$ YEARS.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)



Deciduous dentition — Permanent dentition including enamel organs — Mandibular canal

* See Table 3.4 under Applied Anatomy

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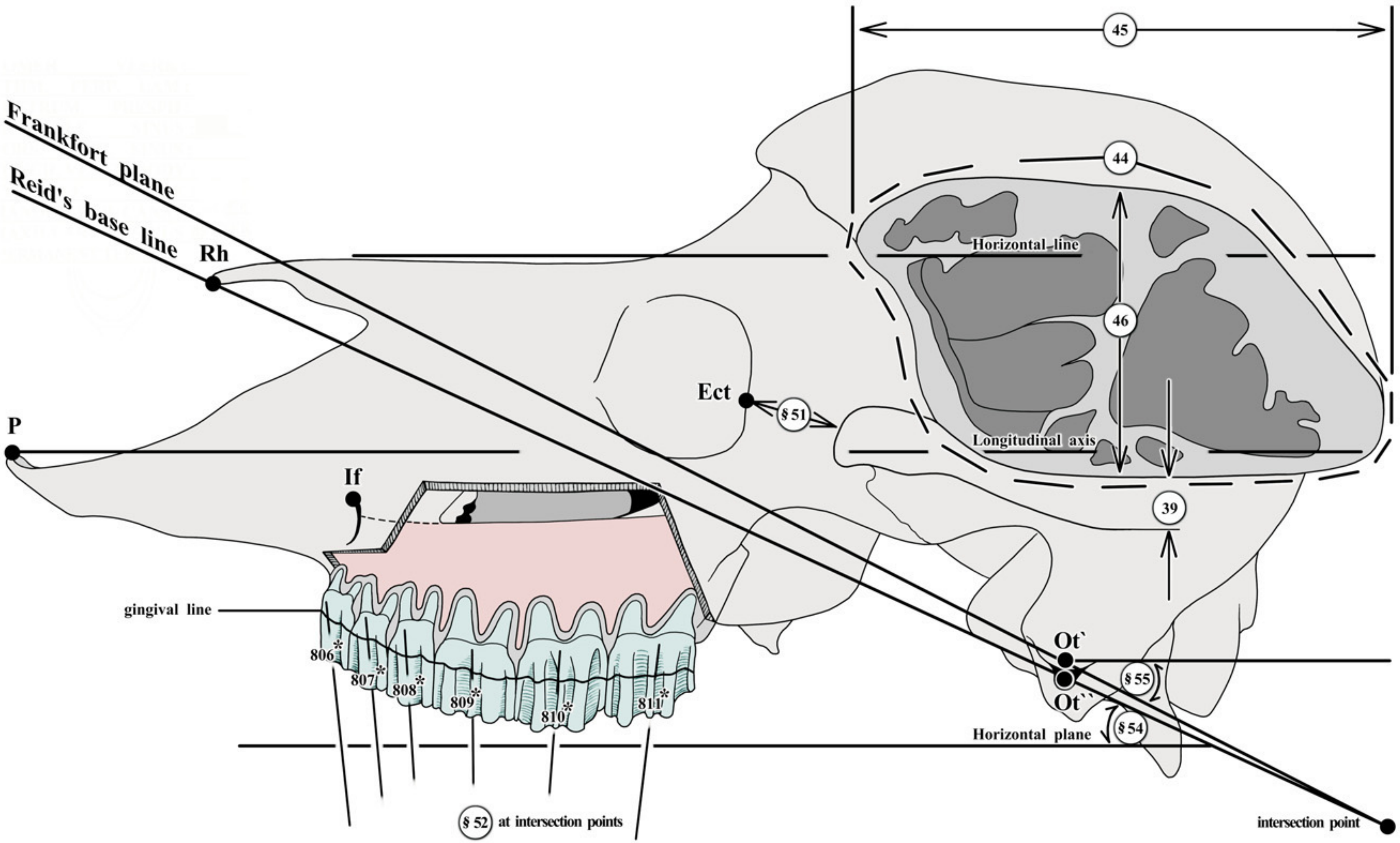
FIGURE 3.69 : CRANIOMETRIC DATA

LATERAL VIEW OF THE SKULL OF AN OLD BULL. THE CORNUAL PROCESS IS CUT AT THE LEVEL OF THE ZYGOMATIC ARCH. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY. PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)

FIGURE 3.69 : CRANIOMETRIC DATA
LATERAL VIEW OF THE SKULL OF AN OLD BULL. THE CORNUAL PROCESS IS CUT AT THE LEVEL OF THE ZYGOMATIC ARCH. BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY. PART OF THE MEDIAL WALL OF THE MAXILLARY SINUS CAN BE SEEN (SEMI-SCHEMATIC)



Frontal sinus | Permanent dentition | Infraorbital canal & septum | Body of ventral concha

* See Table 3.4 under Applied Anatomy

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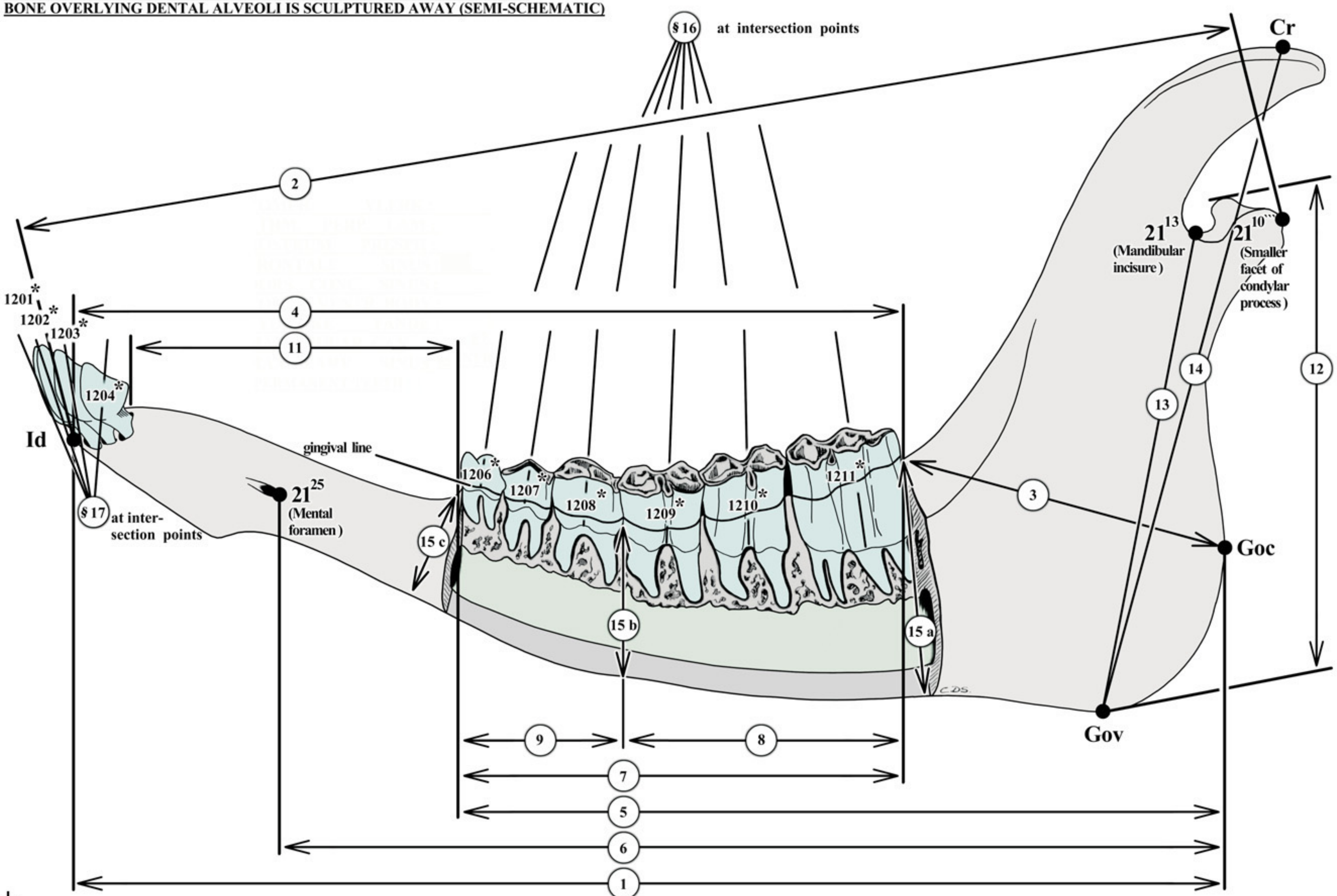
FIGURE 3.70 : CRANIOMETRIC DATA

**LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF AN OLD BULL.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)**

LATERAL VIEW OF THE LEFT MANDIBULAR RAMUS OF AN OLD BULL.
BONE OVERLYING DENTAL ALVEOLI IS SCULPTURED AWAY (SEMI-SCHEMATIC)

FIGURE 3.70 : CRANIOMETRIC DATA



Permanent dentition | Mandibular canal | * See Table 3.4 under Applied Anatomy

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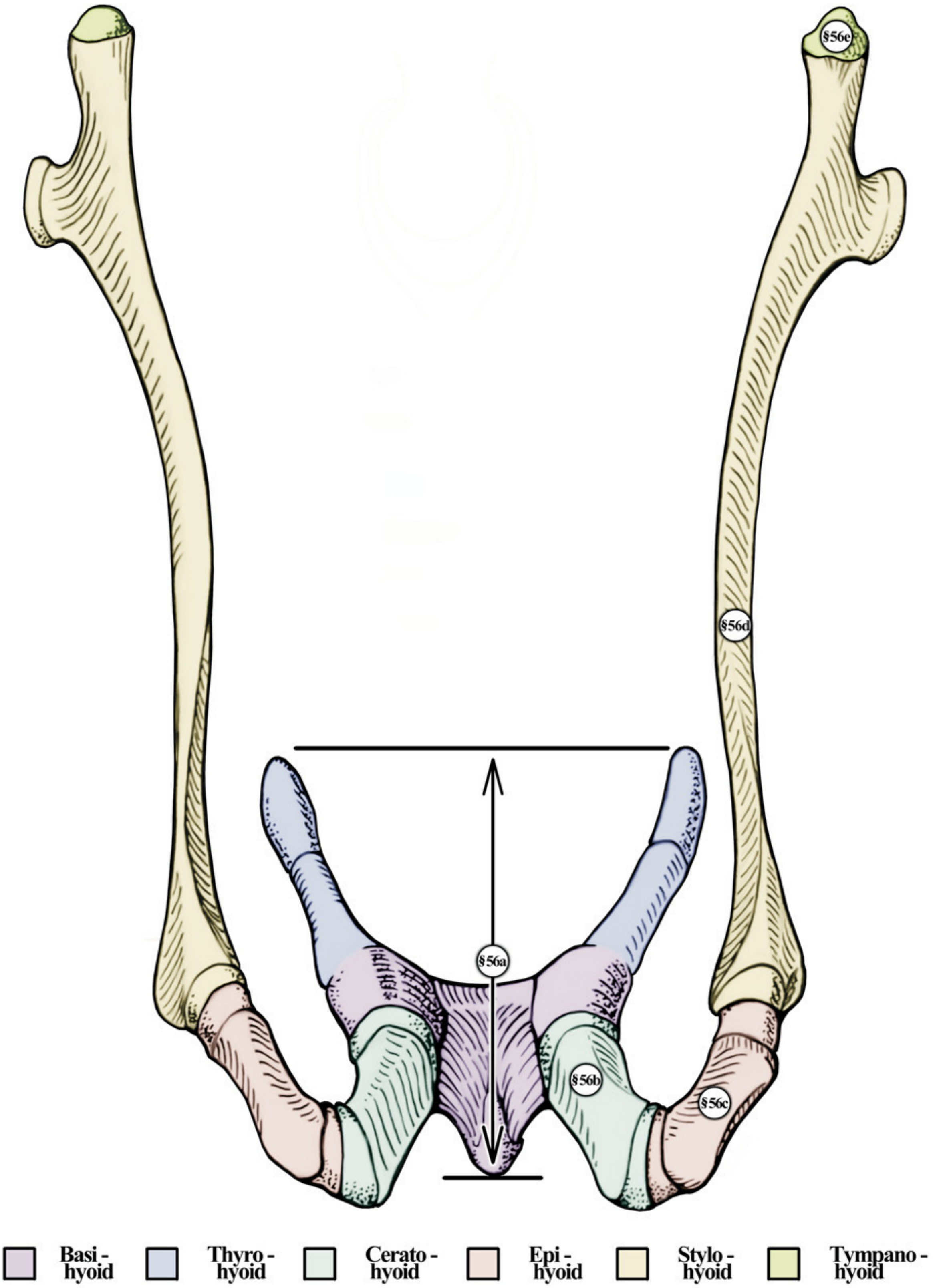
FIGURE 3.71 : CRANIOMETRIC DATA

THE HYOID APPARATUS (LINE DRAWING, ROSTRAL VIEW)



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TERMINOLOGY AND METHODOLOGY :

INTRODUCTION :

Osteo-archaeological terms, developed and used by Palaeontologists, are adopted essentially as it is for this section. (See also **General Introduction**.) Only in the **Glossary of terms** - and not in this section - are these terms (and their abbreviations) indicated by a hash sign # . And because they are not listed in the *N.A.V.*, they are also marked by an asterisk * [160] . Standardized methods, as developed by Palaeontologists, are followed to obtain the data for this section.

PRE-DEFINED AND PRE-EXISTING OSTEO-ARCHAEOLOGICAL POINTS, CONCEPTS AND TERMS USED IN VARIOUS MEASUREMENTS :

Existing concepts and well-established osteo-archaeological **points** (from where measurements of the skull are taken), forms the standard on which this study on the **Craniometric data** of the savannah buffalo is based on. As it is not the purpose of this study to revise or re-defined these concepts and points, they are therefore used according to the standard lists and methodology. However, some minor alterations, additions or corrections had to be made. These adaptations to the standard lists are made to suit the specific needs of this study to record the **Craniometric data** of the savannah buffalo in a **meaningful** way. The correction made to the standard lists, had to be done to bring the terminology in line with this study's section on the osteology (section A). Most are essentially editorial in nature. In essence, the **methods and meanings** of the standard list are therefore kept unaltered according to existing Palaeo-anatomical prescriptions. One exception however is that the first upper and lower molars of the savannah buffalo are regarded by this author as a more accurate indicator of the longevity of savannah buffalo, than the recommended third molars as for the domestic Bovine. (The domestic Bovine served as the standard animal on which the original work was based upon.) Forty-seven (47) standard measurements for the skull and 15 for the mandible are prescribed. Measurement numbers, measurement names (when logic), the

160 Non-*N.A.V.* terms are not indicated by asterisks because it falls outside the scope of this study to review the definitions of these terms or to justify their use in this section on Craniometry. The term "aboral" can serve as an example **:** It is a term foreign to Veterinary Anatomy and is not listed in the *N.A.V.* It will be used in this section as is, but it will appear in the **Glossary** with an asterisk.

relevant points from which measurements are taken, and the figure or figures that illustrate the method best in the savannah buffalo, are supplied in the lists. Units of length are in millimetres, angles in degrees, volume in millilitres, and indexes calculated to the second decimal point. As prescribed, plus and negative signs (+ / -) indicate which measurements are clear and easy to take and which results cannot accurately be accounted for. In this work, only in some rare cases were the measurements obtained doubtful, and these are indicated by a minus sign (-) in the tables. Examples of these are some measurements of the cornual processes and some tooth measurements. The former situation arose because the cornual processes were still covered in some specimens by horn because these skulls could not be damaged. Tooth measurements that could not be taken accurately were due to teeth that were still in the process of erupting. The vestibulo-lingual axes of teeth can also not be measured accurately.

The abbreviations for the standard measuring points and the concepts are listed in alphabetical order below (34 points and concepts in total). Some concepts do not have abbreviations. The un-abbreviated terms and their definitions, are listed alphabetically in the **Glossary of terms**. They are only defined and explained in full in the **Glossary** and not here in this section, as it is taken for granted that Palaeontologists and Osteo-archaeologists know what these terms mean. The alphabetical order of the terms, and the abbreviations for these terms in the list below, differ from each other as can be expected.

LIST OF PRE-DEFINED AND PRE-EXISTING OSTEO-ARCHAEOLOGICAL POINTS, CONCEPTS AND PLANES **:**

A Akrokranion.

B Basion.

Br Bregma.

Cr Coronion.

Ect Ectorbitale.

Ent Entorbitale.

Eu Euryon.

F Frontal midpoint, the median of the line joining the Ectorbitalia (only in carnivores).

- The Frankfort plane * [161] .

Goc Gonion caudale.

Gol Gonion laterale.

Gov Gonion ventrale.

H Hormion.

Id Infradentale * [162] .

If Infraorbitale.

L Lambda.

- Molar tooth row (no abbreviation).

N Nasion.

Ni Nasointermaxillare * [163] . The term for this point is updated to Nasoincisivum in this study.

O Opisthion.

Op Opisthokranion.

---

161 There is no abbreviation for the Frankfort plane. It is an old term of a horizontal plane used in Human Craniometry.

162 The craniometric point 'Infradentale' is the same as the 'Pogonion'. Even though the 'Pogonion' is an existing old term from Human and Veterinary Craniometry, the term 'Infradentale' is used in this study.

163 The "intermaxillary bone" / "premaxilla" is outdated and replaced by the term Incisive bone. The term Nasointermaxillare (Ni) implies that the nasal bone, the maxillary and the incisive bones are all three involved. This can be confusing as in some savannah buffalo individuals, the caudal extent of the nasal process of the incisive bone does not reach the nasal bone to form a nasoincisive suture. Despite that, the point **Ni** can still be used for Craniometric purposes on the savannah buffalo, as per definition, it still is the most aboral* point of the nasal process and it remains visible. The term is therefore changed to the Nasoincisive point.

Ot	Otion.
P	Prosthion.
Pd	Postdentale.
Pm	Premolare.
S	Premolar tooth rows (no abbreviation).
Po	Palatino-orale.
-	Pogonion. (See footnote 162.)
-	Reid's base line * [164] .
Rh	Rhinion.
S	Synsphenion.
Sp	Supraorbitale.
St	Staphylion.
Zy	Zygion.

164 Reid's base line is an old term from Human Craniometry.

NEW REFERENCE POINTS, AND ADDITIONAL MEASUREMENTS **:**

Due to shortcomings experienced in expressing concepts, and to record specific structures that should obviously be taken when data is collected on the skull of the savannah buffalo, additional measurements are proposed and introduced into this section. These measurements also augment the anatomical description (section A) and comply with the needs of this study ***** [165] . The additional measurements proposed for the skull, the hyoid and the mandible of the savannah buffalo are listed separately. They are all denoted by the typographic symbol § . Allocating additional reference points first, was necessary in order to execute the new measurements. These points also make it easier to describe some of the calculations, especially those used in the formulae for indexes. These additional new points are either adjustments of existing osteo-archaeological points, or totally new allocated points. The points are established by adding one or more dashes (` or ``) to the abbreviation of the most suitable existing reference point. **Twelve new points had to be allocated** for this study. In order to marry the standard list of measurements, the new reference points and the additional measurements, **fourteen FINAL COMMENTS** are made and should be read carefully (vide infra). The twelve new points are the following **:**

A`, B`, B``, Eu`, H`, H``, L`, L``, O`, Ot`, Ot`` and P`. (See LIST OF PRE-EXISTING POINTS above.)

A` The point A` is allocated to the existing median point of the intersecting line that joins the most rostral points of the nasal parts of the frontal bones. (See also measurement 9 below as well as figures 3.59 & 3.61.)

B` The point B` is allocated to the rostral end of the rostrum [prae-]sphenoidale (5 [8]) and B - B` forms the basal axis I. (See also measurement §64 below and figures 1.4 & 3.58.)

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165 Three examples may serve to proof that new points are indeed imperative **:** (1) The fact that the savannah buffalo does not have an intercornual protuberance makes the interpretation of the reviewed measurement - now between the points O and O` - much easier than the existing nomenclature ever can. (2) The presence of a prominent rostrum [prae-]sphenoidale has a marked effect on the basal axis\*, and therefore the reviewed measurement B - B` makes a lengthy description obsolete. It also condenses the formula for the cranial index. (3) The width of the lateral boney orbit - as an indicator of the magnitude of the protruding orbital margin of old bulls - is an example of a new measurement that is proposed for the savannah buffalo. It serves the purpose to give a measurable value to sexual dimorphism that is otherwise so subtle that it cannot be described well with existing terms and measurements. (See measurement §51.)

B`` The point B`` is allocated to that point on the summit of the skull that indicates the greatest vertical height of the skull in the region of the squamous part of the frontal bone, as measured from B. (See measurement 40 as well as figures 3.57, 3.58 & 3.64). B - B `` must be differentiated from O - O` which is the least height of the skull as taken in measurement 41.

Eu` The point Eu` is allocated to the least parietal width aborally* in the temporal fossa to indicate the maximum non-pneumatized or true [neuro-]cranial width. It is the same as the ".... least occipital breadth **;** the distance between the most medial points of the aboral* borders of the temporal fossa ...". (See also measurement 30, figure 3.57 and FINAL COMMENT 6 below for further detail.)

H` The point H` is allocated to the rostral end of the keel of the vomer that can sometimes be seen in ventral view. In those cases where no visible part of the keel of the vomer can be seen between the palatine processes of the incisive bone, this point H` is taken at the ventral level of the maxilloincisive suture (16^{3}), as it usually coincides with the rostral end of the vomeromaxillary suture (12^{4}). (See measurement **§**50 (a), figures 3.38, 3.39, 3.60, 3.63, 3.64 & Synsphenion on the intersphenoidal synchondrosis (4^{2}). Also see FINAL COMMENT 7 below.)

H`` The point H`` is allocated to the rostral end of the wings of the vomer as seen in dorsal view. (See measurement **§**50 b and figures 3.38, 3.59, 3.60, 3.61 & 3.63.)

L` The point L` is allocated to a median point on the nuchal crest because the occipitoparietal suture (2^{23}) ossifies, after which the point Lambda (L) cannot be seen anymore. Therefore, L` is then used to indicate the most caudal extent of the frontal sinus complex. At that point the thickness of the external lamina of the occipital bone is approximately 3-5 mm. (See figure 3.57 & 3.58.) L` is preferred because the alternative point "Inion" - as used rarely in Veterinary Anatomy - is dwarfed by the prominent nuchal crest of the savannah buffalo. (See measurement **§**49 and FINAL COMMENT 1 below.)

L`` The point L`` is allocated to the most rostral extent of the nasal sinus which is also the most rostral extent of the whole frontal sinus complex. The point L`` can only be accurately determined when the skull is cut in the median plane or when the nasal bone is sculptured away over the rostral extent of the nasal sinus. However, the nasal sinus is not present in all animals, and its size cannot be judged from macroscopic external view in all intact skulls. Radiographs may help to predetermine the presence of the sinus. (See measurement §49 and figure 3.58.)

O` The point O` is allocated to the least height of the skull, as measured from O. (See measurement 41 and compare it with B - B`` as taken in measurement 40. Also see figures 3.57 & 3.58.)

Ot` The point Ot` is allocated to the most lateral point of the retrotympanic process that bears a tuberous enlargement. (See measurement §68 and figures 3.57, 3.62, 3.64, 3.65, 3.67 & 3.69). It forms the most lateral point of the skull in older animals. The distance Ot` - Ot` is used to measure the maximum width of the [neuro-]cranium in the calculation of the skull index. It is also used in the calculation of the cranial index where the effect of the frontal sinus needs to be included. (See LIST OF INDEXES below.)

Ot`` The point Ot`` is allocated to the centre of the osseus opening of the external acoustic meatus. (See figures 3.57, 3.62, 3.64, 3.65, 3.67 & 3.69). The point Ot `` is also used as one of the two reference points in “Reid’s base line”**;** the other reference point for that line is the point Rh. (See Rhinion, measurement §54 and also see FINAL COMMENT 9 below.)

P` The point P` is allocated to the ridge on the most caudal border of the occipital condyle. P` - P forms the condylar ridge - Prosthion length that is the maximum skull length. (See measurement §63, figures 3.57, 3.58 & 3.64 and FINAL COMMENT 11 below.)

CALCULATION OF INDEXES, DRAWING LINES, PLANES, AXES AND MEASURING ANGLES BETWEEN PLANES AND LINES :

Indexes are helpful to evaluate many aspects of the **Craniometric data** of skulls. Most of the indexes as described in this section are standard and important mainly to Palaeontologists. Some indexes are more useful in the understanding of anatomical concepts. For example, variations in the rostro-caudal dimension of the frontal sinus (L` - L``) can be grasped better by considering the index because both age and individual variations affect the value. Although many more indexes can be calculated, only seven indexes for the skull of the savannah buffalo are computed in this section. The results of the indexes calculated for this section are not intended to be absolutely relevant for the whole specie because only a limited number of skulls were used to compile the data. The most important reason to compute indexes is to do away with size and age factors. The second most important application of indexes, can be to determine the gender of the animal retrospectively. There is however usually not a problem to distinguish gender in older complete skulls as sexual dimorphism in the skulls of savannah buffalo is obvious. Indexes of individual skull bones might then be of value when only parts of skulls have to be classified in one or the other gender, or to determine age, or to identify individual bones of skull fragments of unknown species. However, no indexes have been calculated for fragments or individual bones as it falls beyond the scope of this study. A third reason for computing more indexes may lie in **three-dimensional indexes** that can for instance compare the volume of the [neuro-]cranium to other parts of the skull. Such indexes may help to distinguish between true and perceived disproportionate growth of parts of the skull. (See point 8 under the LIST OF INDEXES below). However, it also falls beyond the scope of this study to do such analysis at this point.

The Frankfort plane and Reid's base line are used as indicators to stress the point that the external auditory canal increases in length over age (especially so in bulls). The increased width of that part of the temporal bone affects planes, lines and indexes. (See measurements §54 & §55.)

The difference between the basal, facial and skull axes might not be all that useful for

Anatomists in general, but these concepts are very handy in descriptive osteology (section A) when the Applied Anatomy also has to be considered (section E).

Angles of a few intersecting lines and planes are drawn because they also render some contribution to the final evaluation on the **Craniometric data** of the skull of the savannah buffalo.

FINAL COMMENTS :

1. The "Inion" - as central surface point on the external occipital protuberance - is not a useful term in the Craniometry of the skull of the savannah buffalo **:** The point L` replaces the "Inion" because the latter are dwarfed by the nuchal crest in the savannah buffalo.
2. The term "premaxilla" is not used in Veterinary Anatomy any more. The correct name for that bone is the incisive bone, *Os incisivum*. (See measurement 19 and footnote 163.) The point referred to by the term "Nasointermaxillare " is therefore updated to Nasoincisivum, but the abbreviation and the point "**Ni**" are still used as is.
3. The "Pogonion" and Infradentale are alternative terms for the same point. The latter term is used in this study as explained under footnote 162.
4. The Akrokranion (A) and the Opisthokranion (Op) is regarded as one and the same point in the domestic bovine on which the standard for ruminants is based. However, in the savannah buffalo they are definitely two distinctly different points. There are two reasons for this **:** First, the Akrokranion is defined as the most caudal point on the vertex of the skull in the median plane. And that is exactly where the skull of the savannah buffalo has an intercornual groove and not an intercornual protuberance, as in the bovine. Secondly, the Opisthokranion is defined as " .... median point on the line joining the most aboral* dorsal points of the cranium". And that point is determined by the bases of the large cornual processes which - in the savannah buffalo - projects much further caudally than in the domestic bovine. The combination of these two factors increases the distance between the two points "A" and "Op", making it essential to differentiate between them, and also to measure the distance between them. (See measurement **§**61 and figure 3.58, but also see figures 3.59 & 3.61).
5. For the savannah buffalo, individual detailed morphometric measurements of the first upper molar (M^{1}) and for the first lower molar (M_{1}), are considered much more significant to note than that of the third molars (M^{3} & M_{3}) to evaluate age and potential longevity of an animal. Also, the occlusal surface of the first upper molar (M^{1}) has more criteria available for species identification than M^{3}, the third upper molar. That detail of the dentition of the savannah buffalo falls beyond the scope of this study. However,

the heights of the clinical crowns are at least measured. Whereas the height of the vestibular side of the upper first molar is measured, the height for the lower first molar is measured on the lingual side. That is because the heights on these specific sides become more critical in the respective dental arches of older animals. (See measurements §57 and 10 for the skull and mandible respectively.)

6. The Euryon (Eu) is defined as the most lateral point (therefore the greatest width) of the non-pneumatized [neuro-]cranium in other domestic species like the horse and camel. In the domestic bovine, the point is defined as the "least occipital breadth", or "the distance between the most medial points of the aboral* borders of the temporal fossa". In some savannah buffalo, the cornual processes can obstruct measurements in the temporal fossa and therefore the latter alternative method for measuring this point Eu - as adapted for the savannah buffalo - is proposed and explained as follows **:**

   The lateral wall of the [neuro-]cranium on the parietal bone - and therefore the point (Eu) in the temporal fossa - can be either (slightly) wider or (slightly) narrower than the "least occipital breadth.....aborally..." - as seen from caudally on the nuchal surface. For all practical purposes the aboral* alternative gives the same measurement (as tested on all the skulls that was available) and therefore it is the preferred point of reference for this measurement in the savannah buffalo. Measuring between these antimeric points indicates the non-pneumatized parietal width of the [neuro-]cranium. This aboral* alternative for the Euryon, is conveniently allocated the point Eu\` on the nuchal surface. The distance Eu\` - Eu\` is used as the true [neuro-]cranial width and this distance is also used in the calculation of the cranial index. (See measurement 30 and LIST OF INDEXES below.)

7. The following aspects pertaining to the vomer and measurements of the vomer, should be noted **:**

   The vomer is a laterally flattened bone. (See section A, and figures 3.38 & 3.39). Usually therefore in skulls cut in the median plane, median as well as some paramedian parts of the vomer are inadvertently destroyed by the blade cutting into the bone. Because the vomer is such a fattened bone, this can occur even if the width of the cut is only about two or three millimetres wide. In ventral view of intact skulls, the

Hormion (H) - which is the caudal border of the vomer in the medial plane - is superimposed over, and coincides with, the Synsphenion (S). (The Synsphenion is also the midpoint of the intersphenoidal synchondrosis. See 4^2 under the basisphenoid bone in section A.) Of further importance, is that the rostral end of the vomer has to be demarcated by two different points especially in older animals. That is because the rostral ends of the wings and keel are not found in the same transverse plane. In this study therefore, the ventrally visible point H` demarcates the rostral end of the keel of the vomer, while the (dorsally visible) point H`` corresponds to the rostral end of the wings of the vomer. (See measurement §50 a & b below.) More important however, is the length of the free ventral part of the keel - that part therefore that remains unfused. (See measurement §50 c.) In the savannah buffalo, the free edge of the keel extends from the intersphenoidal synchondrosis, to a point on or slightly more rostral than the dorsal aspect of the palato-maxillary suture (on the dorsal surface of the osseus palate). In intact skulls seen from ventrally, that rostral end of the free part of the keel would correspond accurately enough to the Palatino-orale point (Po). The most rostral ends of the fused and the free parts of the vomer must therefore be clearly differentiated from each other. The former is important because the fused part of the keel of the vomer is of specific importance in the savannah buffalo as it is involved in the interincisive fissure (13^8). In this species, that fissure is in fact a misnomer. (See section A.) The latter free part of the vomer's keel is important as a differentiating feature between the savannah buffalo and other related species. These three aspects of the vomer can only be studied by careful sagittal cuts of skulls. (See chapter four, **Discussion**, points 14 & 15.)

8. The rostral point on the rostrum [prae-]sphenoidale is indicated by B`. The line connecting the Basion (B) to this point B`, gives the basal axis (AXIS I) of the cranium. (See measurement §64.) The rostro-caudal extent of the basal axis forms the true [neuro-]cranium length. The basal axis is a very useful concept in the osteological descriptions (section A) as well as for describing Applied Anatomical aspects (section E). The point B` must be distinguished from the point B`` which lies on the extreme summit of the skull's horn base. (See measurement 40 below.)

9. The centre of the external opening of the auditory meatus is indicated by Ot``. The point Ot (the most lateral point of the mastoid process) is not used for calculations in this study because although it is supposed to be the widest point of the mastoid region dorsal to the external auditory meatus, that part of the skull immediately dorsal to the external auditory meatus is not the mastoid process in the savannah buffalo, but is part of the squamous part of the temporal bone. (Vide infra and see footnote 60 in section A.) The line connecting Ot`` to the point Rh, forms the so-called "**Reid's base line**". The "**Frankfort plane**" is defined as the "auriculo-infraorbital" plane that connects the most dorsal point on the margin of the external auditory meatus - indicated by Ot` in this study - to the lowest point on the infraorbital margin. Reid's base line and the Frankfort plane intersect each other at a point in space rostral to the skull in younger animals but caudal to the skull in older animals. A larger statistical number of skulls should be used to analyse Reid's base line and the Frankfort plane to determine the significance of the change of intersection positions with age. (See measurements §54 & §55 and footnote 182.)
10. The most lateral point of the mastoid process of the temporal bone can at best be seen in caudal view on the nuchal plane of skulls of young savannah buffalo. However, in old savannah buffalo it cannot be seen any more, even in ventral views, as the tympanomastoid suture ($7^{25``}$) is too well ossified. This therefore differs from standard archaeological prescription on the domestic Bovine, where the point is marked as Ot. (See measurement 25.) In savannah buffalo, the maximum temporal width - which is the maximum width of the [neuro-]cranium (Ot` - Ot`) - is determined by the tuberous enlargement of the retrotympanic process of the temporal bone. (See measurement §68.) The two points, Ot and Ot`, should not be confused with each other and they should also be differentiated from a third point Ot`` which is the centre of the external opening of the auditory meatus as seen from laterally. (See FINAL COMMENT 9 above.)
11. The most caudal border of the occipital condyle lies on a ridge. The medial edge of this ridge is an exact point to work from, and the point P` has been allocated to it. (See also $2^{14``}$ under the occipital bone.) To have a point P` on the condyle gives a more specific point to measuring from than the whole condyle. Thus, the term "condylobasal length" -

as used by Palaeontologists in the standard measurement number 2 - can be done away with. The measurement P` - P gives the maximum skull length which is also used in the formula to compute the skull index. For this study, the condylar ridge (P`) - Prosthion (P) length is therefore the preferred measurement. (See measurement number §63.) This differentiation also avoids possible confusion between the term "condylo**basal** length", and the true **base** of the skull (because the skull is shaped like a pyramid with a **base** and an apex). The true skull base height should strictly be - as is done in this study - from the point B to B``. (See also measurement 40 and the LIST OF INDEXES below.)

12. The greatest palatal width (or breadth) in measurement 38 includes the outer borders of the dental alveoli. This measurement therefore includes the width of the left and the right alveolar processes of the maxilla too, and is therefore an indication of the width of the facial part of the maxilla and not the width of the palate. The greatest width of the osseus palate should be measured as the greatest inter-alveolar palatal width. The greatest inter-alveolar palatal width should give the true maximum interalveolar palatal width. (See measurement §65 and figure 3.64.) This true palatal width is used to compute the palatal index. (See LIST OF INDEXES below.)
13. In the savannah buffalo, the facial width - as measured on the zygomatic arches (Zy - Zy) - can be either (slightly) wider or (slightly) narrower than the greatest width of the squamous part of the frontal bone, measured at the Ectorbitalia (Ect - Ect). Either the Ect - Ect or the Zy - Zy distance (whichever is widest) is used in the calculation of the facial index. The cornual diverticulum obviously has to be disregarded in the calculation of that index. In very young animals, Zy - Zy forms the most lateral points on the skull, and it is wider than either Ect - Ect or Ot` to Ot`. In old animals Ot` - Ot` form the most lateral points (also when one disregards the cornual diverticulum from the three-dimensional configuration). Although the distance between Ect - Ect or Zy - Zy can be used in the calculation of the facial index, the frontal sinus index is calculated by using Ect - Ect without the alternative of using Zy - Zy. The least frontal width (taken in measurement number 32 immediately caudal to the Ectorbitale), gives some indication as to the magnitude to which the orbital margin can protrude when it is compared with the Ect - Ect measurement as taken in measurement 33. (See LIST OF INDEXES below.)

14. The angle of the nasoincisive incisure (13 [10]) may be affected by two factors **:**

    (a) The size of the lateral process of the nasal bone which becomes relatively smaller in older animals. (See Nasal bone under section A.)

    (b) Whether the nasal process of the incisive bone is fused to the nasal bone or not. (See footnote 123 in section A.)

No conclusions could be drawn on the limited number of specimens studied, but the following statistics derived from all the skulls used in this study is informative. Twenty-two percent (22 %) of skulls studied showed complete fusion between the nasal process of the incisive bone and the nasal bone at the nasoincisive suture (18 [7]). In those cases, the suture can be as long as 30 mm in some individuals. In 33 % of cases the nasal process of the incisive bone extended as far caudally as the level of the nasoincisive incisure. In the remaining 45 % of cases, the nasal process did not reach the nasal bone at all. In the latter group of cases, the exposed un-pneumatized part of the maxilla then forms the ventral border of the nasoincisive incisure for a distance of approximately 10 mm. (See 16 [3] and the rest of that paragraph in section A.)

MEASUREMENTS FOR COLLECTING CRANIOMETRIC DATA OF THE SAVANNAH BUFFALO :

LIST OF STANDARD MEASUREMENTS OF THE SKULL :

1. **Profile length :** Akrokranion - Prosthion (**A - P**). See figure 3.61.
2. Condylobasal length **:** occipital condyle - Prosthion. See FINAL COMMENT 11 above.
3. **Skull axis** length (**AXIS III**) **:** Basion - Prosthion (**B - P**)* [166] . See FINAL COMMENT 11 above and see figures 3.58 & 3.63.
4. **Short skull length :** Basion - Premolare (**B - Pm**). See figure 3.64.
5. **Premolare - Prosthion** (**Pm - P**). See figure 3.64.
6. **Basion - Nasion** (**B - N**)* [167] . See figure 3.58 and measurement §64 .
7. **True [viscero-]cranium length :** Nasion - Prosthion (**N - P**). See figures 3.58 & 3.61.
8. **Median frontal length :** Akrokranion - Nasion (**A - N**). See figure 3.61.
9. **Greatest frontal length :** Akrokranion - median point of most rostral ends of frontal bones (**A - A`**)* [168] . See figures 3.59 & 3.61.
10. **Short upper cranium length :** Akrokranion - Rhinion (**A - Rh**). See figures 3.59 & 3.61.
11. **Akrokranion - Infraorbitale** (**A - If**). See figure 3.61.
12. **Greatest length of nasal bones :** Nasion - Rhinion **:** (**N - Rh**). See figure 3.61.
13. Occipital condyle to ipsilateral Entorbitale. See FINAL COMMENT 11 above * [169] .
14. **Lateral facial length :** Ectorbitale - Prosthion (**Ect - P**). See figure 3.62.
15. Occipital condyle to ipsilateral Infraorbitale. See FINAL COMMENT 11 above * [170] .

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166 The skull axis length (axis III) from Basion - Prosthion (B - P) replaces the term "basal length" used in measurement 3. That is because "basal length" can be confused with the "condylobasal length" (measurement 2) and with the true base of the skull. (See measurements 40 & 41.) The skull axis is one of three axes that can be drawn in the skull as seen in medial view. (See ADDITIONAL MEASUREMENTS §64 and §75 for AXIS I and II respectively.) The angles formed between these three axes are measured in measurements §59, §60 and §73 respectively.

167 The distance B - N is not regarded as a suitable "neurocranium" length, because the point N is influenced by the development of the frontal sinus complex. The true [neuro-]cranium - as is used in this study - is measurement §64 from B - B`, the basal axis (AXIS I). The measurement can best be taken when the skull is cut in the median plane.

168 The point A` is a newly allocated point for an existing median point of an intersecting line. (See the **Glossary of terms**.)

169 The measurement "Occipital condyle to ipsilateral Entorbitale" is replaced by the "Condylar ridge - ipsilateral Entorbitale" (P` - Ent) measurement. (See measurement §66.)

170 The measurement "Occipital condyle to ipsilateral Infraorbitale" is replaced by the "Condylar ridge - ipsilateral Infraorbitale" (P` - If) measurement. (See measurement §67.)

16. **Infraorbitale - Prosthion** (**If - P**). See figure 3.65.
17. **Superior dental arch length :** Postdentale - Prosthion (**Pd - P**). See figure 3.64.
18. **Oral palatal length :** Palatino-orale - Prosthion (**Po - P**). See figure 3.64.
19. **Length of nasal process of incisive bone :** Nasoincisivum - Prosthion (**Ni - P**). See figure 3.58, FINAL COMMENT 2 above, and footnote 163.
20. **Cheek tooth row :** mesial surface of second upper premolar - distal surface of last upper molar on vestibular side (**P^2 - M^3**). See figure 3.64.
21. **Molar tooth row :** mesial surface of upper first molar - distal surface of last upper molar on vestibular side (**M^1 - M^3**). See figure 3.64.
22. **Premolar tooth row :** mesial surface of second upper premolar - distal surface of fourth upper premolar on vestibular side (**P^2 - P^4**). See figure 3.64.
23. **Greatest near-horizontal diameter of orbital margin** (**Ect - Ent**). See figure 3.62.
24. **Greatest near-vertical diameter of orbital margin**. See figures 3.62.
25. **Mastoid width :** Otion - Otion (**Ot - Ot**). See FINAL COMMENTS 9 & 10 above as well as figure 3.57.
26. **Greatest width of occipital condyles**. See figure 3.57.
27. **Width of bases of paracondylar processes**. See figure 3.57.
28. **Greatest horizontal diameter of foramen magnum**. See figure 3.57.
29. **Vertical diameter of foramen magnum :** Basion - Opisthion (**B - O**). See figure 3.57.
30. **True [neuro-]cranial width :** Euryon` - Euryon` at least width of parietal bones in temporal fossa on nuchal surface (**Eu` - Eu`**). See figure 3.57 and FINAL COMMENT 6 above.
31. **Least intercornual groove width** between the bases of the cornual processes *[171]. See figures 3.57, 3.59 & 3.61.
32. **The maximum frontal sinus width** which is the least width of the squamous part of frontal bone just caudal to Ectorbitale. See Frontal Sinus Index under the LIST OF INDEXES below. Also see figures 3.59 & 3.61.

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171 The distance between the bases of the cornual processes and the depth of the intercornual groove (which forms subsequent to the enlargement of the cornual bases) gives a measurable dimension to this aspect of sexual dimorphism in the savannah buffalo.

33. **Greatest width of squamous part of frontal bone :** Ectorbitale - Ectorbitale (**Ect - Ect** or **Zy - Zy**). See FINAL COMMENT 13 above, and Facial Index under the LIST OF INDEXES below. See figure 3.59 and see figure 3.64 to compare the two alternative measurements.
34. **Least width between the orbital margins :** Entorbitale - Entorbitale (**Ent - Ent**). See figures 3.59 & 3.61.
35. **Facial width at facial tuberosity *** [172] . See figures 3.59 & 3.61.
36. **Greatest width of nasal bones**. See figures 3.59 & 3.61. Note the difference in position where the measurements are taken.
37. **Greatest width of body and palatine processes of incisive bones**. See figures 3.59, 3.61 & 3.64.
38. **Palatal width inclusive of alveolar processes *** [173] . See FINAL COMMENT 12 above and figure 3.64.
39. **Least distance between temporal lines of frontal and temporal bones *** [174] . See figures 3.62 & 3.69.
40. **Greatest height of the skull, the true skull base height *** [175] **:** Basion - the point in space B`` (**B - B``**). B`` is emphasized by the difference between the summit of the skull in the intercornual region, and the bases of cornual processes. See FINAL COMMENTS 8 & 11 above and figures 3.57 & 3.58. Also see the following measurement.
41. **Least height of skull :** Opisthion - an allocated point O` on the intercornual groove (**O -**

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172 The facial tuberosity (16 [6]) is an anatomical structure. No specific existing osteo-archaeological reference point appears to be available for this structure. It is therefore indicated in the illustrations under this section, by the numerical number allocated to it under section A.

173 An alternative to the greatest palatal width inclusive of the alveolar processes, is the greatest inter-alveolar palatal width as taken in measurement §65. Thereby the true maximum width of the palate is obtained and that can be used in calculating the palatal index. (See LIST OF INDEXES.)

174 The temporal line (7 [8]) delineates the temporal fossa. In old bulls, the temporal line on the frontal bone becomes partially incorporated into the ventral aspect of the cornual process, and cannot be seen clearly in some animals.

175 The point B`` is a newly allocated median point in space. It is determined by the levels to which the bases of the cornual processes project beyond the summit of the skull. It is not homologous to the highest point of the intercornual protuberance of the domestic bovine. (See **footnote 176** for notes on the point O`). B - B`` is a vertical dimension with the skull in the datum plane.

O`)* [176] . See figures 3.57 & 3.58.

42. **The horizontal distance between the distal ends of the cornual processes *** [177] . See figure 3.59.

42a **The total length of both cornual processes**, from distal end to distal end, measured along the outer curves. See figure 3.59.

43. **The greatest tangential distance between the outer curves of the cornual processes.** See figure 3.59.

44. **Cornual process circumference** on a sagittal plane through Ot` * [178] . See figures 3.67 & 3.69.

45. **Maximum horizontal rostro-caudal diameter of cornual process** on a sagittal plane through Ot` with the skull in the datum plane. See figures 3.64, 3.67 & 3.69.

46. **Greatest vertical dorso-ventral diameter of cornual process** on a sagittal plane through Ot` with the skull in the datum plane. See figures 3.67 & 3.69.

47. **Unilateral length of a cornual process** measured along the caudal edge. See figure 3.59.

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176 In the domestic bovine, the least height of the skull would be from Opisthion (O) - on the dorsal edge of the foramen magnum - to the highest point of the intercornual ridge (in the median plane). In the savannah buffalo, that highest point is the newly allocated point O` that lies on a horizontal line, tangential to the intercornual groove in the median plane. (See **footnote 175** to distinguish this point from B``.)

177 In the table where the results are recorded (TABLE 3.1), it will be seen that in the case of the bull, no dimensions are taken. In that specimen, the cornual processes were cut to prevent the specimen from getting stolen. That was done shortly after collection in 1966, and in the years that followed, the cut parts of the cornual processes and horns unfortunately got lost. In the case of the trophy bull, the measurements were taken of the process including the horn. (See also **footnote 101** regarding the terminology problem of the cornual process, having a base and a distal free part, and not a crown - or a corona - and a neck or collum.)

178 The "horncore basal circumference" is impractical to take on intact savannah buffalo skulls because the base extends over nearly the whole dorsal surface of the skull in bulls but not in cows. Therefore, three measurements of the cut surface of the cornual process in a sagittal (paramedian) plane through Ot` are taken. These are the circumference, the greatest dorso-ventral diameter, and the maximum rostro-caudal diameter of the cut surface. Due to practical problems, these measurements cannot be regarded as very accurate in skulls where the horns are not cut, and are therefore indicated in such cases with a minus sign in the results. If, for scientific use (and not for trophy hunters), the length and the curvature of the cornual process have to be measured, it should be done on the centre-line of the process. Such a measurement can best be done by digital computerized means. (Also see **footnote 101**.)

ADDITIONAL MEASUREMENTS PROPOSED FOR THE SKULL AND HYOID APPARATUS OF THE SAVANNAH BUFFALO :

§48 **Volume of cranial cavity**. Cranial cavity volume can be measured by using millet seed to fill the cavity, and then re-measuring the volume of seed used ***** [179] .

§49 **The total length of the frontal sinus complex :** The rostro-caudal extent of the frontal sinus complex of the savannah buffalo must include the nasal sinus when it is present (**L` - L``**). The total frontal sinus length is used in the calculation of the frontal sinus index. See NEW REFERENCE POINTS above and figures 3.58 & 3.59. Also see LIST OF INDEXES below.

§50 (a) **The rostro-caudal dimension of the keel of the vomer** (**H - H`**). See figures 3.60 & 3.63 and FINAL COMMENT 7 above. The height of the keel in the various sections of the vomer, are shown on the lateral view of the vomer in figure 3.60.

(b) **The rostro-caudal dimension of the wings of the vomer** (**H - H``**). See figures 3.60 & 3.63, but also see figures 3.58, 3.61 & 3.64, and see FINAL COMMENT 7 above.

(c) **The rostro-caudal dimension of the free edge of the keel** (**H - Po**). See figures 3.60 & 3.63

§51 **The width of the lateral boney orbit** (/ width of the zygomatic process of the frontal bone / width of the frontal process, if the zygomatic bone is used) measured from the temporal line to the lateral orbital margin at the point Ect (Ectorbitale)***** [180] . See figures 3.62, 3.65, 3.67 & 3.69.

§52 **Intersection point / s for the vestibulo-lingual axes of maxillary cheek teeth**. The vestibulo-lingual axis of a tooth lies centrally on the vestibulo-lingual plane of that tooth. The axes of individual teeth of a specific quadrant in the maxilla, would intersect each other at one or more points, projected in space. The distances to the intersections are

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179 Millet seeds or *manna* is the seed from a *Panicum* species of grass. Much smaller mustard seed - or even digital methods using 3D computer images - would be more accurate to measure the volume of the cranial cavity. However, due to ossification of parts of the meninges especially in older bulls, the volume cannot be measured accurately in any case. The average of three measurements was regarded to be accurate enough. Halved skulls can be used with greater ease as temporary filling of all fissures and foramina can then be done a lot easier. Alternatively, the volumetric displacement of a model of the cranial cavity can be used. Even though this method can be highly accurate, making such a model is time consuming and requires technical skills.

180 The width of the lateral orbital margin gives an indication as to the increase in the width of this structure from young animals to old animals. The increase in width of this structure can be as much as four fold in bulls but slightly less so in cows. This measurement is therefore a sexual dimorphism indicator for the skulls of savannah buffalo.

measured from the occlusal surface of the maxillary cheek teeth * [181] . See figure 3.69.

§53 **Angle of maxillary cheek teeth occlusal surface plane with the median plane**. The occlusal surface plane is formed between the occlusal surfaces of the upper and lower cheek teeth, and the intersection of that plane with the median plane. See figure 3.45.

§54 **Angle of Reid's base line with the horizontal**. Reid's base line is taken by connecting **Ot`` to Rh first. The angle is then measured between the line and the horizontal**. The latter measurement is taken with the skull in the datum plane. See figures 3.62, 3.65, 3.67 & 3.69. Also see the next measurement number §55 and footnote 182 regarding the intersecting points of the two measurements.

§55 **Angle of Frankfort plane with the horizontal**. The Frankfort plane can also be described as an "auriculo-infraorbital plane" **:** It is taken by drawing a **plane through the left and right Ot` points and the lowest points on the antimeric infraorbital margins**. **The angle is then measured between this plane and the horizontal plane**, with the skull in the datum plane. See figures 3.62, 3.65, 3.67 & 3.69 * [182] .

§56 **Dimensions of the different components of the hyoid bone**. See figure 3.71.

(a) Rostro-caudal dimension (- a "radial" dimension-) of the semi-lunar basihyoideum plus thyrohyoideum. This measurement is taken from the rostral end of the lingual process to a median point on the line that connects the caudal ends of the thyrohyoideum.

(b) Length, width and rostro-caudal dimensions of the ceratohyoideum.

(c) Length, width and rostro-caudal dimensions of the epihyoideum.

(d) Length, width and rostro-caudal dimensions of the stylohyoideum.

(e) Length, width and rostro-caudal dimensions of the tympanohyoideum. (Note that it appears as if in old animals, the tympanohyoideum is mostly taken up into the

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181 The vestibulo-lingual axes of the cheek teeth converge distally (whereas the axes of incisors diverge distally). The significance of the converging axes of cheek teeth lie in contact surface wear of teeth. (See **Glossary of terms**). The correlation between the degree of convergence and age was not established. The common point cannot be exactly determined and therefore the distance from the occlusal surface to this common point has to be guesstimated to some extent. Although it is not an accurate measurement, it is nevertheless very significant when the dentition is considered.

182 The intersecting point between Reid's base line and the Frankfort plane, is usually rostral to the temporal bone in young animals, but caudal to the temporal bone in older animals. The Frankfort plane and Reid's base line are used as indicators to stress the point that the external auditory canal increases in length with age (especially in bulls). The increased width of that part of the temporal bone affects planes, lines and indexes. It may be that in animals of intermediate age - between 3 to 5 years of age - the line and the plane might not intersect at all.

ossified proximal part of the stylohyoideum. Also note that in prepared skulls that were boiled, the tympanohyoideum could be damaged or would appear not to be present.)

§57 **Length of enamel covered crown of first upper molar** (**$M^{\underline{1}}$**) on the vestibular side. See figure 3.44. The remaining length of the enamel-covered crown of the first upper molar - sometimes more so than that of the first lower molar in the savannah buffalo - determines the longevity of an animal if the dentition alone is considered. (This differs from the Bovine as discussed in the introductory paragraph under PRE-DEFINED POINTS above.)

§58 **The angle between the general direction of the external acoustic meatus and the median plane**. See figure 3.57.

§59 **The gnathic angle between the basal axis (I) and the skull axis (III)**. See figures 3.58 & 3.63.

§60 **The craniofacial angle between the basal axis (I) and facial axis (II)*** [183] . See figure 3.58.

§61 **The Akrokranion - Opisthokranion distance** (<u>old animals only</u>) (**A - Op**). See FINAL COMMENT 4 above and figure 3.58, but also see figures 3.59 & 3.61.

§62 The **position of Palatino-orale (Po) point on the palatomaxillary suture** (19^5) **relative to the level of either $Dp^{\underline{3}}$, $Dp^{\underline{4}}$, $M^{\underline{1}}$ or $M^{\underline{2}}$** , depending on age related eruption of these teeth * [184] . See figure 3.64.

§63 **Maximum skull length :** Condylar ridge - Prosthion length (**P` - P**)* [185] . See FINAL COMMENT 11 above and figure 3.58.

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183 The third angle - between the facial axis II and the skull axis III - is calculated after the other two angles have been measured. (See measurement §73.)

184 The horizontal part of the palatine bone, relative to the position of the cheek teeth (and the alveolar process of the maxilla), is not only indicative of relative changes with age, but also to mesial drift of teeth. (See palatine and maxillary bones under section A.) This phenomenon is recognized during embryological development in other species too. No attempt was made in this study to interpret the significance of this, apart from being a possible tool in estimating the age of the savannah buffalo among many other parameters. How the horizontal part of the palatine bone relates to the distance between the caudal end of the alveolar processes and the temporomandibular joint in the savannah buffalo, needs a separate investigation. (Also see point 9 under the LIST OF INDEXES.)

185 The condylar ridge - Prosthion length is preferred above the term “condylobasal length”. (See measurement 2 and FINAL COMMENT 11.) “Condylobasal” can be confused with the true base of the skull, measured between B and B``.

§64 **True [neuro-]cranium length** or **basal axis** (**AXIS I**) **: (B - B`)*** [186] . See figures 3.58 & 3.63.

§65 **True maximum inter-alveolar palatal width**. See FINAL COMMENT 12, figure 3.64 and footnote 173.

§66 **Condylar ridge - ipsilateral Entorbitale** (**P` - Ent**). See figure 3.65.

§67 **Condylar ridge - ipsilateral Infraorbitale** (**P` - If**). See figure 3.65.

§68 **Maximum width of [neuro-]cranium** (**Ot` - Ot`**). See figure 3.64.

§69 **Total palatal length :** Prosthion to Staphylion length (**P - St**). See figure 3.64.

§70 **Angle of the nasoincisive incisure**. See figures 3.59 & 3.63.

§71 **Diameter of the combined round and orbital foramen.** See figure 3.58, as well as 4 [12] under section A, and TRAJECTORY I under section E.

§72 **The greatest length, height and width of the cerebral part of the cranial cavity in the horizontal, vertical and transverse planes**. See figure 3.58.

§73 **The angle between the facial axis (II) and the skull axis (III) is determined by calculation** after the gnathic and craniofacial angles have been measured in measurements §59 & §60 respectively. See figure 3.58.

§74 **The angle between the basal axis (axis I) and the horizontal plane with the skull in the datum plane**. See figures 3.58 & 3.63.

§75 **Facial axis** length (**AXIS III**) **: B` - P** . See figures 3.58 & 3.63.

§76 **Volume of maxillary sinus complexes**. This value can be determined by measuring the volumetric displacement of modelled parts in water. See figures 3.55 & 3.56.

§77 **Volume of the frontal sinus complexes**. This value can be determined by measuring the volumetric displacement of the modelled parts. The volume would include the volume of the boney septa of the frontal sinus. See figures 3.55 & 3.56.

Note : Digital means may in future be used to determine the last two measurements. Until such time, these volumes - as well as the volume of the cranial cavity - can be measured accurately enough by the methods described above. (See measurement §48 and footnote 179.)

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186 The basal axis (I) and the true [neuro-]cranial length is discussed under FINAL COMMENT 8 and under **footnote 167** for measurement 6. (See also **footnote 83** in text under section A.)

TABLE 3.1

RESULTS OF STANDARD AND ADDITIONAL MEASUREMENTS FOR THE SKULL AND HYOID APPARATUS OF THE SAVANNAH BUFFALO :

Note : All units of length are in millimetres, and are therefore not indicated in the table. Volume in millilitres (ml) and degrees (E) are however indicated to distinguish these values from units of length.

Measure-ment number	Dimension in heifer	Dimension in bullock	Dimension in cow	Dimension in bull	Trophy sized bull
1	381	425	442	520	542
2	412	448	468	480	503
3	348	409	435	454	470
4	261	279	303	312	321
5	123	130	132	142	149
6	209	219	240	254	265
7	228	245	278	278	280
8	155	180	170	202	240
9	185	213	205	240	261
10	285	333	353	376	426
11	269	304	311	334	362
12	131	158	185	179	187
13	227	246	255	265	281
14	276	292	307	327	332
15	287	313	324	333	350
16	130	144	150	156	159
17	M^3 not erupted Dp's still in wear	265 Erupting M^3 Dp's still in wear	270	276	282
18	180	186	203	210	227
19	121	136	145	154	175

Measure-ment number	Dimension in heifer	Dimension in bullock	Dimension in cow	Dimension in bull	Trophy sized bull
20	M^3 not erupted Dp's still in wear	139 Erupting M^3 Dp's still in wear Premolar EO's present	141	136	134
21	M^3 not erupted	86 Erupting M^3	87	85	84
22	Dp's still in wear	56 Dp's worn	60	58	56
23	64	63	60	64	73
24	57	60	61	61	61
25	176	206	229	251	249
26	98	113	108	121	112
27	132	169	169	189	180
28	30	44	40	32	34
29	35	44	45	38	41
30	98	119	136	126	119
31	55 (-)	45	61	28	20
32	196	206	210	215	240
33	192	207	220	223	235
34	122	134	152	150	151
35	131	141	154	156	155
36	54 (caudally)	51 (rostrally)	67 (caudally)	66 (rostrally)	64 (rostrally)
37	68	85	100	107	114
38	114	130	145	134	145
39	30	26	29	24	13
40	174	189	209	225	280
41	143	155	168	182	204
42	255	390	472	Horns cut. See note 177	673 See note 177
42 a	970 (-)	1410 (-)	1480 (-)	Horns cut. See note 177	1600 (-) Note 177

Measure-ment number	Dimension in heifer	Dimension in bullock	Dimension in cow	Dimension in bull	Trophy sized bull
43	396	695	810	Horns cut. See note 177	940 See note 177
44	220	390	330 (-) intact horns	410	680 (-) intact horns
45	82	140	118 (-) intact horns	151	250 (-) intact horns
46	65	106	70 (-) intact horns	80	160 (-) intact horns
47	265 (-)	565 (-)	610 (-)	Horns cut	660 (-)
§48	460 ml (-)	575 ml (-)	630 ml (-)	530 ml (-)	610 ml (-)
§49	235 (-)	234 (-)	244 (-)	260	280 (-)
§50a	219	223	252	265	282
§50b	219	223	270	282	328
§50c	123	135	145	147	155
§51	15	25	32	33	41
§52	un-erupted permanent premolars and M^3	erupting permanent premolars	300 (-)	400 (-)	500 (-)
§53	60_E	70_E	70_E	65_E	70_E
§54	23_E (-)	23_E (-)	23_E (-)	28_E (-)	23_E (-)
§55	21_E (-)	21_E (-)	24_E (-)	30_E (-)	25_E (-)
§56a	3 - 4 month old specimen: 42 (mostly cartilaginous)	specimen unavailable	59 (-)	75 (-)	specimen unavailable
§56b	3 - 4 month old specimen: 26 x 5 x 7	specimen unavailable	36x7x10	43x6x10	specimen unavailable
§56c	3 - 4 month old specimen: 16 x 6 x 9 (cartilaginous)	specimen unavailable	24x9x14	41x5x8	specimen unavailable
§56d	3 - 4 month old specimen: 91 x 3 x 8	specimen unavailable	130x5x12	130x6x15	145x9x16
§56e	3 - 4 month old specimen: 12 x 6 x 9 (cartilaginous)	specimen unavailable	2x5x12	2x6x15 (-)	specimen unavailable
§57	42 compare to M_1	37 compare to M_1	25 compare to M_1	20 compare to M_1	12 compare to M_1
§58	60_E	65_E	58_E	60_E	60_E
§59	20_E	18_E	skull not halved	24_E	skull not halved
§60	150_E	153_E	skull not halved	141_E	skull not halved

Measure-ment number	Dimension in heifer	Dimension in bullock	Dimension in cow	Dimension in bull	Trophy sized bull
§61	(-)	(-)	20 (-)	25	45 (-)
§62	$Dp^{\underline{4}}$	$M^{\underline{1}}$	$M^{\underline{1}}$ / $^{\underline{2}}$	$M^{\underline{1}}$	$M^{\underline{2}}$
§63	409	445	461	480	500
§64	164	170	185 (-)	191	205
§65	73	82	86	88	91
§66	227	247	255	267	282
§67	287	315	325	332	350
§68	189	216	246	266	269
§69	229	244	274	275	286
§70	29_E (-)	28_E (-)	32_E (-)	40_E (-)	60_E (-)
§71	Not applicable	Not applicable	Not applicable	20 x 17	20 x 17
§72	Not applicable	Not applicable	Not applicable	Not applicable	120 - 130 mm long, 70 - 80 mm high 100 mm wide
§73	10_E	9_E	skull not halved	15_E	skull not halved
§74	152_E	154_E	± 150_E (-)	145_E	± 145_E (-)
§75	235	245	267	289	297
§76	Not measured	Not measured	Not measured	Not measured	740 ml
§77	Not measured	Not measured	Not measured	Not measured	8663 ml

LIST OF STANDARD MEASUREMENTS OF THE MANDIBLE **:**

1. **Gonion caudale - Infradentale** length (**Goc - Id**). See figures 3.66, 3.68 & 3.70.
2. **Caudal border of the smaller facet of condylar process - Infradentale** length. (The smaller facet is numbered $21^{10'''}$ under section A.) See figures 3.66, 3.68 & 3.70.
3. **Gonion caudale - distal border of** $\mathbf{M_{\overline{3}}}$ **:** (**Goc -** $\mathbf{M_{\overline{3}}}$). See figure 3.70.
4. **Distal border of** $\mathbf{M_{\overline{3}}}$ **- Infradentale** length ($\mathbf{M_{\overline{3}}}$ **- Id**). See figure 3.70.
5. **Gonion caudale - mesial border of** $\mathbf{P_{\overline{2}}}$ length (**Goc -** $\mathbf{P_{\overline{2}}}$). See figure 3.70.
6. **Gonion caudale - caudal border of the mental foramen** length. (The mental foramen is numbered 21^{25} under section A.) See figures 3.66, 3.68 & 3.70.
7. **Cheek tooth row** length measured from the mesial surface of second lower premolar - distal surface of last lower molar on vestibular side ($\mathbf{P_{\overline{2}}}$ **-** $\mathbf{M_{\overline{3}}}$). See figure 3.70.
8. **Molar tooth row** length measured from the mesial surface of lower first molar - distal surface of last lower molar on vestibular side ($\mathbf{M_{\overline{1}}}$ **-** $\mathbf{M_{\overline{3}}}$). See figures 3.70.
9. **Premolar tooth row** length measured from the mesial surface of second lower premolar - distal surface of fourth lower premolar on vestibular side ($\mathbf{P_{\overline{2}}}$ **-** $\mathbf{P_{\overline{4}}}$). See figure 3.70.
10. **Length of the enamel-covered crown of the first lower molar** ($\mathbf{M_{\overline{1}}}$) on the lingual side. See figure 3.44. Note that the lingual height of the mandibular first molar, but the vestibular height of the maxillary molar is measured, as the heights of the clinical crowns on these sides are more critical to measure. That is especially so when the longevity of the animal is considered, based on its dentition.
11. **Length of diastema** from the mesial border of $P_{\overline{2}}$ - distal border of $I_{\overline{4}}$ ($\mathbf{P_{\overline{2}}}$ **-** $\mathbf{I_{\overline{4}}}$). See figure 3.70.
12. **Height of mandibular ramus** from the Gonion ventrale - most dorsal level of condylar process. See figure 3.70.
13. **Height of mandibular ramus** from Gonion ventrale - mandibular incision. (The mandibular incision is numbered 21^{13} under section A.) See figure 3.70.
14. **Height of mandibular ramus :** Gonion ventrale - Coronion (**Gov - Cr**). See figure 3.70.
15. (a) **Height of molar part of mandible** at level of $\mathbf{M_{\overline{3}}}$ (distal border). See figure 3.70.
15. (b) **Height of molar part of mandible** at level of $\mathbf{M_{\overline{1}}}$ (mesial border). See figure 3.70.
15. (c) **Height of molar part of mandible** at level of $\mathbf{P_{\overline{2}}}$ (mesial border). See figure 3.70.

ADDITIONAL MEASUREMENTS PROPOSED FOR THE MANDIBLE OF THE SAVANNAH BUFFALO :

§16 **Intersection point / s for the vestibulo-lingual axes of mandibular cheek teeth**. The vestibulo-lingual axis of a tooth lies centrally on the vestibulo-lingual plane of that tooth. The axes of individual teeth of a specific quadrant in the mandible, would intersect each other at one or more points, projected in space. The distances to the intersections are measured from the occlusal surface of the cheek teeth. See figure 3.70 and footnote 181.

§17 **Intersection point / s for the vestibulo-lingual axes of mandibular incisors**. The vestibulo-lingual axis of an incisor lies centrally on the vestibulo-lingual plane of that tooth. The axes of individual incisors of the left and the right-hand sides, would intersect each other at one or more points, projected in space. These points lie caudo-ventral to the incisive part of the mandible, in the intermandibular region. The distances to the intersections are measured from the occlusal surface of the incisors. See figure 3.70 and footnote 181.

TABLE 3.2

RESULTS OF STANDARD AND ADDITIONAL MEASUREMENTS FOR THE MANDIBLE OF THE SAVANNAH BUFFALO :

Note : All units of length are in millimetres, and are therefore not indicated in the table.

Measurement	Dimension in heifer	Dimension in bullock	Dimension in cow	Dimension in bull
1	336	356	384	394
2	353	375	408	411
3	100 M_3 not erupted	92 M_3 incomplete	106	109
4	239 M_3 not erupted	265 M_3 incomplete	279	288
5	211 Dp's still in wear	229 M_3 incomplete Premolar EO's present	250	253
6	278	285	307	302
7	113 M_3 not erupted Dp's still in wear	138 M_3 incomplete Premolar EO's present	148	149
8	57 M_3 not erupted	83 M_3 incomplete	94	92
9	57 Dp_2 - Dp_3	51 Premolar EO's present	53	54
10	52 compare to §57	46 compare to §57	18 compare to §57	29 compare to §57
11	101 Dp_2 - Di_3	105 P_2 - Di_3	101	112
12	135	146	165	171
13	133	143	160	163
14	179	210	223	228
15a	71 M_3 not erupted	77	80	81
15b	55	53	57	57
15c	40	39	46	49
§16	un-erupted M_3 Dp's present	Dp's present Premolar EO's present	160-180 (-)	180-300 (-)
§17	120-200 Di present	120-190 Di & I present	130-250 (-)	110-250 (-)

INDEXES :

Indexes are calculated to do away with the size factor. An index is calculated by dividing the dimension of one particular criterion - for example the width - by the length of a related criterion. The result is multiplied by a hundred to get an index value. It is a very simplified method as only one dimension (- of the three-dimensional anatomical aspect -) is considered.

LIST OF INDEXES FOR THE SKULL OF THE SAVANNAH BUFFALO :

Note : The symbols in the following formulae are chosen at random and primarily in order not to clash with any abbreviations of existing or newly allocated points.

1 Facial index* : $^{Æ}/_{E}$ x 100. Æ in this formula is the maximum facial width and it is measured from Ectorbitale to Ectorbitale or from Zygion to Zygion, whichever is widest. Ect to Ect gives the greatest width of the squamous part of the frontal bone and is taken in measurement 33. (See FINAL COMMENT 13 and figures 3.59 & 3.64.) E in this formula is the true [viscero-]cranial length from Nasion to Prosthion. N to P is taken in measurement 7. (See figures 3.58 & 3.61.)

2 Cranial index* : $^{G}/_{D}$ x 100. Two alternative configurations can be calculated :

(a) Taking into account only the width of the walls of the cranium relative to the length of the basal axis of the cranium. That excludes the effect of the frontal sinus complex :

G in the formula is measured from Euryon\` to Euryon\`, the true [neuro-]cranium width. Eu\` to Eu\` is taken in measurement 30. (See figure 3.57.) D in this formula is measured from Basion to the rostrum [prae-]sphenoidale, the true [neuro-]cranium length. B to B\` is taken in measurement §64. (See figures 3.58 & 3.63.)

(b) Including the effects of the frontal sinus :

In the second alternative, the value of G in the formula is the maximum width of the [neuro-]cranium, measured at the tuberous enlargements of the retrotympanic processes of the temporal bone. Ot\` to Ot\` is taken in measurement §68. (See figure 3.64.) The value for D in the formula here is the measurement which includes the effect of the frontal sinus, which is from Basion to the Nasion. B to N is taken in measurement 6. (See figure 3.58.)

3 Skull index* : $^{K}/_{Y}$ x 100 : K in this formula is the maximum width of the [neuro-]cranium, measured from the tuberous enlargement of the retrotympanic process. Ot` to Ot` is taken in measurement §68. (See figure 3.64.) Y in this formula is the maximum skull length measured from Prosthion to the ridge that is allocated the point P` on the most caudal point of the occipital condyle. P to P` is taken in measurement §63. (See figure 3.58.)

4 Palatal index* : $^{J}/_{I}$ x 100. J in this formula is the true inter-alveolar palatal width taken in measurement §65. (See figure 3.64.) "I" is the total palatal length from the Prosthion to the Staphylion. P to St is taken in measurement §69. (See figure 3.64.)

5 Frontal sinus index* : $^{Œ}/_{M}$ x 100. In this formula Œ is the maximum frontal sinus width just caudal to the Ectorbitale. Ect to Ect is taken in measurement 32. (See figure 3.59 & 3.61). M in this formula is the total frontal sinus complex length measured between L` and L``. "L" refers to Lambda L*# which is replaced by the newly allocated term L` because L disappears due to ossification of the suture. The thickness of the external lamina of the occipital bone at L` is approximately 3-5 mm. L`` is a point allocated to the most rostral extent of the nasal sinus to give the most rostral extent of the frontal sinus complex. L` - L`` is taken in measurement §49. (See figures 3.58 & 3.59.)

6 Index of orbital aditus* : $^{V}/_{W}$ x 100 : V in this formula is the greatest near-vertical diameter of the orbital margin taken in measurement 24. (See figure 3.62.) W in this formula is the greatest near-horizontal diameter of the orbital margin from Ectorbitale to Entorbitale. Ect to Ent is taken in measurement 23. (See figure 3.62.)

7 Nasal index* : $^{Q}/_{R}$ x 100 : Q in this formula is the greatest width of the nasal bones. The nasal width is taken in measurement 36. (See figures 3.59 & 3.61.) In some animals the greatest width lies more caudally, in others more rostrally on the nasal bone. R in this formula is the greatest length of the nasal bones, measured from Nasion to Rhinion. N to Rh is taken in measurement 12. (See figures 3.61.)

8 Calculating indexes using a single dimension can be misleading. For instance, there is no reason why as a second alternative, the facial axis length (measurement §75) can not be taken instead of the true [viscero-]cranial length (measurement 7). In that case, E in the formula can be substituted by the measured value of B` - P and not from N to P. By that same reasoning, the following more complex indexes could also be calculated :

The volume of the cornual process should be compared with the volume of the skull by determining these volumes - preferable by digital means. Such a calculated index will give a volumetric value and might confirm or reject what is perceived as a disproportionate increase in the size of the cornual processes when compared to the size of the skull as a whole. What appears to be another example of disproportionate growth, is that of the retrotympanic process of the temporal bone, and a volumetric value might reflect the true state of this perception. The simplest volumetric value measured, is that of the cranial cavity (measurement §48). Yet it is not compared with any other volume or calculated in any index. Further studies and three-dimensional computer digitization of the skull and mandible of the savannah buffalo are needed before conclusions can be drawn and before suitable complex indexes can be formulated * [187] .

9 The distance from the articular condyle of the mandible to the molar and the incisive parts of the body of all ages should be calculated to record the longitudinal growth of the mandible. (See footnote 184 in this regard as well.)

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187 The intention of this study is not to scientifically confirm all the observations but to recognize and describe perceptions and to give terms to structures where necessary for use in describing the osteology and the **Craniometric data**. That was done by also keeping the macroscopic description of the Myology, Neurology, Angiology and the Splanchnology of the head of the savannah buffalo in mind. Three-dimensional computerized studies falls beyond the scope of this study.

TABLE 3.3

COMPUTED INDEXES FOR THE SKULL OF THE SAVANNAH BUFFALO :

Note : **The symbols in the formulae are chosen at random but primarily in order not to clash with any abbreviations of existing or newly allocated points. In the dimension collum for the formulae, reference points are given where possible with the relevant measurement number (or additional measurement number) in brackets.**

Number	Index	Formula x 100	Dimension	Index in heifer	Index in bullock	Index in cow	Index in bull	Trophy sized bull
1	Facial	Æ/E	Ect - Ect (33) N - P (7)	0.84	0.84	0.79	0.80	0.84
2 (a)	Cranial	G/D	Eu` - Eu` (30) B - B` (§ 64)	0.60	0.70	0.74	0.66	0.58
2 (b)	Cranial	G/D	Ot` - Ot`(§ 68) B - N (6)	0.90	0.99	1.03	1.05	1.02
3	Skull	K/Y	Ot` - Ot`(§ 68) P` - P (§ 63)	0.46	0.49	0.53	0.55	0.54
4	Palatal	J/I	(§ 65) P - St (§ 69)	0.32	0.34	0.31	0.32	0.32
5	Frontal sinus	Œ/M	Ect - Ect (32) L` - L`` (§ 49)	0.83	0.88	0.86	0.83	0.86
6	Orbital aditus	V/W	(measurement 24) Ect - Ent (23)	0.89	0.95	1.02	0.95	0.84
7	Nasal	Q/R	(measurement 36) N - Rh (12)	0.41	0.32	0.36	0.37	0.34

CHAPTER THREE

RESULTS

SECTION E : APPLIED ANATOMICAL ASPECTS

(See figures **3.72 - 3.83**. Also see 1.2 - 1.4, 3.1, 3.2, 3.5, 3.7, 3.11, 3.14, 3.31, 3.44, 3.49, 3.58, 3.59 & 3.63 - 3.70.)

Anatomically teeth actually fall under the digestive system, but their presence and intimate relationship with the skull and mandible justifies Applied Anatomical consideration to both the dentition and the skull as a whole.

GENERAL INTRODUCTION:

Utilization of savannah buffalo as a source of food, or culling of buffalo for ecological reasons, or in hunting, demands instant killing. Killing a dangerous animal like the savannah buffalo instantly - under unfavourable conditions in the wild, and while standing a safe distance away from the animal - is not easily done. Instant death under those circumstances can be inflicted optimally by accurately shooting a projectile (bullets or arrows that has sufficient inherent dynamic energy) into the brain. When sudden death needs to be inflicted, acute and massive damage to the brain should be the primary goal. Secondary acute intra-cranial haemorrhage would also be fatal but would not necessarily cause sudden death. The bones of the skull of the savannah buffalo have been described in detail in the previous sections. Based on that osteological study, three different approaches to the brain - referred to as trajectories I, II and III - will be considered in this section.

The topographical anatomy of the visceral organs of the neck, thorax and abdomen of the savannah buffalo correlates well with that of the domestic bovine. A complete three-dimensional concept of the anatomy of the vital organs - not only of the head but also those of the neck and thorax - should therefore be prerequisite knowledge of all hunters. Equipped with that knowledge, big game hunters would know of other alternative sites elsewhere in the body that can be used in case an ideal shot to the brain cannot be carried through. The less favourable alternative lethal targets are - apart from the brain - the spinal cord, brachial plexus, heart, thoracic aorta and lungs. Unlike the elephant, but similar to that of domestic animals, the lungs are situated within pleural cavities that can cause the lungs to collapse when air enters penetrating thoracic wounds of large enough diameters. Technically however, it becomes a highly involved exercise for a novice to understand the intricacies of the splanchnological, topographical and functional details of these vital organs. It becomes even more so when one has to integrate all that information into an applied way in the instant killing of dangerous animals during very limited time frames. It falls beyond the scope of this study to discuss all those possible lethal targets in the body, and therefore only brain-shots via three different trajectories will be considered here.

The trajectory through the combined round and orbital foramen - regarded as the ideal route for a brain shot in the savannah buffalo (vide infra under Trajectory I) - can also be used as an alternative route for taking small histological specimens of the brain. Taking brain specimens using biopsy instruments in this way, avoids the backbreaking task of opening up the skull by conventional methods, by using saws and lots of physical effort.

Age determination by using the shape of the horns, as well as tooth eruption and wear, is documented in the literature for the savannah buffalo. Some of these descriptions lack detail and accuracy, or some cannot be applied under difficult field conditions. For instance, when examining the exposed parts of teeth in the mouth of a live but tranquillized savannah buffalo - either to determine the age or to do dental work when it can still gnash its teeth - becomes a totally different story. Usually, a fairly accurate determination can be made if the animal is under the age of approximately six years, because aging by using the incisors is easy to carry out under most conditions. In older animals, determining the age becomes less accurate because the cheek teeth cannot be exposed properly for visual inspection. This is due to anatomical restrictions in opening the mouth large enough. And there are no other easier ways to determine the age. Even in properly prepared skull collections that include all the teeth, it remains a daunting task to understand the complex three-dimensional structure of teeth. That is so even when both the exposed as well as the embedded parts of all teeth can be seen. Since savannah buffalo are farmed with as "game ranch animals", it became even more important for Veterinarians and game farmers to be able to age buffalo. Therefore, basic guidelines will also be discussed in this section because it forms the basis on which to estimate the remaining lifespan of an animal **even if the birth date is known**. As an additional aid, radiographs centred over especially on the lower first molar tooth can be taken. That procedure is strongly advocated. However, that is not easily done in field conditions either. Even so, correct age determination (when needed), as well as calculating an estimated life expectancy for the individual animal - based preferably not only on the teeth but also on other health parameters too - should be important factors in determining the price of an animal. The longevity aspect of an animal probably becomes more relevant than the age, because of the ever increasing prices of especially disease free savannah buffaloes that are used in breeding programmes.

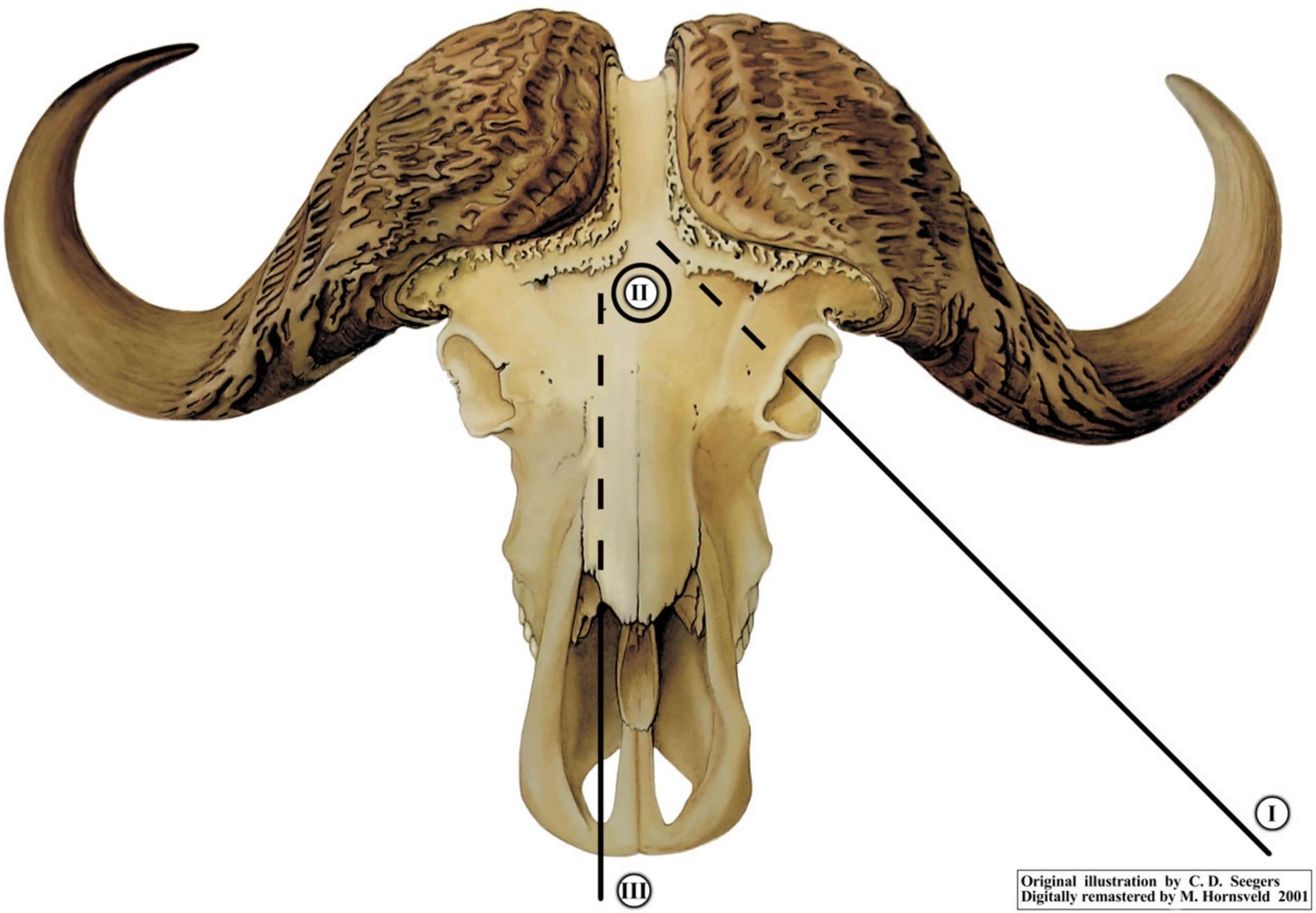
Table 3.4 (vide infra) supplies a complete **Dental Chart** of all the teeth, including the enamel organs of the savannah buffalo. Enamel organs in that chart are abbreviated **EO** or **eo** for enamel organs of permanent and deciduous teeth respectively. The digital numbering system as summarized in the table, also reflects the enamel organs as seen in radiographs of younger animals or in sculptured skull collections.

FIGURE 3.72 : APPLIED ANATOMY

DORSAL VIEW OF THE SKULL OF AN OLD BULL, INDICATING TRAJECTORIES I, II AND III THAT SHOULD BE CONSIDERED WHEN SHOOTING A BULL (SEMI-SCHEMATIC)

FIGURE 3.72 : APPLIED ANATOMY

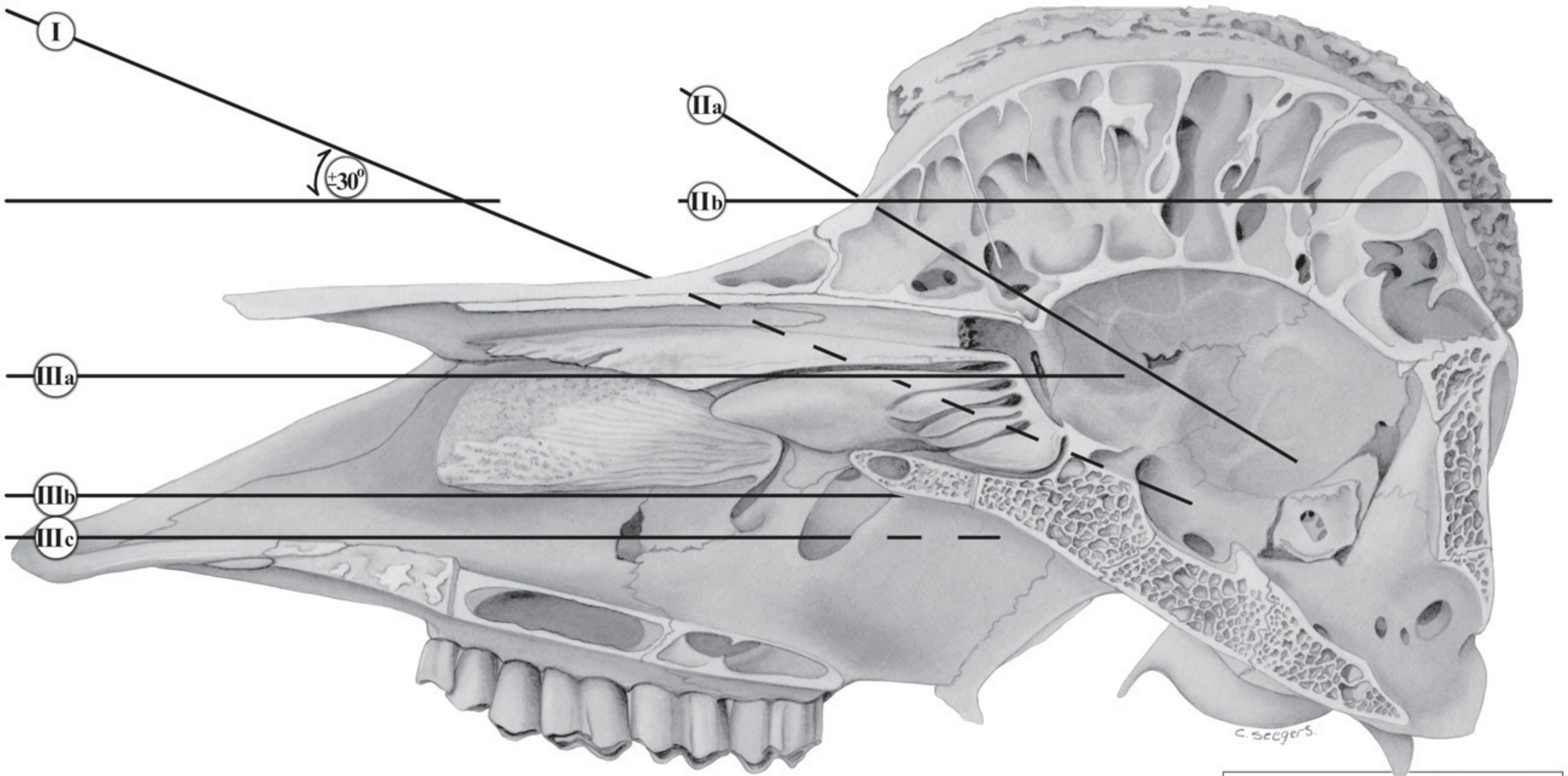
DORSAL VIEW OF THE SKULL OF AN OLD BULL, INDICATING TRAJECTORIES I, II AND III THAT SHOULD BE CONSIDERED WHEN SHOOTING A BULL (SEMI-SCHEMATIC)



Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.73 : APPLIED ANATOMY

MEDIAL VIEW OF THE SKULL OF AN OLD BULL, INDICATING TRAJECTORIES I, II (a), II (b), III (a), III (b) AND III (c) THAT SHOULD BE CONSIDERED WHEN SHOOTING A BULL (SEMI-SCHEMATIC)



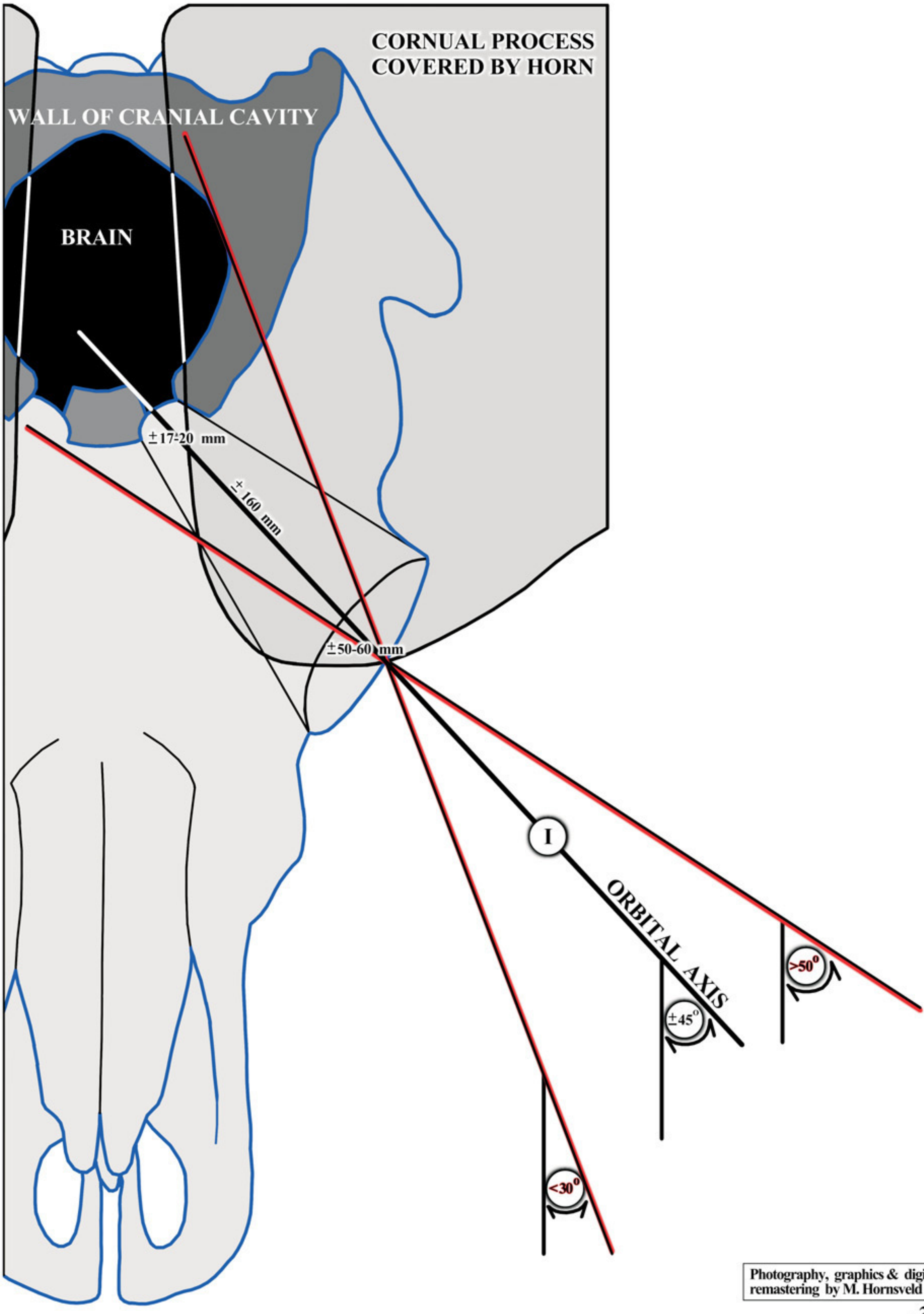
Original illustration by C. D. Seegers
Digitally remastered by M. Hornsveld 2001

FIGURE 3.73 : APPLIED ANATOMY

MEDIAL VIEW OF THE SKULL OF AN OLD BULL, INDICATING TRAJECTORIES I, II (a), II (b), III (a), III (b) AND III (c) THAT SHOULD BE CONSIDERED WHEN SHOOTING A BULL (SEMI-SCHEMATIC)

FIGURE 3.74 : APPLIED ANATOMY

ILLUSTRATION OF THE ORBITAL AXIS IN DORSAL VIEW :
ASPECTS TO CONSIDER WHEN SHOOTING A BULL ALONG THE ORBITAL AXIS (SCHEMATIC)

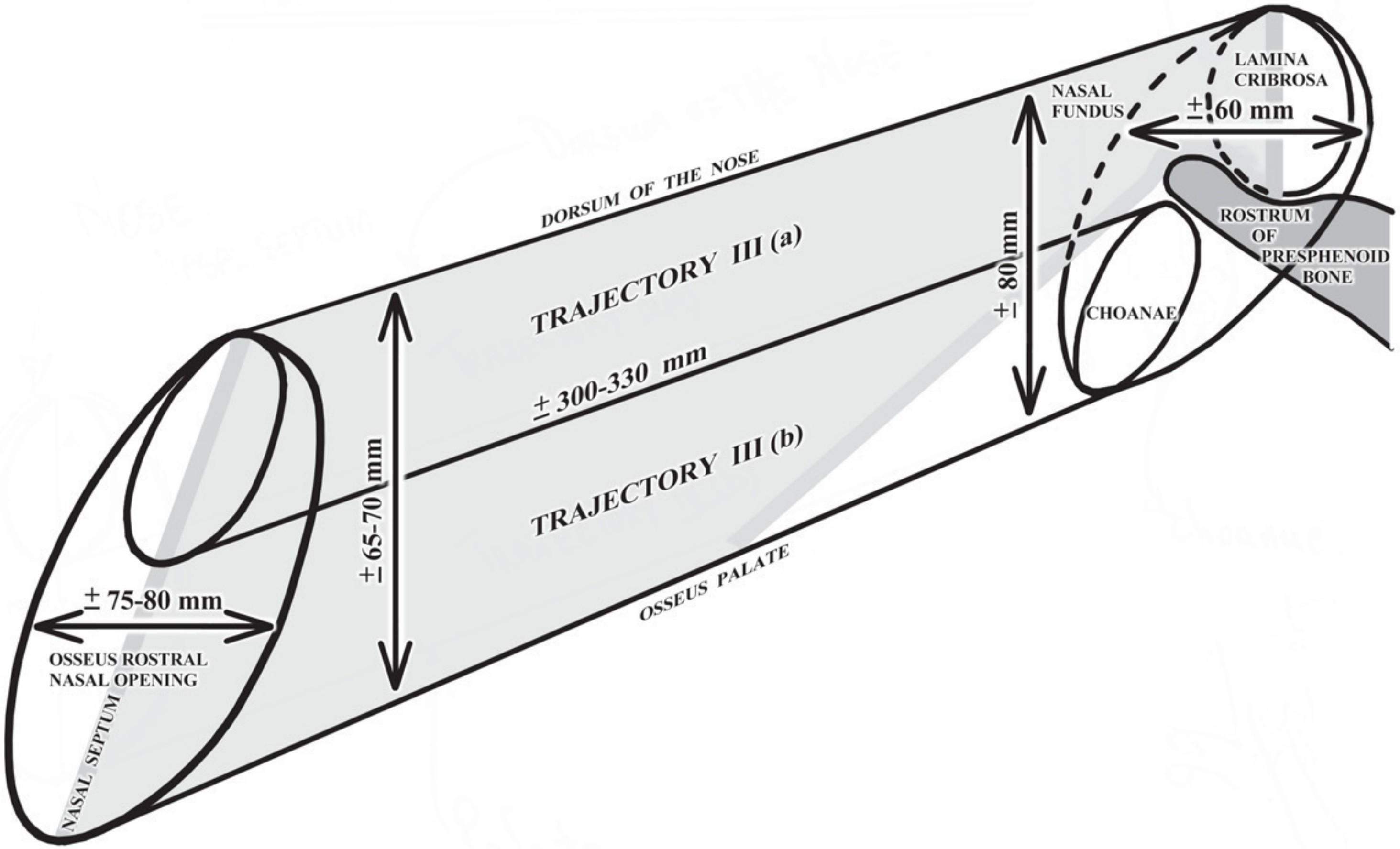


Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.75 : APPLIED ANATOMY

ILLUSTRATION OF THE NASAL CAVITY IN OBLIQUE LATERAL VIEW :
ASPECTS TO CONSIDER WHEN SHOOTING A BULL VIA A NOSTRIL (SCHEMATIC)

FIGURE 3.75 : APPLIED ANATOMY
ILLUSTRATION OF THE NASAL CAVITY IN OBLIQUE LATERAL VIEW :
ASPECTS TO CONSIDER WHEN SHOOTING A BULL VIA A NOSTRIL (SCHEMATIC)



Photography, graphics & digital remastering by M. Hornsveld 2001

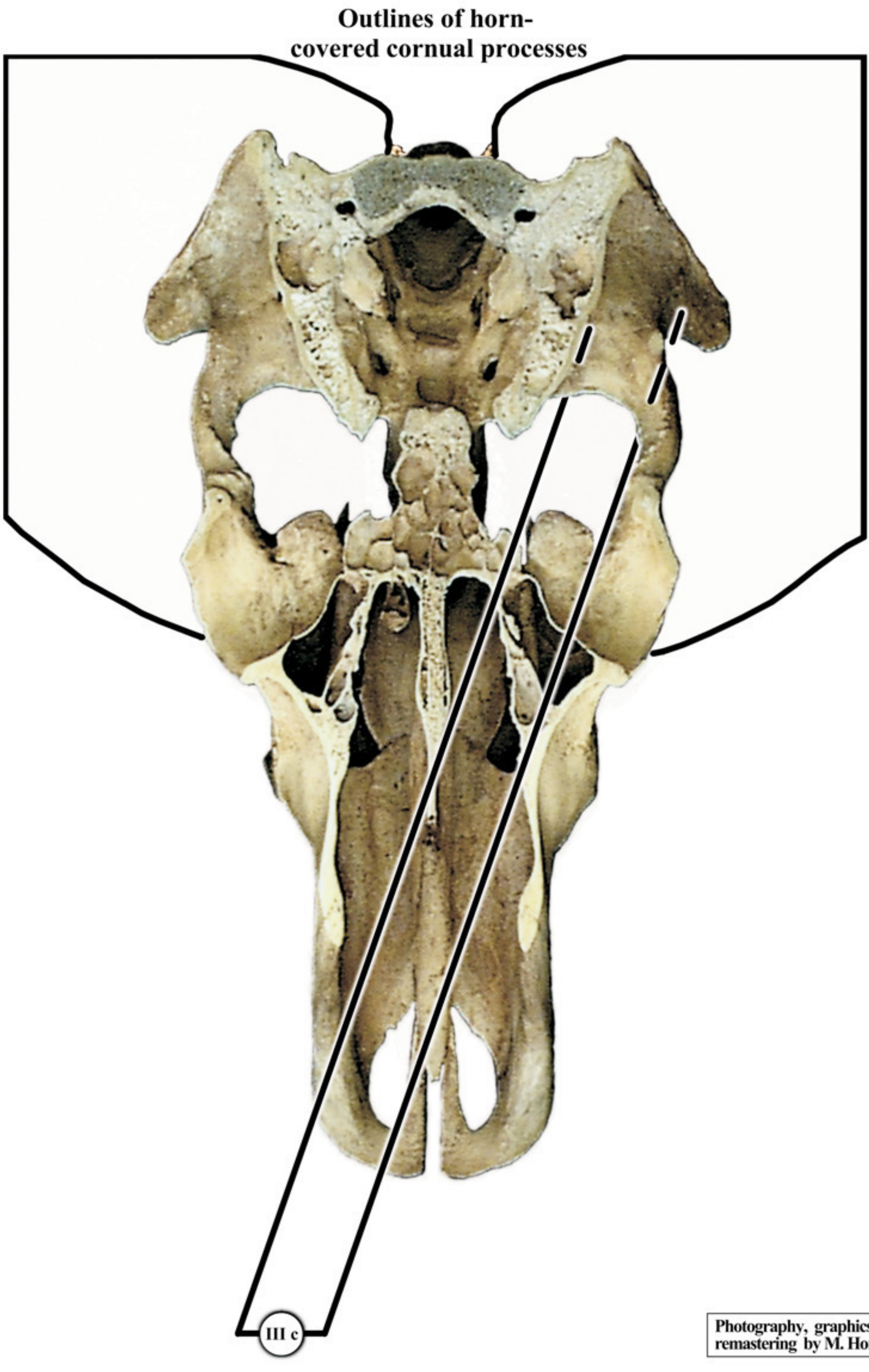
FIGURE 3.76 : APPLIED ANATOMY

DORSAL PLANE CUT THROUGH THE CENTRE OF THE *FORAMEN ORBITOROTUNDUM* (LATERAL VIEW)

Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.77 : APPLIED ANATOMY

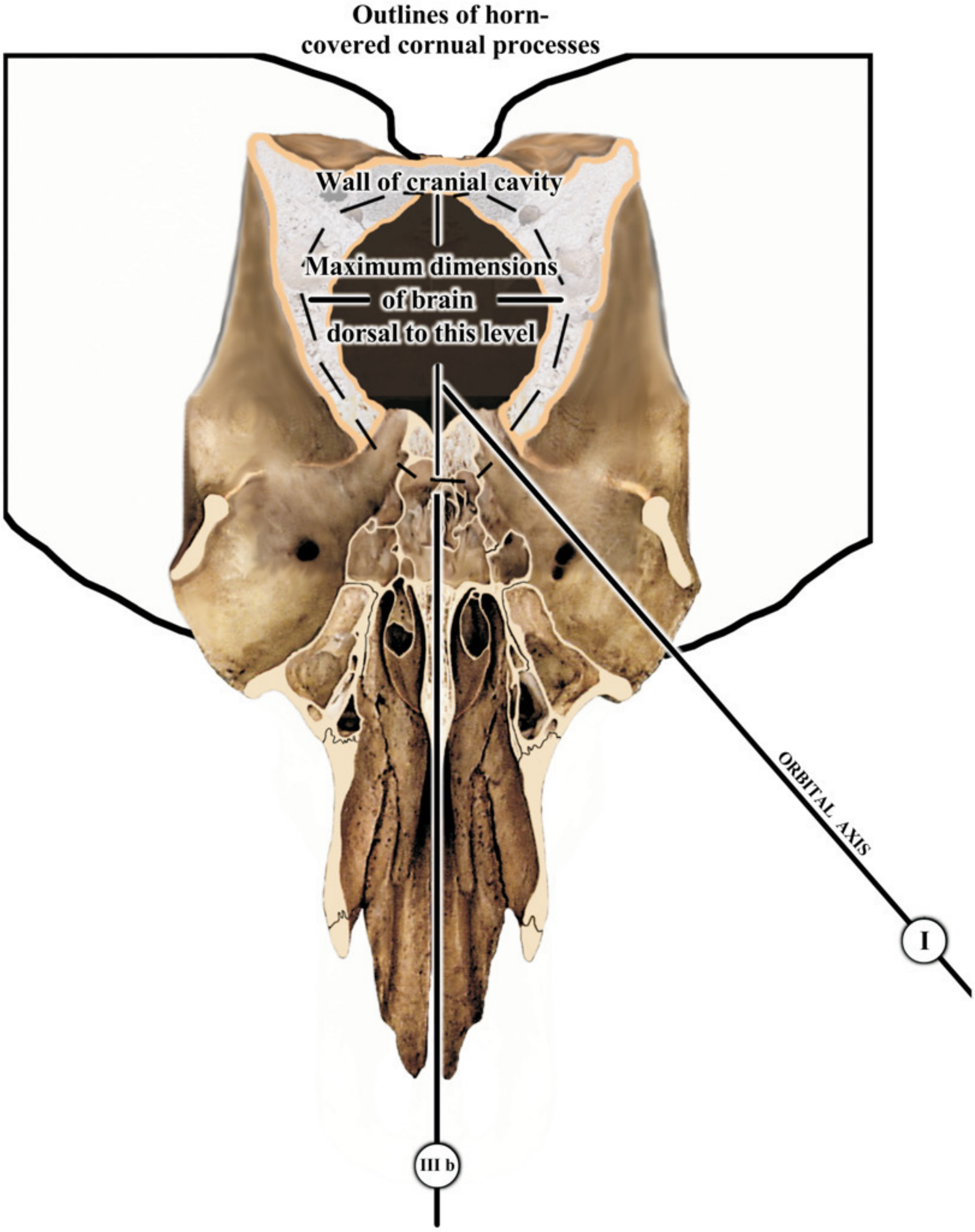
VENTRAL HALF OF SKULL CUT IN THE DORSAL PLANE THROUGH THE *FORAMEN ORBITOROTUNDUM*, INDICATING TRAJECTORY III (c) (DORSAL VIEW)



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.78 : APPLIED ANATOMY

DORSAL HALF OF SKULL CUT IN THE DORSAL PLANE THROUGH THE CENTRE OF THE *FORAMEN ORBITOROTUNDUM* (VENTRAL VIEW)



Photography, graphics & digital remastering by M. Hornsveld 2001

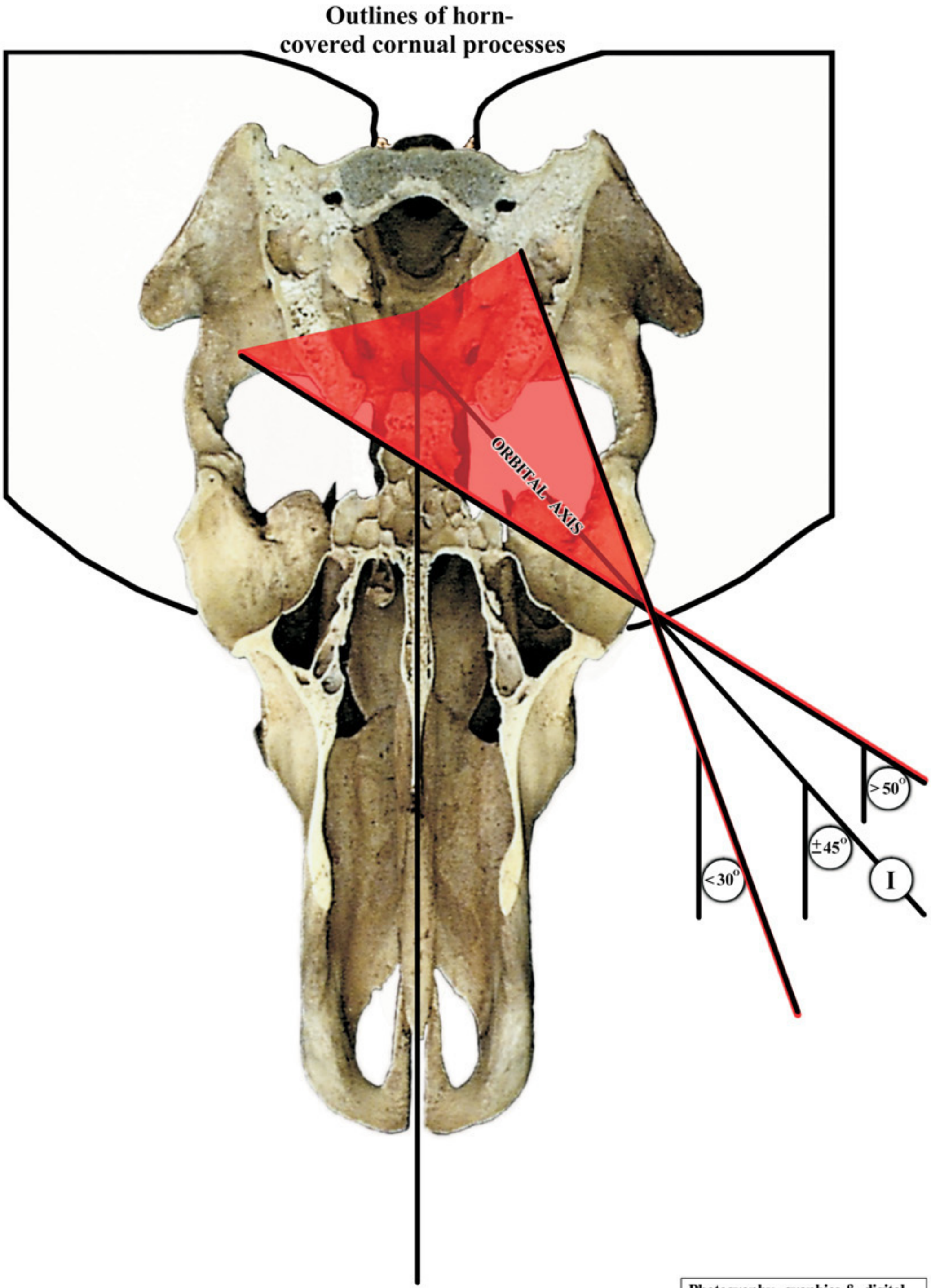
FIGURE 3.79 : APPLIED ANATOMY

VENTRAL AND DORSAL HALVES OF SKULL SUPERIMPOSED OVER EACH OTHER WITH HORNS COVERING THE CORNUAL PROCESSES. TOPOGRAPHICAL POSITION OF THE CRANIAL CAVITY RELATIVE TO THE SKULL AS A WHOLE (SEMI-SCHEMATIC)

Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.80 : APPLIED ANATOMY

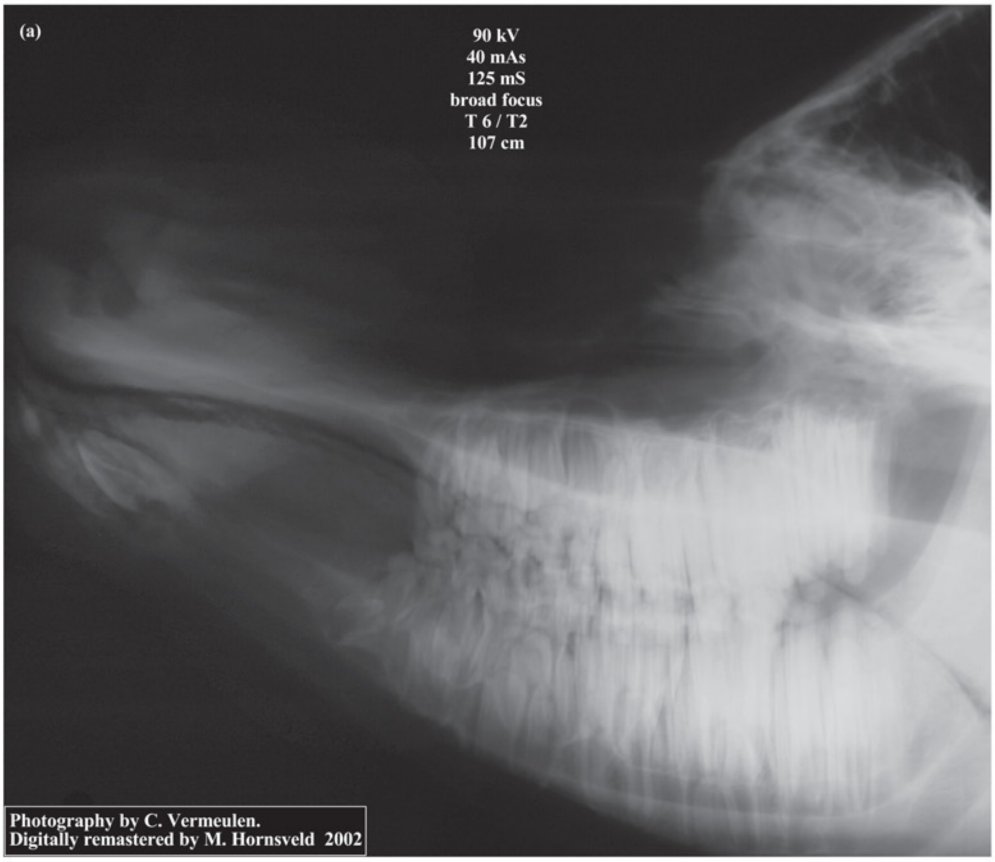
ANGLES AT WHICH PROJECTILES CAN ENTER THE CRANIAL CAVITY VIA THE *FORAMEN ORBITOROTUNDUM*.
DORSAL VIEW RELATIVE TO THE VENTRAL HALF OF THE SKULL OF A BULL (SEMI-SCHEMATIC)



Photography, graphics & digital remastering by M. Hornsveld 2001

FIGURE 3.81 : APPLIED ANATOMY

RADIOGRAPH OF AN IMMATURE ANIMAL IN (a) LATERAL AND (b) DORSAL VIEWS



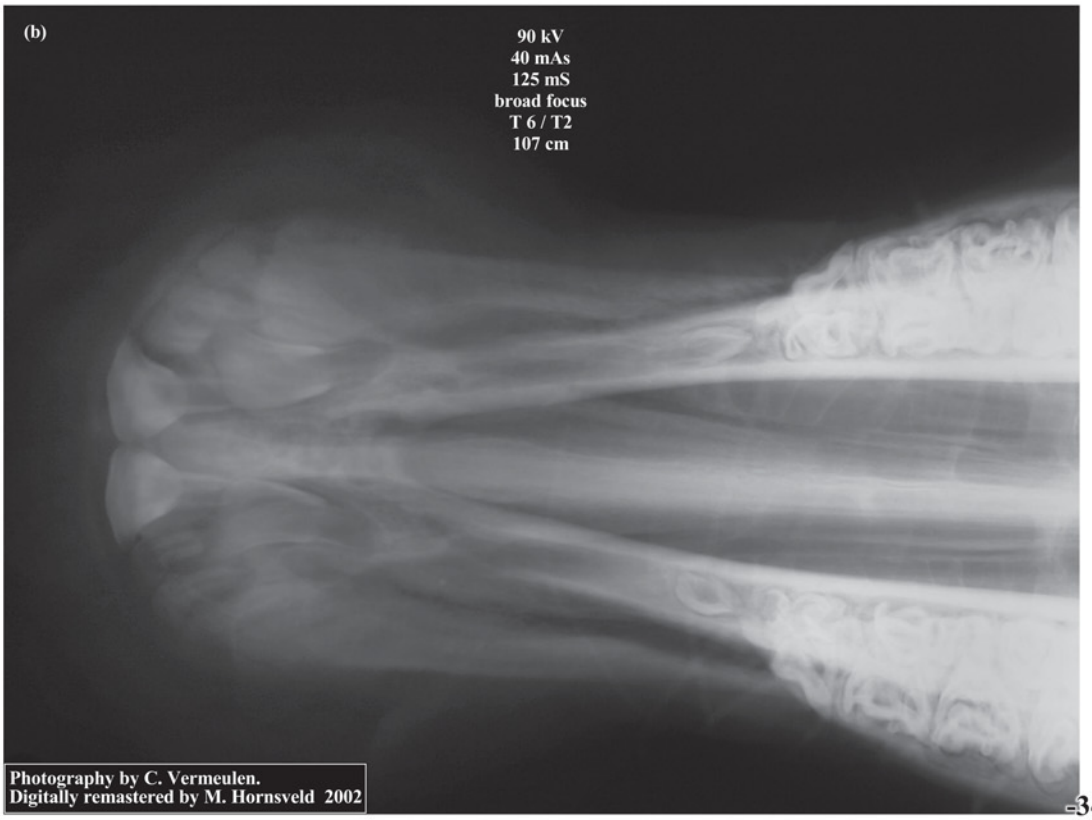


FIGURE 3.82 : APPLIED ANATOMY

RADIOGRAPH OF A SKULL OF A MATURE ANIMAL (DORSAL VIEW)

Note : The skull used for this radiograph is the same skull as was used for figures 3.54 and 3.76 - 3.80

FIGURE 3.83 : APPLIED ANATOMY

SCHEMATIC PRESENTATION OF THE FORCES IN THE SKULL RELAYED BY THE INFRAORBITAL PILLAR

ROSTRAL VIEW **OBLIQUE LATERAL VIEW**

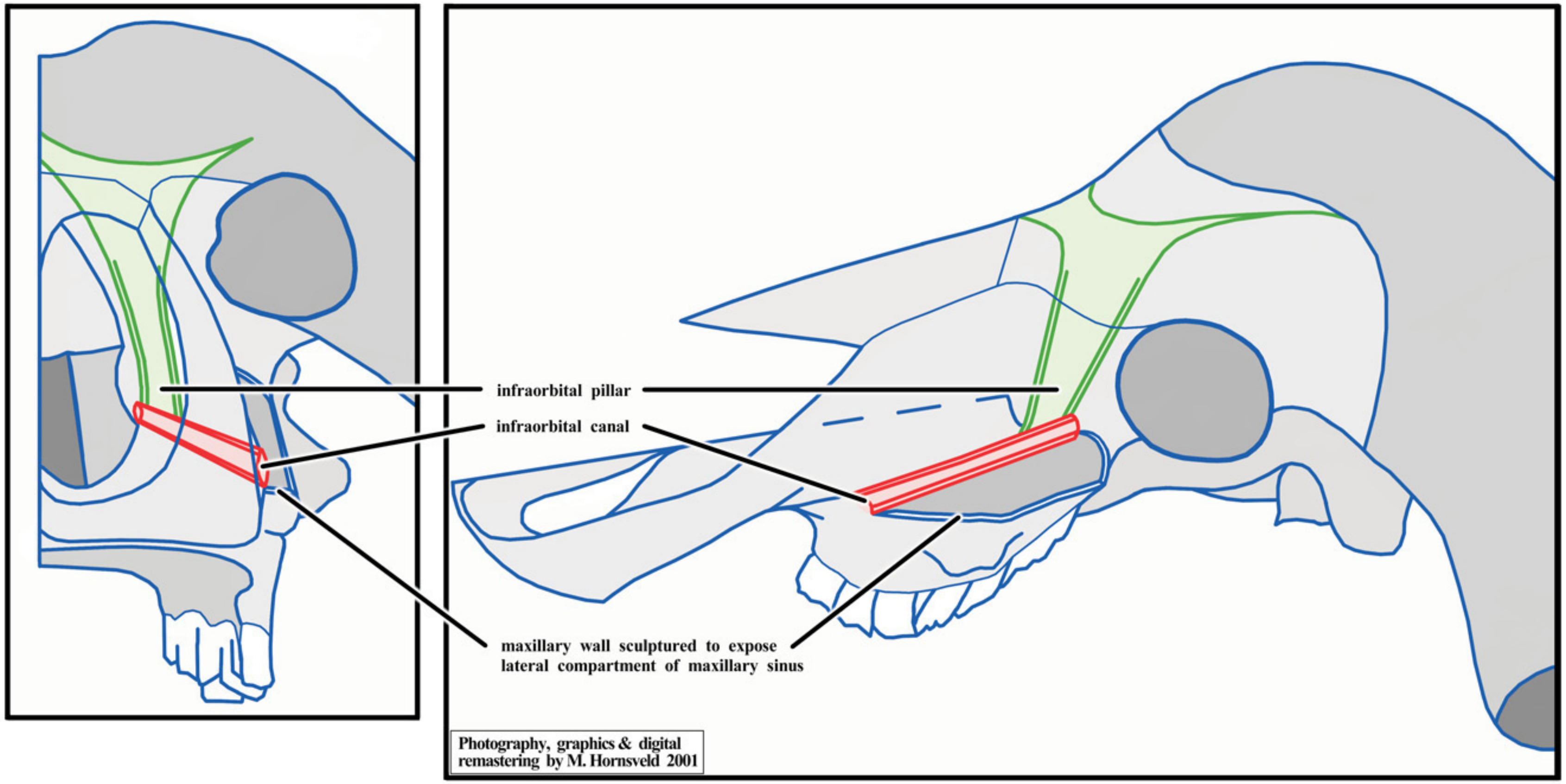


FIGURE 3.83 : APPLIED ANATOMY
SCHEMATIC PRESENTATION OF THE FORCES IN THE SKULL RELAYED BY THE INFRAORBITAL PILLAR

APPLIED ANATOMICAL ASPECTS OF THE SKULL OF SAVANNAH BUFFALO, AS RELATED TO HUNTING.

(See figures **3.72 - 3.80**.)

INTRODUCTION:

If the deliberate attempt of a person is to kill an animal like the savannah buffalo, instantly, and by using a suitable projectile and rifle, one should aim for the brain and not any of the other vital organs. Alternatively, and by far the second best method, one can destroy the spinal cord in the neck region. However, both the brain and the spinal cord are surrounded by bones. The brain is surrounded by the bones of the skull and the cervical spinal cord by seven vertebrae. Dorsally and laterally in bulls, the brain region is protected by different parts of the cornual processes that are covered by horn. Horn is a very dense epidermal product that covers the entire cornual process. The thickness varies dorsal and lateral to the brain region and measures on average between 18 and 25 mm respectively in these areas. The thickness can be even more substantial in some old bulls, ranging from a minimum of 10 mm to a maximum of 38 mm. Horn - even as thin as 10 mm - would severely affect any projectile. The cornual process itself consists of bone, which at the proximal end contains a lateral extension of the frontal sinus. The sinus contains air. The sinus in the cornual process as well as of the frontal bone, is subdivided by boney septa that strengthens skull-cornual process junctions mechanically. The proximal osseus part of the cornual process consists peripherally almost entirely of compact or solid bone. The brain is therefore extremely well protected, effectively shielded from projectiles like bullets and arrows from almost all possible angles. The horizontal, transverse and vertical dimensions of the cerebral part of the brain of a mature savannah buffalo (excluding the smaller cerebellar part and the narrow junction with the spinal cord caudo-ventrally), is approximately 120 - 130 mm long, 70 - 80 mm high (maximum 90 mm) and approximately 100 mm wide. (See measurement § 72 under section D, **Craniometric Data**.) The rest of the spinal cord is nearly as long as the body of the animal. For humane reasons, only the cervical part of the spinal cord should ever be considered in an attempt to kill an animal. Whatever the size of the brain or the length of the spinal cord, the unobstructed entrance to these two parts of the central nervous system is very limited. The detailed study of the skull of the savannah buffalo (section A), reveals that the brain is not covered by bone in the region of two foramina - of significant diameters - one on either side of the skull. These openings are the combined round and orbital foramina, the *Foramen orbitorotundum*. Each opening is situated at the deep aspect of the eye in the boney orbit (13 [21]). When looking at a skull, the foramina can be easily visualized in the depth of the boney orbits, as their horizontal and vertical diameters are 17 mm and 20 mm respectively. (See measurement **§** 71 under section D, **Craniometric Data**.)

The absolute diameters of these foramina are important, as well as the absolute and relative sizes of the brain. The diameter of the spinal cord at the point of exiting the skull should also be compared to the diameter of the combined round and orbital foramen to get a proper perspective of the sizes of the larger foramina of the skull. The diameter of the *Foramen magnum* (where the spinal cord leaves the skull), varies between 32 - 41 mm. Further down in the cervical region - for instance at the level of the fifth neck vertebra - the diameter of the boney canal that contains the spinal cord diminishes to only approximately 30 mm.

The seven segmental cervical vertebrae have robust dorsal, lateral and ventral projections. These projections can form severe obstructions to the pathway of any projectile. The canal for the spinal cord is only interrupted by small openings between vertebrae, but these are insignificant for practical use. Although the dorso-ventral measurement of the neck vertebrae is 140 - 180 mm high, the exact topographical position of the spinal cord within the vertebrae is difficult to visualize in the living animal. (See figure 3.11.) Due to the small diameter of the cervical spinal cord (as discussed in the previous paragraph), the use of the cervical spinal cord will therefore not be discussed any further as an alternative vital organ in the savannah buffalo.

AIMING FOR THE BRAIN:

The topographical position of the whole brain is difficult to visualize. For practical descriptive purposes, only the cerebral part of the brain and the brainstem will be considered for fatal shots in this discussion. Therefore, disregarding for a moment the ballistic properties and penetration potential of modern projectiles through skin, bone, horns or soft tissues (like nerve, muscle and connective tissue), it is suggested that the modern hunter should consider to make use of the *Foramen orbitorotundum* referred to above. Each foramen (one on each side of the skull) can allow unobstructed entrance to the brain. (See figures 3.72 - 3.74 and 3.76 - 3.80). Theoretically, this pathway also has the least chances of deflecting projectiles away from the brain as the route passes through soft tissue all the way. Furthermore, the cone shape of the boney orbit would rather tend to direct projectiles towards the *Foramen orbitorotundum* - and thus also to the brain - and not away from it. Closed eyelids could only affect the visual point on the body to take aim at. Before explaining this approach to the brain via the eye and the boney orbit (13 [21]) - referred to as a **trajectory along the orbital axis** - the following five comments warrant detailed attention. (Also see section A.)

1. The skull - but also the head in general - has a four sided pyramidal shape with the apical end rostrally at the nose, and the caudal blunt end of the skull - or the base - at the head-neck junction. The skull therefore has a general longitudinal axis. In lateral view - by convention of the datum plane for this animal - this axis lies parallel to the dorsal surface of the nasal bone, the *Dorsum nasi*. (See **Glossary of terms** and the section on the **Craniometric data**.) Viewed from dorsally, the longitudinal axis extends from the caudal (basal) to the rostral (apical) ends of the skull in the median plane. (The longitudinal axis is to be differentiated from the axis of the bones that make up the base of the cranium to form the basal axis, **axis I**). A horizontal plane drawn through the longitudinal axis would be parallel to any of the dorsal planes and parallel to the dorsal aspect of the nasal bone. (See figures 1.3, 1.4 & 3.76.)
2. The suggested trajectory for projectiles along the orbital axis and via the combined orbital and round foramen into the brain, makes an angle of approximately 45 degrees with the longitudinal axis, i.e. to the front of the animal. (See figures 1.2, 1.3, 3.7, 3.72, 3.74 & 3.80.) The orbital axis is also approximately 30 degrees (ranging between 25 to 35 degrees) higher than the horizontal plane of the skull. (See figures 1.2, 3.73 & 3.76.)
3. Aspects like the thickness of different bones in different areas of the boney orbit - as well as other soft tissue structures en route - have to be considered as they may influence the

pathway of the projectile or the projectile itself. (Only high quality projectiles that would not deform under impact can be considered when shooting savannah buffalo.) Bone immediately surrounding the *Foramen orbitorotundum* lies directly against the brainstem. The stem of the brain is positioned more towards the floor of the cranial cavity. Therefore, if the foramen is missed, the projectile should still break the bone surrounding the combined round and orbital foramen and damage the brainstem with the same fatal results. That is if the projectile has enough potential energy to shatter that surrounding bone.

4. In discussing the theoretical pathway a projectile has to follow to penetrate the brain, one also has to speculate about other possible scenarios if it does not follow the theoretical route - in this case if it does not travel all the way along the orbital axis.
5. The paranasal sinuses have to be considered too, because their size and shape affects the topographical position of the brain. Also, deflected projectiles could - in a non-lethal way - just traverse through the air-filled sinuses and may even exit the skull. Boney partitions inside the sinuses may also play a role in the pathway of projectiles when other routes but the orbital axis is considered.

The paranasal sinuses have been discussed under the different parts of the frontal sinus complex under section A. (See for instance footnote 27.) A thorough knowledge of all these and other osteological aspects will be a prerequisite to understand what follows in this section. Three possible pathways or trajectories are discussed under the following headings respectively, each with its own pros and cons.

TRAJECTORY I : AIMING FOR THE BRAIN ALONG THE ORBITAL AXIS

(See figures **1.2, 1.3, 3.2, 3.7, 3.72 - 3.74, 3.76, 3.78 & 3.80**.)

The orbital axis passes through both the centre of the orbital margin as well as the centre of the combined round and orbital foramen. The orbital axis makes an angle of approximately 45 degrees with the longitudinal axis of the skull, i.e. to the front of the animal. (See figures 1.2, 1.3, 3.7, 3.72, 3.74 & 3.80). The orbital axis also lies approximately 30 degrees (ranging between 25 to 35 degrees) higher than the horizontal plane of the skull. (See figure 1.2, 3.73 & 3.76). This axis can be imagined in the live animal as passing through the centre of the cornea and the pupil and might even travel for some distance along the optic axis, but the two axes must be differentiated from each other as they are not the same. To define the pathway of the orbital axis however, needs some further clarification. That is because there are other equally important or even more important aspects to consider, than just to aim for the centre of the eye. The reason for that can be found in the third dimensional aspect (depth) that is substantial in the case of the savannah buffalo. Therefore, the direction of travel of the projectile (or biopsy needle) on the deep side of the eye (caudo-medial to the eye) is critical and more important than a central point of entry in the region of the pupil. (See figures 3.74 & 3.80).

For all practical purposes, the boney orbit (13[21]) is situated around and behind the eye. The entrance to the boney orbit at the orbital margin has a diameter of approximately 50 - 60 mm. (See measurement 23 & 24 under section D, **Craniometric Data**.) This opening is fairly round, or somewhat oval, and in some individuals the maximum horizontal dimension may be as much as 70 mm. The medial aspect of the wall of the boney orbit, lies directly lateral to the brain. Ideally, a projectile should follow a pathway along the orbital axis in order to penetrate the brain directly through the foramen, but at least four different scenarios should be considered if the pathway of the projectile would deviate from the intended angle. Deviations can be either medially, dorsally, laterally or ventrally. In other words, the deviation can be either to the inside, above, to the outside or below, that part of the orbital axis that lies behind the orbital margin. The multitude of other possible directions between the four main directions will not be considered here. The resultant scenarios of the four main deviations are as follows **:**

1. A slight medial deviation is not of major concern as the medial wall of the boney orbit (13 [21]) also form the rostro-lateral wall of the "cranial cavity", containing the brain. However, it does imply that the projectile has to be able to penetrate this part of the wall of the cranial cavity which is approximately 15 - 20 mm thick. It consists mostly of compact solid bone. If however, the angle from the front is too much, approaching approximately 55 degrees to the longitudinal axis (instead of 45 degrees), the projectile would deviate so much more <u>medial from the intended orbital axis</u>, that it would pass rostral to - or in front of - the brain. It would then only penetrate and traverse the caudal part of the nasal cavity. That would not be fatal to the animal. (See figure 3.80).

2. If the approach is from the correct angle (45 degrees) but the projectile is directed (and travels) along such a pathway that it goes <u>dorsal to the intended orbital axis</u>, the dorsal part of the dorso-medial wall of the boney orbit (13 [21]) will be penetrated. (It would happen when the approach is from a position lower than the level of the eye, approximately in the horizontal plane of the skull.) That part of the boney wall of the orbit that will be penetrated is formed by the frontal bone of the skull. If the projectile would go straight on (i.e. not get diverted due to the impact with bone), it would pass dorsal to the brain. It would then just traverse the frontal sinus. However, due to the obtuse angle a projectile would make with the conically shaped wall of the boney orbit, such a projectile may be deflected partially or totally. If it is reflected ventrally it might still penetrate the brain.

3. If the approach is from an angle of approximately 30 degrees to the front (instead of 45 degrees), the projectile would go <u>lateral to the intended orbital axis</u> and two possible scenarios should be considered **:** Firstly, when it is directed and travels more dorsally in a <u>dorso-lateral deviation from the axis</u>. The projectile would then just penetrate the base of the horn - which contains part of the frontal sinus. That would not

be fatal to the animal at all. Secondly, if the projectile is directed and travels in a ventro-lateral deviation, it would enter the temporal fossa. (The temporal fossa is allocated the number 1 [9] under section A.) If the impact of the projectile is great enough, and if it does not get redirected, it could theoretically penetrate the lateral wall of the cranial cavity that forms the temporal fossa. Due to the obtuse angle that such a trajectory makes with the squamous part of the temporal bone, the projectile would most probably just ricochets off (instead of busting the lateral wall of the cranial cavity). The projectile would then just pass through the temporal muscle, between the base of the horn and the skull itself. The projectile would exit the head caudal to the horn-covered cornual process in the region of the dorso-lateral aspect of the head-neck junction. Obviously, this would also not fatally wound the animal.

4. The fourth scenario is where the projectile is aimed and travels from the right angle in front of the animal (at 45 degrees), but when it travels along such a pathway that it goes more ventrally than the intended orbital axis. When directed too much in a ventral direction from an angle of approximately 35 - 40 degrees to the dorsal plane of the skull (instead of the 25 - 35 degrees), the following can occur **:**

   If the projectile goes in a straight line, it could damage the base of the skull. The base of the skull consists out of the bodies of three rod-shaped bones viz. the basisphenoid, presphenoid and the occipital bones. If these bones at the base of the skull implode on impact towards the cranial cavity, it could be fatal to the animal as it would at least cause acute secondary intra-cranial haemorrhage if not sudden death. Note that the body of the basisphenoid bone at this level measures from left to right approximately 40 mm. The basisphenoid body in old bulls has a solid boney synostosis in front (to the body of the presphenoid bone) as well as behind (to the body of the occipital bone). It consists of external and internal laminae with trabecula between the layers that strengthens it. (See figure 3.2.)

   If the projectile is directed even more ventro-medially than the intended orbital axis, that is when the angle is more than approximately 45 degrees to the horizontal plane (instead of 25 - 35 degrees), the following can happen **:** The projectile can penetrate the medial pterygoid muscle, the perpendicular lamina of the palatine bone, the pterygoideus process of the wing of the basisphenoid bone and the lateral boney wall of the choana. Further on, the projectile will probably pass through soft tissue structures like the nasopharyngeal cavity, then the caudal end of the oro- and laryngopharynx, the trachea, possible also the hyoid bone and the ventral muscles of the neck, to eventually exit the animal in the region of the ventral neck-line. Those hunters who are familiar with these anatomical structures would know that damage to these structures would not be acutely fatal. (See **Glossary of terms** for short definitions of these anatomical structures.)

Therefore, if the approach is from the correct angle - that is approximately 45 degrees to the side but in front of the animal, and approximately 30 degrees dorsal to the horizontal plane of the skull, one has the best change that the projectile would travel along the intended orbital axis. The head of un-alerted, resting savannah buffalo, is essentially already kept in this position as seen from a hunter's point of view. Towards the lateral side, only monocular vision will be possible. Therefore, a trajectory along the orbital axis in resting animals has advantages specifically linked to that position of the head and skull of relaxed savannah buffalo. The orbital axis route of a projectile could then penetrate the cranial cavity and the brain via the *Foramen orbitorotundum.* That is possible even without having to break any bone as the size of the foramen is adequate to allow the passage of most projectile sizes and shapes. Anatomically, a projectile would pass through the following parts of the eye **:** The cornea, approximately 150 mm of orbital contents that includes fluids and fluid-like substances of the eye, the lens, the caudal wall of the eye (or *Sclera*) at the back, retractor bulbi and perhaps some other extrinsic eye muscles, the optic nerve, possibly some fat as well as surrounding minor blood vessels and nerves. If the eye of the animal was closed, another 10 mm or more have to be added for the eyelids. An eyelid consists of an outer layer of skin, some connective tissue, a delicate muscle, and conjunctival mucous membrane on the inside, facing the cornea. That is in total then not more than approximately 160 to 170 mm of soft tissue with a fairly homogenous structural resistance. Dissections showed that the skin anywhere else in the head and neck regions would have more resistance to projectiles than the eyelids. The crux of using this route successfully would be to determine the orbital axis accurately enough. An oblique view of the head of the animal with the head in the normal resting position would help to visualize this trajectory. The relative position of the hunter, compared with the position of the head of the buffalo is important and not the position of the body of the animal. In un-alerted animals, even a pure lateral approach to the body of the animal would also allow this trajectory when the head of the animal is moved to that side of the body from which the hunter is approaching. This is advantageous above other trajectories for alerted buffalo, because under these conditions the head and the body tend to be kept together and in a straight line, moving together as a unit.

TRAJECTORY II : AIMING FOR THE BRAIN VIA THE FOREHEAD:

(See figures **3.72 & 3.73**.)

Savannah buffalo, especially bulls, often shows a clear indentation on the forehead. The position of the indentation or concavity is situated between the eyes and the bases of the horns in front of the summit of the skull. Osteologically, the area is known as the glabella. (The glabella is allocated the number 10[12``] in section A, and lies in the centre of the frontal fossa numbered 1[14] . The frontal fossa is best illustrated in figure 3.7.) When a hunter would aim for the brain using the glabella as mark, the following has to be considered **:**

If the direction of the projectile is exactly in the median plane - even though it might be perfectly in line with the brain - it has to penetrate the following osseus structures **:** Firstly the external layer (lamina externa) of the frontal bone, then the septum of the frontal sinus and then the internal lamina of the frontal bone. Both the external and the internal laminae are 3 - 5 mm's thick, consisting of compact or solid bone. The septum itself is also solid bone, and although only about 1 mm thick, it is paired, and connects the external and internal lamina for approximately 60 - 90 mm (measured in a horizontal plane). It is strengthened and supported by multiple septa. A trajectory exactly on the median plane would therefore not be as good as one that travels in the paramedian plane or slightly obliquely, even crossing the median plane. Ideally, the direction of the projectile along trajectory II should be parallel but dorso-caudal to the basal axis (**axis I**) of the skull. (See trajectory **II (a)** in figure 3.73, and see figure 1.4 or 3.58 for the basal axis.) However, the trajectory of a projectile parallel to the longitudinal axis - and plane - on the level of the glabella, would pass dorsal to the brain. Such a projectile would pass through the frontal sinus complex. The frontal sinus complex only contains air and irregular boney septae, and such a trajectory for a projectile that does not become deflected in its passage, would not mortally wound the animal. (See Trajectory **II (b)** in figure 3.73.)

TRAJECTORY III : AIMING FOR THE BRAIN VIA A NOSTRIL

(See figures **3.2, 3.72, 3.73, 3.75, 3.77 - 3.79**.)

The third alternative for a brain shot is to aim for the brain via one of the nostrils. It is often discussed and is well known as an aiming point, as it fits in with the behaviour of alerted buffalo. Alerted buffalo tend to look at the point of disturbance of the approaching hunter, by "looking over their noses" - apparently in binocular vision. Such a frontal approach allows a hunter only one alternative and that is to aim for the brain via the nostril. Although this trajectory has its "advantages" (but predetermined by the circumstances), the trajectory that the projectile follows, actually passes through the whole length of the nasal cavity before it reaches the brain. For this reason, as well as for other reasons that will be discussed below, this trajectory may be plagued with undesirable complications. To start with, at least two scenarios should be considered as the trajectory of the projectile can pass either through the dorsal half or through the ventral half of the nasal cavity. In both instances however, the projectile might also exit the nasal cavity through a large opening (the sphenopalatine foramen) and by that, totally bypass the cranial cavity. (Vide infra under trajectory III c which is discussed under "Further comments on the approach via the nostril".)

The undivided diameter of the boney entrance to the nasal cavity (including both the left and the right osseus borders behind the fleshy nostrils), is approximately 75 - 80 mm. That is when measured from the extreme left to the extreme right. The combined rostral osseus nasal opening is approximately 65 - 70 mm high, as measured from dorsal to ventral with the skull in the datum plane. Theoretically, these measurements give a large entrance to the skull if one disregards the nasal conchae and the nasal septum contained within the nasal cavity. The slight conical shape of the boney walls of the nasal cavity however tapers down caudally. That is caused mostly by the lateral walls of the nasal cavity that become somewhat narrower at the caudal end. The caudal end of the nasal cavity, at the caudal end of the fundus nasi (allocated the number 13 [13] in section A), optimally has an area of 60 mm wide by 80 mm high (measured in a transverse plane). What is favourable of this area is that lies appropriately in front of the brain. (See figure

3.75.) The horizontal and vertical dimensions of the brain that lies behind this area are slightly greater, measuring approximately 100 mm wide and 85 mm high. If the trajectory of the projectile is parallel to the ground, it would require the dorsum of the nose also to be parallel to the ground, or alternatively stated, horizontally placed in the datum plane. Only in this ideal plane would the rostral nasal opening and the caudal boney limit of the nasal cavity be optimally in line with each other and the brain. What is important to note about this approach apart from the above, is that the distance from the rostral opening to the caudal end of the nasal cavity is approximately 300 to 330 mm long. Furthermore, when buffalo bulls "look over their noses", it does not necessarily mean that the dorsum is properly placed (i.e. horizontally). This is aggravated by the prerequisite that the projectile has to penetrate the facial part of the skull (at the nostril) between two parallel and horizontal lines viz. that of the dorsum of the nose and the boney palate (or for that matter the occlusal surface of the upper cheek teeth). Neither the palate nor the occlusal surface of the teeth can be seen in the live animal, and the level of the dorsum of the nose is not so obvious to see from the front in all animals. This is because a "Roman nosed" bull cannot be judged easily from the front as having its head in the correct plane, by using the nasal bone alone. The following might be an aid **:** The levelled skull should be in the correct plane if viewed from the front when the centres of the nostrils lie on a plane that would pass just ventral to the (ventral) margin of the boney orbits. Also note that the pathway of the projectile in this approach has to be not only ventral to the dorsum of the nose but also ventral to the internal surface of the nasal bone. That is because the nasal bone is thick and long, often curved, and always consists of compact bone in older animals. Furthermore, this trajectory must not only be parallel to the occlusal surface of the upper cheek teeth but also dorsal (apart from being parallel) to the boney palate. What complicates this trajectory via the nostril even more, is that preferably, the projectile should not travel in the ventral half of the nasal cavity although it might appear to the uninformed to be more spacious. One reason for this is that because the boney palate should be avoided, one would generally prefer a trajectory that is further away from the palate as it can be highly resistant to projectiles. Especially rostrally, at the rim of the entrance to the nasal cavity, the palate consists out of solid bone. The rim of the osseus rostral nasal opening would severely resist the route and energy of projectiles. Finally, one must also not forget that the boney nasal septum divides the nasal cavity into equal halves and the nasal septum is therefore also approximate 300 to 330 mm long. In cross section, the shape of the nasal cavity (to the one side of the nasal septum), is effectively semilunar with the flat side in the paramedian plane and against the nasal septum. Measured from dorsal to ventral, or medial to lateral, the radius of this semilunar tube-like route to the one side of the nasal septum, is maximally 30 mm. With the length of the nasal cavity - that has to be traversed by the projectile before it will reach the brain - being approximately 300 - 330 mm long, a small lateral movement of the nose, will miss-align the whole pathway. The following might be important considerations in this regard **:**

(1) Placing the shot to the one side of the median plane, in order to avoid the nasal septum. The septum is attached dorsally to the nasal bones and ventrally to the boney palate and the vomer. These attachments strengthen the region. The rostral third of the septum might be cartilaginous in younger animals, but most of it in older bulls is osseous. The length of the osseous part of the nasal septum in young animals is at least approximately 200 mm long. The width of the nasal septum varies from one or two millimetres to up to 10 mm at the caudal end. The septum consist of spongy bone - filled with fat and blood vessels - and covered on either side by a thin layer of solid bone. Fortunately, the type of bone the septum consists of is not as compact and as solid at the other bones of the skull. (That of the vomer and of the nasal conchae are even less compact.)

(2) The cone shape of the nasal cavity.
Because the lateral walls of the nasal cavity narrows down caudally, the distance the projectile has to travel through the nasal cavity is significantly important.

(3) The thickness of the lateral nasal wall.
The thickness of the wall varies, but it can be 10 - 15 mm thick at places. The rim

of the rostral nasal opening is even thicker, especially ventrally, where it also forms the rostral end of the palate. The lateral nasal wall consists of solid bone for at least a third of the distance.

(4) Other possible obstructions in the nasal cavity.

(a) The ventral half of the caudal end of the nasal cavity contains the rostrum of the presphenoid bone. It projects rostrally into the nasal cavity for approximately 50 - 60 mm. The direction of this process lies along the axis of the base of the skull in the median plane and makes an obtuse angle of approximately 145 degrees with the dorsal plane. The rostrum of the presphenoid bone consists of spongy bone, covered by external layers of solid bone (dorsally and ventrally) and may contain a sinus of its own. It is supported by parts of the vomer and the ethmoid bone, to which it is intimately fused.

(b) Dorsal to the rostrum, the fundus nasi (13 [13]) at the caudal end of the nasal cavity contains thin-walled ethmoidal conchae and their septa.

(c) The nasal cavity is separated from the brain by the cribiform plate which is only approximately 2 mm thick. The lamina cribrosa consists out of solid bone.

(d) The nasal conchae and the nasal mucosa contained in the nasal cavity.

One must realize that the nasal cavity is not a large open cavity, as in the living animal it is almost completely filled by all the conchae. Even though the conchae are delicate structures, they are covered by mucosa that lines the whole inner surface of the nasal cavity, including the outer surfaces of all the conchae as well as any air filled spaces contained within the conchae. The air passages that remain between the conchae and the dorsal nasal wall (or the one above the osseus palate), are not voluminous. The conchae and the soft tissue structures, including the spongy nasal septum, and any blood and fat they may contain, may act either as soft tissue or even “hydraulic decelerators”. Aggregates of the abovementioned structures could absorb much of the energy of oncoming projectiles, as deceleration of projectiles can be expected to occur due to the length and the tunnel-shaped nature of the nasal cavity.

Further comments on the approach via the nostril (and the nasal cavity) to the brain **:**

As said in the above, trajectories through the nasal cavity via the nostrils, are plagued with undesirable complications and has to be elaborated upon. Due to the tapering effect of the nasal cavity, and the solid nature of the rim, the lateral walls as well as of the roof of the cavity (formed by the incisive, maxillary and nasal bones respectively), this route may either stop a projectile or - once the projectile is inside the nasal cavity - may certainly also redirect or reflect it. For instance, a projectile can be redirected either towards the fundus nasi (in the dorsal half) or totally away from it. If the projectile enters the fundus nasi, dorsal to the rostral tip of the rostrum of the presphenoid bone, it should penetrate the lamina cribrosa. (See trajectory **III (a)** in figure 3.75.) That is the ideal situation. If however the pathway of the projectile goes ventro-medially, and into the ventral half of the nasal cavity, the rostrum of the presphenoid bone might adversely affect the direction and momentum of the projectile. If the projectile exits the caudal end of the nasal cavity even more ventrally - trajectory **III (b)** - then the bodies of the presphenoid, basisphenoid and occipital bones would be directly in the pathway of the projectile. (See figure 3.73.) These bones form the base of the skull (the basal axis or **axis I**) which is very strong. It consists of spongy bone that is covered by both a lamina externa and a lamina interna. These laminae are of solid bone. (See figure 3.2 for the situation in a young animal and figure 3.73 for an older bull.) Also said above, is that the bones at the base of the skull make an obtuse angle of approximately 145 degrees with the horizontal. That angle, relative to the trajectory of the projectile, has to be kept in mind. Apart from that also, is the fact that these bones that form the base of the skull, are rod-shaped and 30 - 40 mm in diameter. However, when measured in the horizontal plane - along the expected horizontal pathway of a projectile - the thickness of these bones will measure as much as 50 - 60 mm. And that is a lot of bone that effectively separates the projectile from the brain.

Another possibility that counts against an approach via a nostril should be mentioned **:** If the projectile travels obliquely through the nasal cavity - by crossing the median plane (even if it is on the correct dorsal plane) - it might exit the nasal cavity through the sphenopalatine foramen (13 [31] & 19 [15]). That would occur after only breaking the delicate shells of the nasal conchae on either side of the septum, and of course the septum itself. (See trajectory **III (c)** in figures 3.73, 3.77 & 3.79.) A projectile travelling along this trajectory will continue - after exiting the nasal cavity - to the contralateral squamous part of the temporal bone (on the other side) until it ends near or at the temporomandibular joint of that side. If the projectile ricochets away from either the ventral surface of the skull base or the squamous part of the temporal bone (due to the obtuse angle in which the projectile would meet these surfaces), or the coronoid process of the mandible, it would penetrate into the ventral neck region. It might then proceed further down the neck muscles, trachea or oesophagus, along the ventral aspect of the cervical vertebral. Such a route would definitely not cause sudden death. By a small change, the cervical vertebrae may be shattered if the projectile still has enough dynamic energy at that stage. That will be hardly likely if the angle at which the trajectory pathway will make with the cervical vertebrae is considered if the animal was shot while "looking over its nose". (See figure 3.11.)

In summary therefore, the theoretical pathways of projectiles along any of the three options of trajectories, all have their pros and cons. These have to be weighed up by the hunter under the various topographical positions in which the head can be kept (relative to the hunter's position), and his or her rifle. Hours of training in three-dimensional concept formation of moving targets of savannah buffalo would be necessary before correct split-second decisions can be made as to when the trigger should be pulled.

APPLIED ANATOMICAL ASPECTS OF THE TEETH OF THE SAVANNAH BUFFALO:

(See figures **3.65 - 3.70**. Also see figure 3.11.)

GENERAL INTRODUCTION:

Although a detailed study on the teeth of the savannah buffalo does not form part of this study on the osteology of the skull, some aspects of the dentition have to be discussed here. It helps to interpret relevant parts of the **Osteology** and **Craniometric data** sections. For instance, tooth formation and subsequent eruption has an effect on the size of the maxillary sinus and other anatomical structures like the infraorbital canal. Furthermore, the development of each premolar set is associated with the formation of a set of temporary gubernacular canals. These canals - as discussed in section A - cannot be discussed or interpreted without a prior study on the dentition. (See 16 [37] and the paragraph that precedes 21 [31] .) Neither can interpretations for the section on the **Craniometric data** be made, if the complete dentition is not understood.

INTRODUCTION TO THE FORMATION AND ERUPTION OF SAVANNAH BUFFALO TEETH:

As in most other mammalian species, all the temporary teeth (excluding the molars) are replaced by permanent teeth. And, as with the temporary teeth, the permanent teeth develop in the tooth bearing parts of the maxilla and the mandible. In savannah buffalo, the complete crowns as well as the complete roots of lower permanent incisors have developed before they erupt. However, in the case of the permanent premolars and the molars, only the distal parts of the crowns are fully developed at the time of eruption. Complete root development in these teeth only occur shortly after eruption. The proximal parts of the crowns of especially molar teeth are completed during that time that elapses between eruption and the time the tooth comes into “wear”. The crowns of premolars tend to be more fully developed by the time they erupt. Detail on maturation of enamel falls beyond the scope of this study. The roots of the cheek teeth as well as the incisors continue to develop (elongate and increase in substantial thickness) over the extended period of wear of the whole dentition, and that is usually as long as the animal lives. The roots are therefore at their longest when most of the crowns have been worn away. Prior to eruption, the enamel organ (vide infra and see **Glossary of terms**) of a developing tooth, erodes away surrounding bone (usually from an interradicular position in a particular dental alveolus). This erosion process also includes destruction of the proximal parts of initially the roots of a temporary precursor that is still in use at that time, but later also to some extend even the proximal crowns. That process continues until the permanent tooth is just about fully developed. This intricate process appears to also allow for the direct re-use of minerals of the deciduous tooth and eroded bone, during the formation of that specific permanent tooth. Adjacent teeth and their dental alveoli are spared. Initially, a tooth erupts at an enhanced rate and does so till it comes into full occlusion. After that, the rate of eruption equals the rate that a tooth wears down at the occlusal surface. But that rate is usually determined by the wear rate of a whole tooth row table and not just by a single tooth, except in the early phases of the first molar set. At any particular time in the life of an animal, a cheek tooth row table is made up of at least three to four teeth. Once again in the case of the first molars, the others may be only the dental caps of the deciduous premolars which are not properly anchored anymore and not necessarily totally functional.

In general, it is known that the enamel organs for the set of permanent teeth (abbreviated as "**EO**" in the table below) take origin from the oral mucosa of the mouth. For the savannah buffalo, this is however divided into a prenatal phase for the incisors and molars, and into a postnatal phase for the premolars. That therefore differs from what has been known about the development of the enamel organs and the teeth they form. Histological sections of the gingiva and underlying basement membrane of savannah buffalo will reveal more of the microscopic processes, but such a study falls beyond the scope of this study. This different and totally separate process for the permanent premolars can be clearly seen macroscopically in serial dissections of complete savannah buffalo heads of various selected ages. (See Chapter two, **Materials and Methods**.) The postnatal process by which the permanent premolar teeth form, differs in various other ways also from the prenatal developmental process for the permanent incisors and the molars. In the latter case - for incisors and molars - the already designated enamel organs remain dormant (in the dental alveolus of the deciduous tooth) until such time as the deciduous precursor has to be replaced (in the case of incisors), or until the specific tooth has to form (in the case of molars). Obviously, deciduous teeth are also formed by enamel organs (abbreviated as "**eo**" in the table below) but these processes will not be discussed here. When ready to give origin to a permanent incisor or a molar, the enamel organ develops further (inside the tooth bearing parts of the mandible or maxilla) by being there in that position in the first instance (due to a pre-natal process). However, as already stated above, in the case of the permanent premolars of savannah buffalo, designation of enamel organs takes origin from certain localized areas of the oral mucosa, and that occurs postnatally. What triggers the localized areas of gingiva to start off the process is not yet clear, but the areas are situated directly lingual to the deciduous tooth that has to be replaced. The process of gingival epithelium growth (which should be a process of hypertrophy), occurs by growth that takes place on the deep side of the gingiva. Histological evidence as to the position and role of the basement membrane during this process, and in the process of piercing right through compact bone on the lingual sides of the deciduous tooth - to form a gubernacular canal - falls beyond the scope of this study. The enamel organs for the permanent premolars remain attached to the gingiva in a pedunculate manner. The distal end of the outgrowth contains the functional enamel organ which eventually - or finally - will obtain its interradicular position. The stalk of the enamel organ is usually small in diameter. (See figure 3.49 for an apparent non-pathological exception.) It remains in the osseus gubernacular canal apparently until at least the enamel organ has matured to a size of approximately 10 or 20 mm in diameter. The gubernacular canals (16 [37]) that form in the premolar bearing parts of the maxilla and mandible are therefore temporary as discussed in section A. (Grass awns may penetrate and pathologically destroy enamel organs by secondary bacterial infection. In those cases the gubernacular canals may be pathologically larger in diameter and be present for a longer period of time. Further details of pathological conditions during odontogenesis however fall beyond the scope of this study.) The gubernacular canals are clearly visible macroscopically, and the direction of formation of the canals (from the gingiva to the interradicular position and not vice versa) serves as evidence of this different mechanism by which the enamel organs of savannah buffalo premolars obtain their final positions in the dental arches. As is standard, the preset number and position of enamel organs of deciduous and permanent teeth - whether by the prenatal or the postnatal mechanisms or by both - determine the number and position of teeth in the adult dentition. In the early development phases of all enamel organs, each enamel organ develops at some point or the other into a cuplike structure that surrounds tissue that will be enclosed into the dental cavity of the future tooth to be formed. That tissue then forms the dental pulp after the enamel layer has formed the crown of the tooth by way of a casting process. The enamel casting process is polarized and is completed distally before it is finished proximally. That is especially clear to see in the molars of savannah buffalo. The three-dimensional shape and the detail of the enamel folds into evaginations and invaginations, are predetermined by genetic factors - factors that ultimately precipitate in the enamel forming part of the enamel organ. The detail of these folds also falls beyond the scope of this study, but is distinctly different from the enamel folds of the cheek teeth of the domestic bovine. Details of these folds may be used - at least in part - as another "fingerprinting" technique in the identification of species. Casting of the enamel layer (from ameloblast cell activity) must not be confused with a growth process, as it ceases at or shortly after eruption. Another part of the enamel organ deposits dentine. That deposition process (from odontoblast cell activity) occurs inside the crown for as long as a tooth remains viable, and in the case of savannah buffalo usually as long as the animal lives. Peripherally, and prior to eruption, but as part of the whole process and as part of the function of the enamel organ, the peripheral part of the enamel organ erodes away bone as well as the roots of predecessor teeth when present. That has been discussed above. Furthermore, an ever enlarging "cavity" that contains the enamel organ itself, and eventually also the near-complete tooth, is thereby formed. The trabecular bone that surrounds the "cavity" (which contains the enamel organ), becomes the dental alveolus of that particular tooth. After eruption, the dental alveolus will continue to remodel itself around the embedded part of the (ever erupting) tooth.

The eruption process of savannah buffalo teeth can for descriptive purposes of this section be divided into the following three phases **:**

Firstly, when the recently formed tooth has to **migrate** from its position in the bone where it was formed, to its semi-final position in the dental arch. It is best seen in incisors that develop up to 35 mm's away from their final positions. Each incisor also rotates around its own longitudinal axis during the migrating process before it attains its final position. As said above, the crowns of incisors are completely formed by the time they erupt. That differs from molar teeth, as the final formation process of molars occurs at and shortly after erupting through the gingiva. A migration phase for molars and premolars can therefore not be seen as clearly as for incisors.

The second phase of eruption starts after the migration phase at the point when the tooth pierces the gingiva. At that point the tooth is said to "erupt". This phase is marked by an **enhanced eruption rate** whereby the crown and the dental alveolus rapidly move out of the tooth bearing parts of the particular dental arc. This causes the distal crown of the tooth to come into contact with the occlusal surface of teeth of the opposing arch, or in the case of incisors, with the dental pad.

The third phase is a **phase of retarded eruption**, the rate of which is directly proportional to the rate of wear at the occlusal surface of a tooth. This retarded eruption lasts until the tooth is worn away.

Note **:** (1) "Erupting" and "eruption", either refers to the three phased processes of eruption (vide supra), or to a point in time (age of the animal) which is when the tooth pierces the oral gingiva to "erupt". The phrase "coming into wear" is when a newly erupted tooth starts to make contact with the opposing teeth (or in the case of the incisors, with the dental pad) at the occlusal surface. "Wearing" is the continuous abrasion that occurs at the distal end (the occlusal surface) and "a worn tooth" means that the largest part of the crown of a tooth has worn away.

(2) Remnants of the crowns of deciduous teeth are simply shed once properly de-rooted by the action of the enamel organ. Eruption of the successor tooth helps in the shedding process.

(3) The semisolid anchoring of all incisors, premolars and molars, play a significant role in the mechanical and dynamic function and wear not only of the occlusal surfaces of teeth of the savannah buffalo, but also wear at the contact surfaces.

(4) Contact surface wear between the distal ends of all adjacent teeth of savannah

buffalo (including incisors, premolars and molars) is a major cause of mesial drift of individual teeth. Mesial drift of tooth rows must be distinguished from this, but dental drift in general forms but another mechanism by which the movement of teeth around various axes (whether as part of eruption, rotation, semisolid anchoring or retarded eruption) can be described.

Thus, when one considers a functional set of teeth in the mouth of a living savannah buffalo (in other words looking at those visible parts of teeth that projects beyond the gingiva into the oral cavity), it must be realized that complex developmental processes have preceded the existence of each tooth, and that some or the other form of constant movement of a tooth - or of all the teeth - is a continuous process. That has partly been described above but needs further elaboration. The developmental process by which tooth pairs are formed (left and right), should be considered as delayed embryological development that occurs in the already overcrowded tooth bearing parts of the head. And, except for the incisors, it occurs in both arches. The process also occurs in a near exact bilaterally symmetric sequence, starting already some time before birth in the case of the deciduous teeth and also for the first molars. Development, as well as eruption of the cheek teeth in the inferior dental arc, tends to be slightly advanced ahead of similar-numbered teeth of the superior arc. Each tooth in the deciduous set (consisting of 20 teeth) is replaced, and additional to that, three extra molars are also formed in each cheek tooth row. Eventually the process ends approximately at the age of 5½ years of age when all in all, 32 new teeth have formed for the permanent set. (Detail of the re-connection of the nerve supply to the permanent incisors and premolars falls beyond the scope of this study.) At the time the crown of a tooth has formed - after eruption but before coming into wear - the unworn crown of that specific tooth is at its longest. Thus, once the enamel of a tooth has been moulded into its shape and size in the process of formation, that quota of tooth length has to serve for life. No further growth of the enamel part can take place, simply because that part of the enamel organ (coming from the ameloblast layer) is not functional anymore. The proximal part of the enamel organs of molars however - which are much longer than other teeth and are clearly polarized - continues to deposit enamel for some time. But that also ceases more or less at the time the molar tooth comes into occlusion. From then on, the crown can only become shorter as it wears away at the distal occlusal surface, even though the roots will continue to elongate. Elongation of the roots (or root "growth"), counteracts the shrinking anchoring capacity of the embedded crowns. The intra-oral height of the clinical crowns of totally worn individual cheek teeth may be maintained for a while by additional movement of individual dental alveoli, or by the eruption of all the dental alveoli of a whole cheek tooth row. Eruption of whole cheek tooth rows in old animals, can be appreciated best when the repositioned cheek teeth alveolar margins of the maxilla and mandible of old animals are compared with that of immature ones. Apart from individual movement of individual teeth (or of cheek tooth rows and their dental alveoli as described above), dental drifting not only of individual teeth occurs but also of complete tooth rows. As can be expected, such drifting is also in a mesial direction. Drifting of teeth and their alveoli occurs constantly in the dentition of savannah buffalo of all ages. Relative positions of dental alveoli of individual cheek teeth or of cheek tooth rows -relative to other bones of the skull - have been discussed and considered under the **Osteology** and **Craniometric data** sections.

DENTAL FORMULAE OF THE SAVANNAH BUFFALO:

The deciduous set of teeth in the savannah buffalo consists out of four lower incisors, no upper incisors and three premolars on each side of the upper and lower dental arches. In a mathematical or algebraic form, the deciduous set can be represented by the following formula **:**

$$Di\,\tfrac{0}{4}\quad Dc\,\tfrac{0}{0}\quad Dp\,\tfrac{3}{3}\quad x\,2 = 20$$

The permanent set of teeth in the savannah buffalo consists out of four lower incisors, no upper incisors, three premolars as well as three molars on either side of the upper and lower dental arches. Expressed as a formula, the permanent set of teeth can be represented as follows **:**

$$I\,\tfrac{0}{4}\quad C\,\tfrac{0}{0}\quad P\,\tfrac{3}{3}\quad M\,\tfrac{3}{3}\quad x\,2 = 32$$

The designated abbreviations are as per international anatomical terminology.

THE ERUPTION SEQUENCE OF TEETH AND HOW TO USE THAT INFORMATION TO AGE SAVANNAH BUFFALO**:**

(See figures **3.65 - 3.70**.)

The formation and eruption of premolars, molars and incisors are spread over more than six years, starting from prenatally, to approximately 5½ years of age (postnatally). During this period, both the mandible and the skull increase in length and width to accommodate the development of more and larger teeth. Except for the intermandibular synchondrosis, the mandible has no other growth plate, yet it keeps up with the length and width increases of the skull. This occurs in such a balanced way that the occlusal surfaces of deciduous and permanent teeth in the upper and the lower arches remain in proper apposition, until all the teeth have erupted. That occurs even in older animals where as a result of contact surface wear between teeth, tooth rows become shorter and proper apposition is therefore also maintained. The development of permanent teeth usually occurs in sets of four (left and right and in upper and lower arches, as one set or a pair of four teeth). A subsequent set overlaps with previous and following sets of four in such a way that eruption of pairs of teeth are staggered in a specific sequence **:**

Between the first week of life and approximately the 4 th month of age, all the temporary teeth have erupted and are in wear. Thereafter, the sequence of formation and eruption of permanent teeth, and how that fits into roughly six-monthly intervals (printed in bold below), can be summarized as follows **:**

The first upper and lower molars (M $\frac{1}{\overline{1}}$) are the first permanent teeth to form, erupt and come into wear. They start to erupt approximately at **age 9 months to one year**. At that time, the primordia of the second upper and lower molars have already formed but the formation process has not been completed yet. Eruption of the second upper and lower molars (M $\frac{2}{\overline{2}}$) follows approximately at **1½ years of age** and at that time, the primordia of the central lower incisors (I $_{\overline{1}}$) are formed. At this stage, the alveoli of the second lower incisors (I $_{\overline{2}}$) and the upper and lower second and third premolars (P $\frac{2}{\overline{2}}$ and P $\frac{3}{\overline{3}}$) are in the process of getting eroded away by their respective enamel organs. Erosion, formation and eruption of the upper and the lower fourth premolars ($P\frac{4}{4}$) lags a little behind that of the third. At approximately **2 years of age**, the upper and lower third molars ($M\frac{3}{3}$) erupt, and they are followed by the eruption of the central lower incisors ($I_{\bar{1}}$). The latter pair come into wear approximately at **2½ years of age**. The third upper and lower molars ($M\frac{3}{3}$) come into wear approximately at the **age of 3**, by which time the second lower incisors ($I_{\bar{2}}$) start to erupt, coming into wear at approximately **3½ years of age**. At this stage the primordia of the third lower incisors ($I_{\bar{3}}$) have formed completely but still has to erupt. The primordia of the upper and lower second, third and fourth premolars ($P\frac{2}{2}$, $P\frac{3}{3}$ and $P\frac{4}{4}$) have all formed completely, and are ready to erupt. Of these premolars, the fourth premolars ($P\frac{4}{4}$) are the last to erupt but they are all in wear at approximately **4 years of age**. At this stage the dental alveolus of the fourth lower incisors ($I_{\bar{4}}$) are in the process of getting eroded away by the enamel organs. After enamel deposition, the third lower incisors ($I_{\bar{3}}$) erupt and are in wear approximately at the **age of 4½ years**. The fourth lower incisors ($I_{\bar{4}}$) are the last teeth to form and to erupt, and come into wear approximately at the **age of 5½ years**.

DENTAL CHARTS**:**

Dental formulae, based on anatomical convention, have limitations which are overcome by **Dental charts**. Various systems exist and clinicians lately used a **three-digit "Triadan" system**. That system is an adaptation from the human two-digit system. Although some systems have advantages over others, none of these satisfy a reference system that also includes the developing enamel organs of teeth that do, as well as those that do not, have successors. This is necessary because during their development, both the enamel organs and their precursors (as well as enamel organs of teeth that do not have successors) are present in the dental arches. That can be clearly seen on radiographs and sculptured skull collections. Because the enamel organs - especially of large wild animals such as the savannah buffalo - are such huge macroscopic structures, they cannot be ignored by Anatomists, Radiologists, Dentists or Zoologists. Therefore enamel organs (whether they do or do not have precursor teeth), not only should, but must, be included in a digital system. Presently, the three-digit

"Triadan" system designates the permanent set from mesial to distal in the four quadrants of the two arches as follows **:**

Right upper quadrant	**:**	101 to 111
Left upper quadrant	**:**	201 to 211
Left lower quadrant	**:**	301 to 311
Right lower quadrant	**:**	401 to 411

The enamel organs of the deciduous teeth, plus the deciduous teeth themselves, and the enamel organs of the permanent teeth as well as the permanent teeth themselves, can all be denoted in an anatomically correct and logical system by adapting the "Triadan" system to a **four-digit system** as is developed for this study on the savannah buffalo. This four-digit system designates the complete dentition of the four quadrants (of both arches), digitizing each tooth including all the enamel organs of deciduous as well as of permanent teeth as follows **:**

Right upper quadrant	**:**	101 to 411
Left upper quadrant	**:**	501 to 811
Left lower quadrant	**:**	901 to 1211
Right lower quadrant	**:**	1301 to 1611

The enamel organs of deciduous and permanent teeth are abbreviated as "**eo**" and "**EO**" respectively in the following semi-schematic table (TABLE 3.4). Eruption direction and relative positions of teeth in the table are shown by vertical and horizontal arrows, respectively therefore either \ , [, Y or Z. (Although both the latter two arrows indicate mesially directed eruption - which do not occur in the savannah buffalo - this standardized and all-applicable dental chart, can be used to indicate the eruption direction of the molars of all animals, including the African elephant.)

TABLE 3.4
DENTAL CHART FOR THE SAVANNAH BUFFALO.

jZ DISTAL Y MESIAL Z DISTALYk

111 No eo	110 No eo	109 No eo	108 Dp4 eo\	107 Dp3 eo\	106 Dp2 eo\	105 No eo	104 No eo	103 No eo	102 No eo	101 No eo	501 No eo	502 No eo	503 No eo	504 No eo	505 No eo	506 Dp2 eo\	507 Dp3 eo\	508 Dp4 eo\	509 No eo	510 No eo	511 No eo
211 No tooth	210 No tooth	209 No tooth	208 Dp 4	207 Dp 3	206 Dp 2	205 No tooth	204 No tooth	203 No tooth	202 No tooth	201 No tooth	601 No Tooth	602 No Tooth	603 No Tooth	604 No Tooth	605 No Tooth	606 Dp 2	607 Dp 3	608 Dp 4	609 No tooth	610 No tooth	611 No tooth
311 M3 EO\	310 M2 EO\	309 M1 EO\	308 P4 EO\	307 P3 EO\	306 P2 EO\	305 No eo	304 No eo	303 No eo	302 No eo	301 No eo	701 No eo	702 No eo	703 No eo	704 No eo	705 No eo	706 P2 EO\	707 P3 EO\	708 P4 EO\	709 M1 EO\	710 M2 EO\	711 M3 EO\
411 M3	410 M2	409 M1	408 P4	407 P3	406 P2	405 No tooth	404 No tooth	403 No tooth	402 No tooth	401 No tooth	801 No Tooth	802 No Tooth	803 No Tooth	804 No Tooth	805 No Tooth	806 P2	807 P3	808 P4	809 M1	810 M2	811 M3
R	I	G	H	T		U	P	P	E	R	L	E	F	T		U	P	P	E	R	
R	I	G	H	T		L	O	W	E	R	L	E	F	T		L	O	W	E	R	
1611 M3	1610 M2	1609 M1	1608 P4	1607 P3	1606 P2	1605 No Tooth	1604 I 4	1603 I 3	1602 I 2	1601 I 1	1201 I 1	1202 I 2	1203 I 3	1204 I 4	1205 No Tooth	1206 P 2	1207 P 3	1208 P 4	1209 M 1	1210 M 2	1211 M 3
1511 M3 EO[	1510 M2 EO[	1509 M1 EO[	1508 P4 EO[	1507 P3 EO[	1506 P2 EO[	1505 No eo	1504 I 4 EO[	1503 I 3 EO[	1502 I 2 EO[	1501 I 1 EO[	1101 I 1 EO[	1102 I 2 EO[	1103 I 3 EO[	1104 I 4 EO[	1105 No eo	1106 P2 EO[	1107 P3 EO[	1108 P4 EO[	1109 M1 EO[	1110 M2 EO[	1111 M3 EO[
1411 No tooth	1410 No tooth	1409 No tooth	1408 Dp 4	1407 Dp 3	1406 Dp 2	1405 No Tooth	1404 Di 4	1403 Di 3	1402 Di 2	1401 Di 1	1001 Di 1	1002 Di 2	1003 Di 3	1004 Di 4	1005 No Tooth	1006 Dp 2	1007 Dp 3	1008 Dp 4	1009 No tooth	1010 No tooth	1011 No tooth
1311 No eo	1310 No eo	1309 No eo	1308 Dp4 eo[	1307 Dp3 eo[	1306 Dp2 eo[	1305 No eo	1304 Di 4 eo[	1303 Di 3 eo[	1302 Di 2 eo[	1301 Di 1 eo[	901 Di 1 eo[	902 Di 2 eo[	903 Di 3 eo[	904 Di 4 eo[	905 No eo	906 Dp2 eo[	907 Dp3 eo[	908 Dp4 eo[	909 No eo	910 No eo	911 No eo

lZDISTAL Y MESIAL Z DISTALYm

Note : (a) A dental chart is a schematic representation of a rostral view of the oral cavity. This schematic chart for the savannah buffalo therefore shows all the teeth can be present at any stage in the mouth (pre- or postnatally). Each tooth or its enamel organ is designated digitally as well as according to standard anatomical terminology.

(b) The position of teeth in the quadrants makes superscript and subscript numbers obsolete in dental charts.

IMPLICATIONS OF THE ERUPTION SEQUENCE ON THE EXPECTED LONGEVITY OF INDIVIDUAL SAVANNAH BUFFALO:

In general it can be said that eruption of a permanent tooth is preceded by a critical period of time during which the enamel casting process takes place. Premature eruption would therefore cause an incompletely formed tooth to come into wear. If such premature eruption caused an ill-formed enamel crown, such a crown would severely jeopardise not only the resistence of that particular tooth to wear but probably also the resistence to wear of a whole cheek or incisor tooth row. Furthermore, a delay in the eruption of a subsequent pair or set of teeth would not just aggravate the situation but could also have a cascade effect on the eruption timing of other teeth or sets still to follow. Such a cascade effect (more applicable for molars that for incisors) can be counterbalanced by compensatory eruption (timing and / or rate) of teeth to follow, if total obstruction to the eruption of a tooth or a tooth pair (usually referred to as “impaction”) has not occurred. Resistance to wear of cheek teeth is based to a much great extent on the thickness of the various enamel folds on the occlusal surface, as these folds are absent on the occlusal surfaces of incisors.

Of all the sets of teeth of the savannah buffalo, the formation, eruption and coming into wear - at the most critically correct time - is the timing of eruption of the first upper and lower molars ($M\frac{1}{1}$). The development of this particular tooth pair starts off shortly before (or possibly in some animals after) birth, and terminates when the animal is approximately one year old. During the time that the temporary premolars are shed, and before the second upper and lower molars ($M\frac{2}{2}$) come into wear (approximately one year later, at the age of two years), the first upper and lower molars ($M\frac{1}{1}$) undergo a heavy wear rate as they have to contribute in a major way to the grinding surfaces of the cheek teeth rows in the arches. That is because the deciduous premolars are all in the process of getting shed. Any delays in the eruption and coming into wear of the second upper and lower molars ($M\frac{2}{2}$), as well as any delays in the eruption and coming into wear of the premolar rows (to contribute to the cheek tooth rows), causes further attrition of the already compromised first molars. In old animals it can be seen that the crowns of the first molars are usually the first teeth to be totally worn. This is usually the result of the scenario that is described above, but it can also be due to other abrasion factors of normal rumination or of pathological conditions, or of both. Any deformity, or lack of crown length, or inferior quality of the enamel of the upper and lower first molars (M^{1}_{1}), but especially the timing of eruption in the whole sequence of events that have to follow, therefore appears to critically affect the longevity of savannah buffalo. It is therefore strongly suggested that radiographs be taken whenever any animal is traded at whatever age they are, to see whether the length of the upper and lower molars (M^{1}_{1}) - or any other tooth for that matter - is of a critical length. Although a limited number of specimens (in which the birth dates were not even known either) were studied, it could be calculated roughly from the above information and from the **Craniometric data**, that the attrition rate of molar teeth (once all the molars are in wear and the cheek tooth rows are complete), is in the order of approximately 2 to 2,5 mm per year. Based on that, one can roughly estimate the remaining life expectancy of any animal at any age, based on the remaining length of specifically the crown of the lower first molar (M_{1}). The length of premolars does not appear to ever become critical in the savannah buffalo, even though they may appear to the uninformed as small teeth compared with the molars. The current selling prices of savannah buffalo as a game farming animal, surely calls not only for accurate age determinations, but also for longevity predictions.

CHAPTER FOUR

DISCUSSION

(See figures **4.1 - 4.4**. Also see other applicable illustrations referred to under specific Discussion points.)

In the final analysis of the osteology of the skull of the savannah buffalo, detail of the osteology has to be evaluated in view of ontogenetic developmental aspects, as well as the post-natal sexual hormonal effects on both the skull and on the teeth. Apart from that, the purpose of this study - as was originally planned - affects the context and viewpoint of this Discussion. As stated in the General Introduction, the purpose was to obtain an accurate description of the osteology in order to ultimately describe the gross anatomy of the muscles, the blood vessels and the nerves as well as the splanchnological detail of the head of the savannah buffalo. Concluded during this study, is that a discussion of the skull of the savannah buffalo should not exclude an evaluation from either a developmental point of view (both ontogenetically as well as phylogenetically) or from a relative comparative point of view (comparing it with similar Bovidae's). But because the original purpose of this study excluded ontogenetic and phylogenetic studies, the expected embryological development in this case, can only be considered in retrospect, based on what is known for the mammalian skulls much smaller than the savannah buffalo. Therefore, this discussion of the skull per se and its individual bones therefore remains the main emphasis, but is balanced out by also considering developmental and comparative issues.

Comparing the osteological features of the skull of the savannah buffalo to what is already known for the skull of the domestic bovine (*Bos*) [101] and that of the Egyptian Buffalo (*Bubalus*) [68] , has restrictions of its own, as neither of these species is necessarily the most logical species to compare the savannah buffalo with. From a Veterinary Anatomists' or an Osteo-archaeologists' point of view [101 & 105] , the former seems more logical, but from a Zoologist point of view, comparison with the latter would seem more logical. Other viewpoints for comparison and analysis should therefore also be considered, and in the context of the African continent, it could be the fossils of *Syncerus* of Africa [33] , or even

FIGURE 4.1 : DISCUSSION

THE RESUTLING SCAR THAT MIGHT REMAIN IN THE TEMPORAL FOSSA OF OLD ANIMALS DUE TO THE SPHENOID FONTANELLE (LATERAL VIEW)

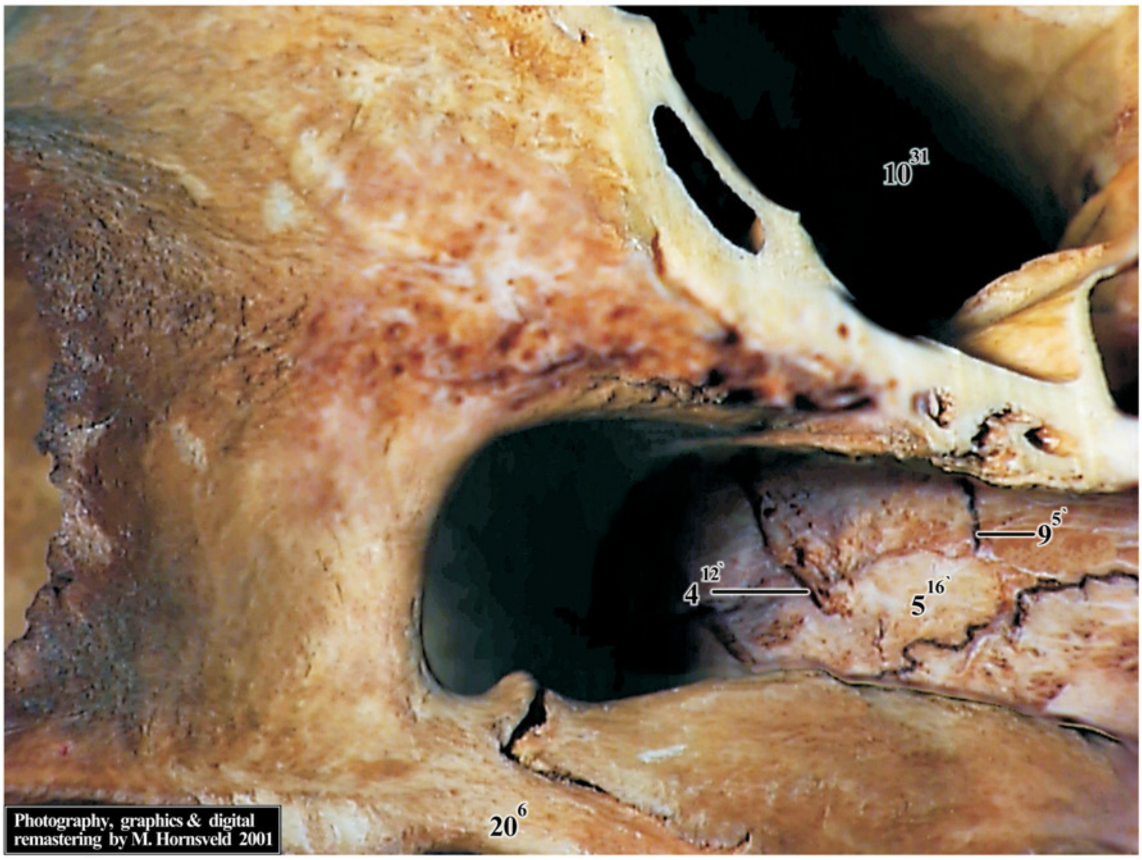


FIGURE 4.2 : DISCUSSION

THE RESULTING TRUE AND FALSE MARKS THAT MIGHT REMAIN ON THE LINGUAL SIDE OF THE MANDIBLE OF (a) VERY YOUNG, (b) IMMATURE AND (c) OLD ANIMALS DUE TO MECKELS' CARTILAGE OR A PROTRUDING CHEEK TOOTH ROOT (MEDIAL VIEW)

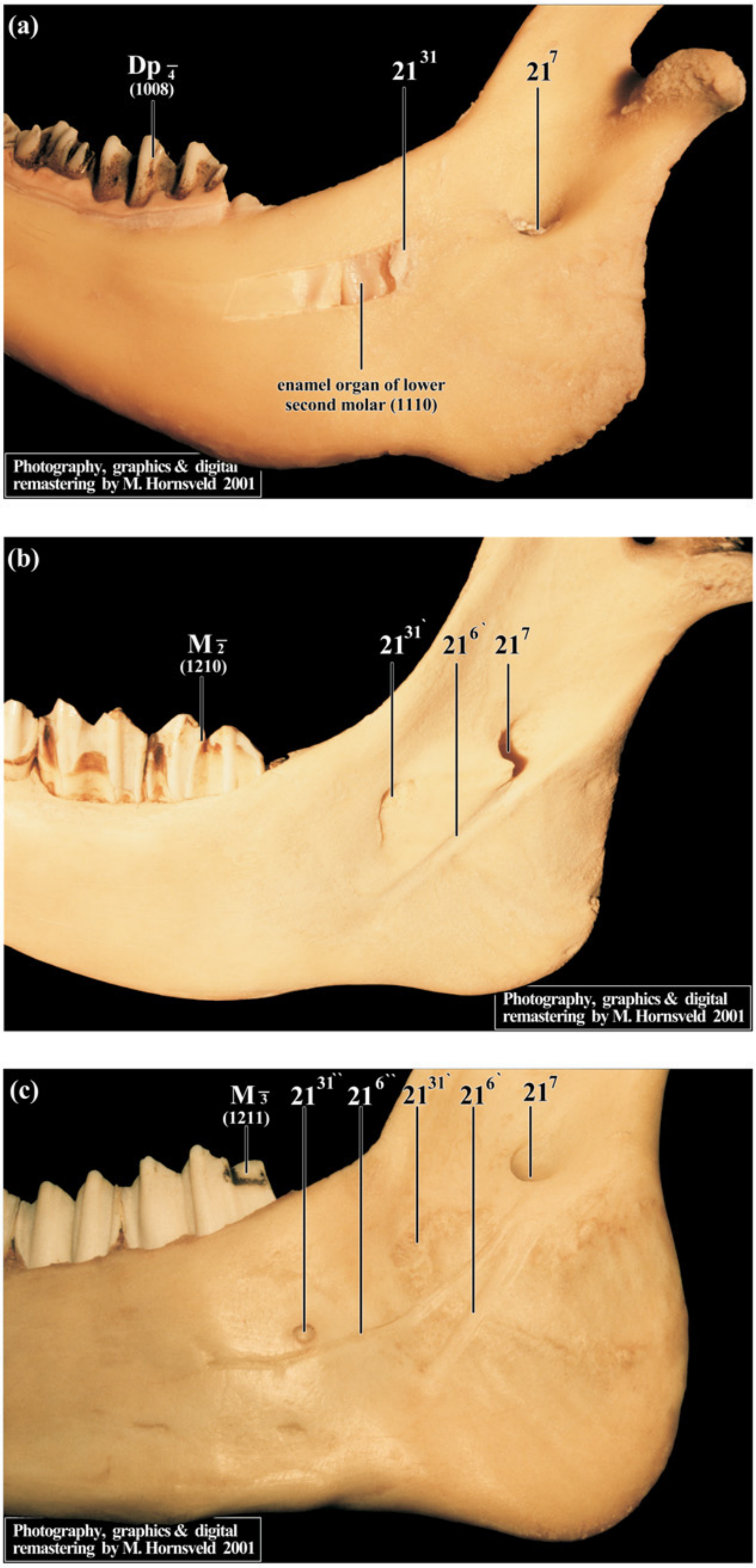
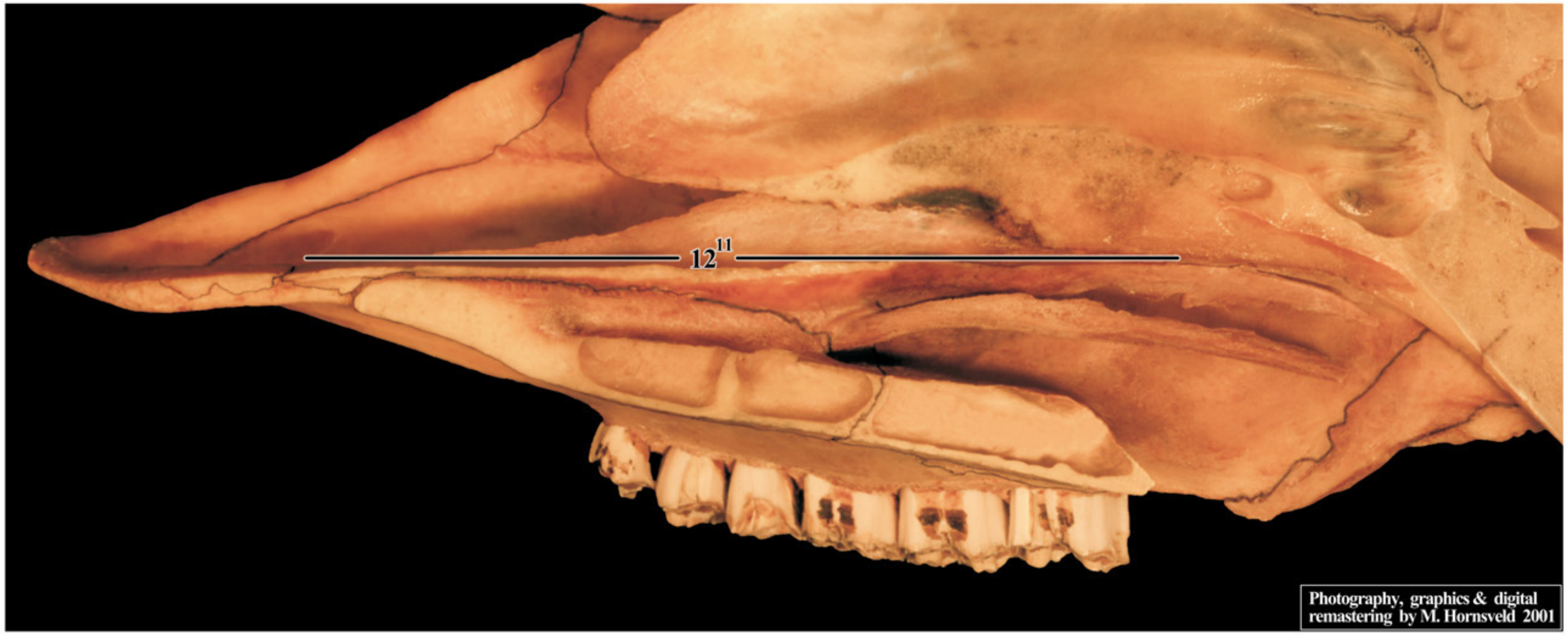


FIGURE 4.3 : DISCUSSION

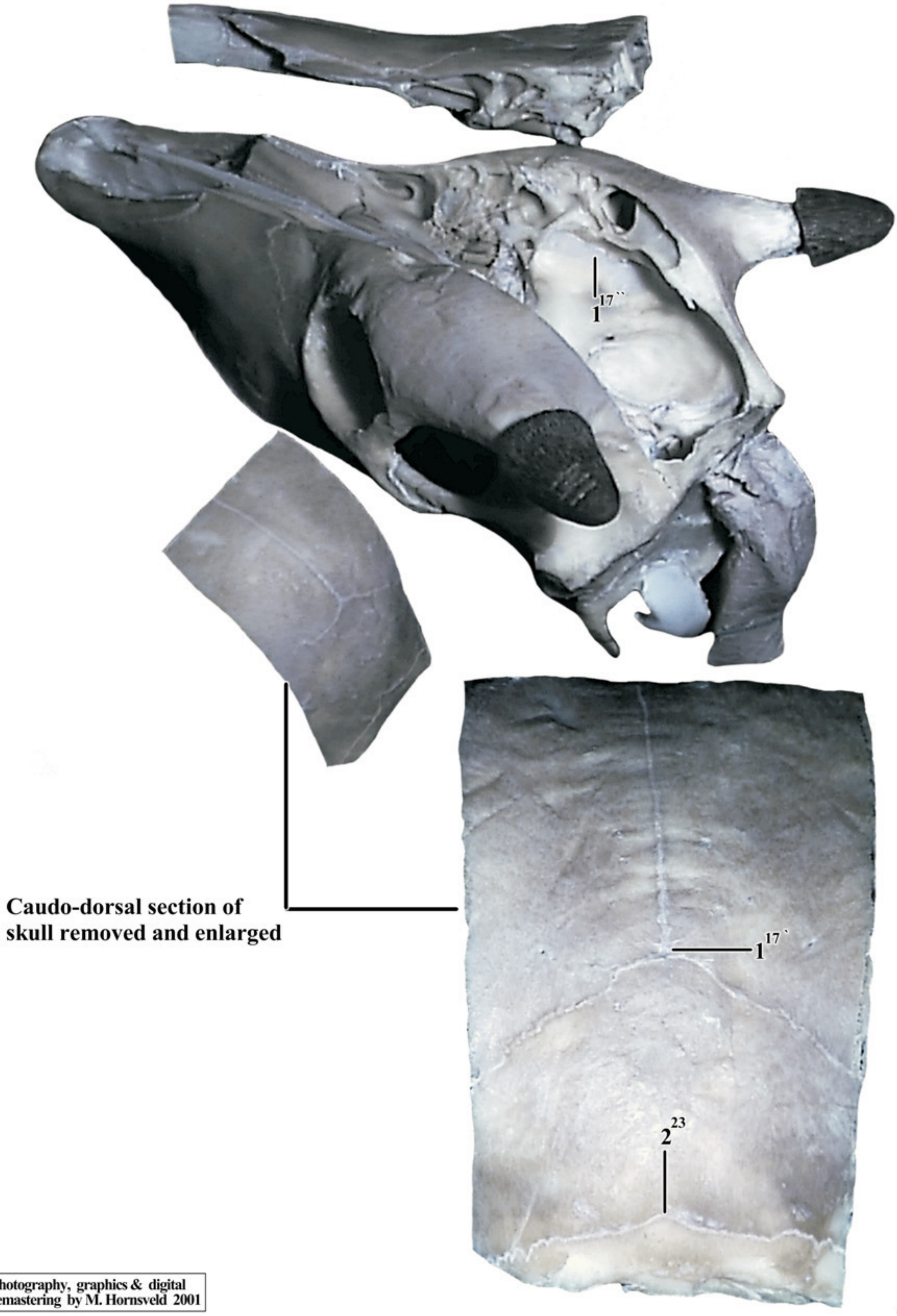
THE VOMERAL CANAL (MEDIAL VIEW)



THE VOMERAL CANAL (MEDIAL VIEW)
FIGURE 4.3 : DISCUSSION

FIGURE 4.4 : DISCUSSION

THE UNPAIRED FRONTOPARIETAL FONTANELLE IN A YOUNG CALF OF APPROXIMATELY 3 - 4 MONTHS OF AGE (DORSAL VIEW)



Photography, graphics & digital remastering by M. Hornsveld 2001

‘*Bubalus* types’ from Africa [26 & 32] . Seen in an even wider context, fossils from Europe on *Bos* [88] , or *Bison* [112] or “house buffalos” [106] , can also be considered for comparison. Ultimately, in the widest sense and seen from a phylogenetic viewpoint, the skull of the savannah buffalo should also be compared with skulls of other size-related ruminants of Africa, Europe, Asia and America, whether of fossil origin or of living species, and to mammals and vertebrates in general. Nevertheless, for such comparison, the prerequisite should be that fine detailed anatomical descriptions of a multitude of criteria are available. Unfortunately, that is not always available for all skulls. Furthermore, disparity in terminology between different scientific fields (also because they were written in different time-frames of history when different terms were official), often complicates such comparisons in so many ways, that it cannot be done in a meaningful way.

For more introductory comments to this Discussion, also see an OVERVIEW OF THE SKULL AS A WHOLE, as described under section B **: The Skull as a Whole**.

ONTOGENETIC DEVELOPMENTAL MODEL OF MAMMALIAN SKULLS:

In broad terms, and based on what is known of the ontogeny of skulls of animals that have been studied in more detail [7, 84 &102] , it appears as if the individual bones of the skull of the savannah buffalo are similar to those of the bovine. The development of the skull of the savannah buffalo as a whole, also appear to be not too dissimilar from that of other mammalian skulls like the pig, dog or human - and when seen in a wider context - even from other vertebrates [42, 128 & 129] . Therefore, the gross morphology of individual bones and their fusion or partial fusion to each other - to form the skull as a whole - can be judged to be compatible to the norm in the absence of any outstanding criteria against doing so.

Obvious aspects of variation, like the position, size and development of the cornual processes of the frontal bone, and other specific anatomical differences, will be addressed under specific headings to follow. (Vide infra.) However, before these can be discussed, the point of departure - for the purpose of this Discussion - has to be elaborated upon. Two approaches are available along which the embryological or ontogenetic development can be dealt with for this study. One is to describe the possible development retrospectively from the point of view of paraxial and neural crest origin. Such an approach can only be considered if pure embryological and histological studies were done. Another approach is to analyse the development of the skull of the savannah buffalo against a standard model of ontogenetic development of mammalian skulls [101] . That model deals with the development of the skull, based on the basic origin of each bone. The model divides the bones of the skull, mandible, hyoid and auditory ossicles, into two main groups. The first group of bones are those that develop from a cartilaginous anlage. The other group are classified as bones that do not form by endochondral ossification, but rather by ossification of non-cartilaginous membranous components. Adding to the cartilage and membranous components, is supporting connective tissue. In that model therefore, connective tissue can contribute to any of the main groups, to form a third element. In summary, the following origins of skull bones are therefore identified according to the model **:**

1. <u>The primordial [neuro-]cranium</u>.
2. <u>The primordial [viscero-]cranium</u>.

Bones originating from both these primordial cartilage types, start to ossify from a central point. Ossification then spreads out peripherally.

3. The desmocranium.

The connective tissue or desmocranium that supports both the above groups, can therefore be divided further into two membranous types **:**

3(a). desmocranial [neuro-]cranium and

3(b). desmocranial [viscero-]cranium.

The former produces membranous bones of the [neuro-]cranium, and the latter lead to the membranous bones of the [viscero-]cranium.

The cartilage that remains between ossification centres, and the connective tissue that remain between un-ossified membranous parts, form the respective sutures, synchondroses and fissures of the skull. If the development of the skull of the savannah buffalo is evaluated against the parameters of this model - as seen retrospectively on postnatal appearance - the following similarities and differences stand out and should be mentioned **:**

POSSIBLE ONTOGENETIC DEVELOPMENT OF THE SAVANNAH BUFFALO'S SKULL AS A WHOLE:

1. The primordial [neuro-]cranium **:**

The model has it that the primordial [neuro-]cranium starts off as a uniform hyaline cartilage capsule, the **chondrocranium**. The primordial [neuro-]cranium of the savannah buffalo could have been a cartilaginous capsule but not necessarily uniform in shape and outline. Centrifugally spreading ossification centres of these individual cartilage components, is said to give origin to all the parts of the occipital bone, the petrous part of the temporal bone, all the parts of the basisphenoid and presphenoid bones, the complete ethmoid bone as well as the ventral nasal conchal bones. In the savannah buffalo, these bones can be identified as such and they do fuse fairly evenly to each other and to other bones of the skull, except for the ventral nasal conchal bones. (Vide infra.) Typically, bones that are derived from the primordial [neuro-]cranium, form both paired and unpaired components. The ethmoid and the temporal bone are exceptions because they do not have unpaired bodies like the other components of the [neuro-]cranium and this is also so in the savannah buffalo. However, a median unpaired part of the ethmoid bone - the perpendicular lamina of the ethmoid bone - is continuous with the rostrum as well as with the body of the presphenoid bone without the intervention of any suture or synchondrosis. In skulls of three to four months post-natal age, the undivided cartilaginous origin is clear to see. This is in contrast to what one would expect to see viz. at least one synchondrosis between the presphenoid and the perpendicular lamina of the ethmoid. At three to four months of age, the perpendicular part of the nasal septum of savannah buffalo, is clearly separated into a small osseus fundic and a much greater cartilaginous nasal part. The ossified fundic part is continuous with the gallic crest and cribiform plate. That region appears to be the centre of ossification. The nasal part, that is still cartilaginous, is continuous with the presphenoid bone, specifically the rostrum which at that age is also still cartilaginous. This makes it hard to belief that the complete perpendicular plate belongs to the ethmoid and not (at least in part) to the presphenoid and / or its rostrum. This part of the fused nasal septum-cum-presphenoid, remains separated by the groove of the vomer - almost along their entire lengths - to form a longitudinal vomeral canal. (Vide infra.) The vomeral canal is neither a typical suture nor a fissure, as the concept of this canal is the same as for other canals found in the skull **:** It contains connective tissue as well as small arteries. The vomeral canal remains as an osseus canal, and even becomes quite spacious in very old animals. Therefore, the situation in the skull of the savannah buffalo regarding these bones and the vomeral canal, cannot be predicted by extrapolation from models of human, dog or bovine skulls. The synchondroses rostral and caudal to the ossified centre of the basisphenoid bone - separating basisphenoid from presphenoid and basisphenoid from occipital bone respectively - are standard for mammal skulls.

The ethmoid bones have paired as well as unpaired laminae, and it is generally described as a single bone (as seen in adult mammalian skulls). However, the ethmoid bone originally (phylogenetically) started off from paired sub-components. Such a paired origin, surely fit into what is seen in the savannah buffalo.

In contrast to the intimate fusion between parts of the ethmoid and the presphenoid bones, the ventral nasal conchal bone of the savannah buffalo is incompletely fused to the maxilla, the palatine and the lacrimal bones. The ventral conchal bone and the ethmoidal conchae have some features in common **:** Firstly, they have paired conchal scrolls on either side of - and unattached to - the nasal septum. Secondly, the basic morphology of the scrolls is similar. Thirdly, both the ventral conchal bone and the ethmoidal conchae are attached to the internal surfaces of the surrounding bones of the face and not the cranium. (Parts of the ethmoid - but not the conchal scrolls though - do fuse by means of reciprocal septae (11[4]) to the frontal bone.) Both bones therefore also contribute to "line" the internal aspect of the nasal cavity without participating in the formation of any external surface of the facial part of the skull. The ventral nasal conchal bone is however classed differently - and possibly due to its position - under the facial bones by the *N.A.V.* That classification is also in contrast to the classification of other bones like the vomer. (See vomer below.)

2. The primordial [viscero-]cranium :

According to the model, the cartilages of the primordial [viscero-]cranium give origin to the parts of the hyoid bone, the malleus and incus, as well as the thyroid cartilage of the larynx. The cartilages that make up the primordial [viscero-]cranium is also referred to as the **splanchnocranium**. The splanchnocranium develops from five different clasps or branchial arches. The hyoid is said to develop from the second and third clasps, the malleus and incus from the first clasp, and the thyroid cartilage from the fourth and the fifth clasp. No clear-cut deviation from this is seen in the savannah buffalo. It is not clear whether a lenticular bone is formed or not and there is no reason to belief that the stapes could not have been formed by Reicherts' cartilage. The articulations between the different components of the hyoid bone of the savannah buffalo are however different and presents more synovial joints than is generally acknowledged. The basihyoid-thyrohyoid synchondrosis - a structure that is clearly seen in the savannah buffalo - fits the model, as both these hyoid components are said to take origin from the third clasp.

Another component of the primordial [viscero-]cranium is Meckels' cartilage which is part of the first clasp. It renders only a basic framework for the mandible, to which desmocranial components (vide infra) are added to complete the mandible. In the savannah buffalo, a remnant of Meckels' cartilage can be still seen on the lingual surface of the mandible of calves of three to four months of age. In old animals, an osseus scar or rather a mark (21[31`]), might be retained in some animals on the medial side of the mandible.

The membranous or desmocranial bones of the primordial [neuro-]- and [viscero-]craniums produce the following remaining bones of the skull by ossification of the connective tissues :

3 (a). The desmocranial [neuro-]cranium.

The membranous [neuro-]cranial components produce the frontal and parietal bones, (including also any interparietal components), as well as the squamous part of the temporal bone. The following - on how their formation in the skull of the savannah buffalo varies from the model - can be said **:** Excessive and continuous postnatal enlargement of the cornual process of the frontal bone is seen in the case of male animals. The base of the cornual process eventually engulfs the convex roof of the skull and actually "seizes" nearly the complete external lamina of the frontal bone. The frontal bone is so well developed rostrally in old bulls that if forms a pronounced summit or vertex (1 [12]). The facial part of the frontal bone is concave again where it joins the nasal bones of the face to form a frontal fossa and a glabella. Such a summit with a frontal fossa and even a glabella is more typical of some dog breeds and man. The external contours of the external lamina of the frontal bone, do not correspond to the contours of the internal lamina in the case of the savannah buffalo, due to the overdeveloped frontal sinus. Similar to the domestic Bovine, the parietal bones form part of the nuchal surface. What is described for dogs, humans and the "domestic buffalo" [51, 106 & 127] , is that the position of the interparietal bone lies between the parietal and the frontal bones. The exact position of the interparietal bone or bones was not established for the savannah buffalo as it needs a study on skulls of prenatal animals. However, circumstantial evidence based on the position and presence of (what could only be) the tentorial process, could indicate that the original developmental position of the interparietal lies more rostrally, towards the frontoparietal suture (9 [5`]), and not further caudally, towards the occipitoparietal suture, as in the domestic bovine [70 & 146] . (In the savannah buffalo, the occipitoparietal suture ossifies externally between the ages of 16 - 24 months and internally the suture remains as a deep groove or recess. The frontoparietal suture is completely ossified after the age of approximately two years although some evidence of it might still be seen on the internal surface.)

3 (b). <u>The desmocranial [viscero-]cranium</u>.

Ossification of the membranous [viscero-]cranial components lead to the formation of the following bones **:** The maxilla, the incisive bone, the nasal, lacrimal, zygomatic and palatine bones, the pterygoid and vomer, as well as the membranous components of the mandible, according to the model. Regarding the desmocranial bones of the [viscero-]cranial part of the skull of the savannah buffalo, they appear to fit the model except for certain aspects of the vomer and the pterygoid bones. The vomer and the pterygoid bones are odd in that the vomer appears to be an unpaired bone in the median plane and it extends caudally to the intersphenoidal synchondrosis (in the region of the primordial [neuro-]cranium). The pattern of fusion of the ventral margin of the keel of the vomer to the maxillary, but not the palatine part of the boney palate, is not typical for the savannah buffalo alone, as it is also seen in the domestic bovine and other mammals. But in *Bubalus* species of buffalo - at least in the Egyptian buffalo - the ventral margin of the keel of the vomer is also fused to the palatine part of the boney palate [68 & 119] . The vomer of the savannah buffalo differs further and from *Bubalus*, in that the rostral part is fused to the incisive part of the palate. (See below under Discussion point number 15.) In the savannah buffalo, the pterygoid bone is a paired bone (as in other domestic mammals), but it differs from what is generally seen in mammal skulls in that it has another part - a body - which is intimately fused between the different wings of both the sphenoid bones. The body of the pterygoid therefore also forms part of the lateral wall of the cranium (externally only) and by that also part of the medial wall of the pterygopalatine fossa. The vomer and the pterygoid bones of the savannah buffalo, thus behave in most respects (definitely topographically) like facial bones and not cranial bones as per *N.A.V.* listing. There is phylogenetic evidence that the vomer and the pterygoid bones were originally a single bone [42] . If that was the case, then the vomer could be interpreted as to have been the unpaired component, and the pterygoids the paired components, of what originally were a single [neuro-]cranial bone. Only on that basis would they fit the classification of the *N.A.V.* as it stands, despite their inclusion in the model as [viscero-]cranial in origin.

Thus, apart from the minor differences noted and discussed above (the continuous presphenoid-perpendicular lamina, the existence of the vomeral canal, a clearly separate ventral conchal bone with a body, and the dubious classification of the vomer and the pterygoids as cranial bones), the skull of the savannah buffalo compares well with the ontogenetic model. Therefore it can be concluded that the skull as a whole conforms to what can be expected in a large herbivore of the Bovini Tribe, and that it is indeed very similar - but not identical - to that of the domestic bovine. However, when individualizing osteological differences of the savannah buffalo's skull is considered - some of which are based on the above ontogenetic differences, while others are based on the gross morphology - 23 significant points of more outstanding differences need to be discussed in more detail. (See SPECIFIC ANATOMICAL ASPECTS OF THE CRANIAL AND FACIAL BONES OF THE SAVANNAH BUFFALO below.)

ZOOLOGICAL CLASSIFICATION AND HISTORICAL BACKGROUND:

The savannah buffalo, ranking among the antelopes under the Bovidae family, and under the subfamily Bovinae, belongs zoologically speaking to the Bovini tribe [73 & 121] . In the Southern African context therefore, the skull of the savannah buffalo should be comparable to other species of its own tribe, including the domestic bovine (*Bos*) of both types. And if seen globally, then the savannah buffalo should also be comparable to European or Asian species of the tribe (*Bubalus*), or even to other extinct or near extinct species. Theoretically, morphological parameters of the skull of the savannah buffalo, should compare best with members of the close related *Tragelaphini* tribe viz. the Sitatunga, the Njala, the Kudu, the Eland and the Bushbuck that also fall under the Bovinae subfamily.

Criteria for zoological classification of related living species of Southern Africa, relies heavily on external morphological features, some of which are as general as the size and shape of the whole animal. That is in total contrast to genetically based methods like chromosome counts and other more modern methods such as amino acid sequencing and DNA studies that are available for some species. Other morphometric criteria for zoological classification may relate to structures of ectodermal origin such as hair, glands of the skin, the mammary glands, or even the horns (not the cornual process). And then finally, also to some features pertaining to the skull and teeth specifically, which are mesodermal and meso-ectodermal in origin respectively. (That is if the interaction between the skull per se and the brain - which is also of ectodermal origin - can be disregarded for a moment.) If the anatomy of an animal as a whole is considered, then these aspects mentioned above, only pertains to a very small sector of the anatomical spectrum of knowledge that can possibly be used to classify animals in a Linnaean system. Yet, scientists like Archeologists, Osteo-archaeologists, Palaeontologists and Zoologists often have to rely only on the most limited section of the spectrum (skull, teeth, or other skeletal remains) when fossils are considered for classification. Using that small a spectrum of the anatomy only, makes their endeavour to find relationships between extinct and living species, a daunting task.

The osteology of the appendicular skeleton of the savannah buffalo has been compared with that of the ancestral *Bos primigenius F. taurus* (Bojanus 1827), but the skull was excluded from the study [105] . The skull has also been excluded in another comparative study between a European "native buffalo" and the ox [59] . The general lack of detailed descriptive studies on the skulls of wild animals can possibly be found in the fact that the skull is a complex and problematic part of the anatomy to master, and to describe. From the point of view of a Veterinary Anatomist - admitting the constraints under which scientist in other fields had to work for ages - one gets the perception that when non-Veterinary Anatomists consider aspects of the skulls of living and extinct creatures, they look essentially at the following **:**

Firstly the <u>horns</u> **:** What is most often considered are the size and shape of the horns and their presence, but obviously also if they are absent in both genders or just in either the male or the female animal. In those rare cases where more than one pair of horns occur in a species - being unusual - it is strikingly significant although it can be due to a mutation.

The absence of horns (iatrogenic and natural) has been recorded in domesticated breeds of *Bos,* as well as the effect it has on the gross morphology of the skull, including that of other species [24, 38, 39 & 40] . Apparent natural absence of horns, has also been recorded for an unspecified species of buffalo in Indonesia [76] . The extreme opposite is also possible and that is abnormal excessive development of a set of horns. Such a case - whether pathological or just a rare individual case - has in fact been recorded for the savannah buffalo [44]. Sexual dimorphism and even texture of the surface of the <u>horn</u> per se, is well recognized in the savannah buffalo, and is also considered by Zoologists. The horn and its change in shape and size with age, is related to the continuous enlargement of the <u>cornual process</u> of the skull. But the horn as an ectodermal derivative is part of the skin, and should not be confused with the cornual process which is mesodermal in origin. Although both are genetically determined, the horn and the cornual process are mutually inducive for each other. No one on its own determines the ultimate dimensions of the combined structure. However, the horn-cornual process interaction (as a postnatal structure) apparently does not affect the size and shape of the [neuro-]cranium as the gross morphology of that part of the skull is rather predetermined by the brain since prenatal times. If in zoological classification, the combined structure of the horn and cornual process is considered when the gross morphology of the whole skull should be considered, then only one single aspect of the frontal bone is considered to the exclusion of many other criteria of the skull.

The second aspect of importance for classification (that non-Veterinary Anatomists apparently consider with emphasis), is the presence or absence of ethmoid "fissures". In the case of the Bovini tribe, the ethmoid fissures should be absent. Apparently though, sutures are meant, because in this study, a temporary ethmoidonasal fissure (14[9]) and a concho-ethmoidal suture & fissure is described (17[3`]). Neither fissure could possibly be meant, as the former becomes a suture, and the latter remain a large fissure. The latter fissure is also seen in the domestic bovine. (See footnotes 125 and 144 respectively, and note the comments that neither are listed in the *N.A.V.*) The remaining other ethmoid sutures on the other hand, are complex and - apart from this study - have not been studied in much detail in most of the domestic species, except in the pig [27, 28 & 29].

Concisely, the following can be said of the ethmoid sutures of the savannah buffalo **:** Ossification of parts of some of the sutures - like the vomeroethmoidal (12[10]) and the sphenoethmoidal sutures (5[9]) - apparently occur early postnatally and over a short period. It can be considered as a first phase of what can happen to the sutures of, and immediately around, the ethmoid bone. The second phase can be described as a delayed fusion of all the remaining ethmoid sutures that did not fuse in the first instance. Some of them remain visible till later in life but from approximately 2 years of age they are always very unclear to see. Without specifying therefore exactly which sutures (or "fissures") of the ethmoid bone are referred to when they are considered for zoological classification purposes [121] - and in the absence of detailed comparative information on the subject - the 'absence of ethmoid fissures' (to classify the savannah buffalo under the Bovini tribe), cannot be accepted. Even as a generalized archetype from the level of the tribe up to the level of family (Bovidae), can any references to ethmoid fissures or sutures only be of limited value. And that would most definitely always be so if the age of the animal is not known or cannot be determined accurately due to a lack of aging criteria. Based on the known pattern of fusion of the ethmoid bone to the surrounding bones of the [neuro-] and [viscero-]cranium for domestic species and the savannah buffalo, it can be said without much doubt, that the ethmoid sutures will probably remain to be those structures (in the skull) which are least studied and worst understood of all.

To base zoological classification on such structures, should be re-addressed.

In contrast to the above two considerations for classification, are those bones of the skull (and their sutures) that have been well studied in various species, and which can potentially be of use for zoological classification.

A good example of this is the variations in the fusion of different bones that contribute to form the region of the occiput and the nuchal surface. This topic has been studied to a great extent in various animals including man [34, 70, 94, 95, 106, 113 & 146]. Many possible permutations appear to exist, and each permutation seems significant enough to be typical for at least one species. It might be typical for the savannah buffalo too, or at least, is different to that of other Bovidae. (See footnote 28.) Although ontogenetic studies need to be done to confirm what is seen postnatally, this should be explored for used in zoological classification. (See below under Discussion point number 2 **:** The caudal aspect of the skull regarding the formation of the occiput and the formation of a paired fontanelle in the temporal fossa).

In conclusion therefore, it must be emphasized that to consider the "horns" and the wide concept of the ethmoid "fissure" - or rather sutures - alone, is incomplete as it would consider only two aspects of the myriads of structures and permutations of anatomic variables. Thus, the practice to consider the horns and the ethmoid fissures or sutures as main criteria - without prior accurate determinations of the age of the animal by tooth eruption and wear - are very relative. Moreover, due attention should be given to ossification of other skull sutures too, and the state of remaining fissures. It can therefore be stated categorically, that doing so for the savannah buffalo, would be bordering on the erroneous. Admitting that other osteological aspects are duly considered when aspects or structures are species-specific, they can only be of value if they have been identified previously, and written up in detail in an anatomical study. For instance, in the savannah buffalo, the ventral margin of the keel of the vomer - in its articulation with the osseus palate - typically does not articulate with the palatine part of the palatine bone. In some old animals, it can be seen that the vomer of the savannah buffalo actually always fuses (after having articulated) with the incisive part of the osseus palate. Conversely, it is typical and well known that the vomer is fused to all three parts of the osseus palate (including the palatine bone) in the Egyptian type of buffalo (*Bubalus*) [68 & 119]. Details of the fusion of bones along many different sutures can and should therefore be used to distinguish between related Bovidae effectively.

The shape of the [neuro-]cranium is said to be determined more phylogenetically whereas the shape of the [viscero-]cranium is said to be determined more ontogenetically [84] than vice versa. Obviously, that statement ignores momentarily the effect that structures like the teeth, the masticatory muscles and the paranasal sinuses could have on the maximum potential growth and shape of the [viscero-]- and [neuro-]crania respectively.

In an analysis of the above three points, it appears as if leaving the confusing issues of comparative osteology of the skulls as well as the cumbersome detailed descriptions unaddressed, is probable what happened through the ages. This study attempts to address some of the deficiencies in our knowledge on the skull on the savannah buffalo per se, by considering the detail of the bones, the sutures and the general morphological features per se. But because comparative information of other wild Bovini is not available, it is not intended to be used to claim or disclaim any zoological classification. On the contrary, it is astonishing that the zoological classification of animals, based on the limited gross morphological criteria alone, is as accurate as it appears to be.

SEXUAL DIMORPHISM AND ITS INFLUENCE ON MORPHOLOGICAL PARAMETERS:

Sexual dimorphism among other species comparable to the savannah buffalo, might not be outspoken enough to render bases for comparison. However, sexual dimorphism in the skull of the savannah buffalo is usually a distinct feature that can be readily seen. In some instances, some of these traits can simplistically be measured one- or two-dimensionally. Visually, dimorphism becomes more striking when skulls of different sexes of comparable ages are placed next to each other. However, due to the large interspecies variations of the gross morphology in savannah buffalo, it needs a well-trained eye to differentiate between genders in less individualistic skulls. To distinguish gender on most of the sub-components of the skull, and also between immature animals, borders on the impossible. It is interesting to note that in older literature on Veterinary Anatomy [30] , the angles between parts of bones as well as between different bones were measured, and proportional growth between the facial versus the cranial parts of the skull were critically evaluated [93] . These are surely measurable criteria that could be applied to differentiate gender or species. However, to do an osteological study on all species into that much detail as was done more or less a hundred years ago, is prohibitive in modern times. Such detailed studies fell into disuse over time in Veterinary Anatomy, but were fortunately taken over in the specialized field of Craniometry.

As reflected in the Craniometric data section, specie-specific criteria for gender identification are suggested in this study. For instance, in the savannah buffalo, the width of the lateral orbital margin (formed by the frontal and the zygomatic processes of the zygomatic and frontal bones respectively) can fairly easily be measured. (See section on **Craniometric data**.) Also, indexes for bones or more complex concepts like the index of a sinus, can be computed. Computer-aided technology should in future be able to help with less outspoken sexually dimorphic aspects. Examples of these may be the following **:**

> The "Roman nose" appearance of some savannah buffalo bulls can theoretically be used, but a standard measurement for the degree of curvature of this bone in the savannah buffalo was not undertaken as in some bulls the nasal bones are flat. (A curved nasal bone is a feature that is also seen in some breeds of horses, typical though of the breed,

and not necessary of the gender. A “Roman nose” is also seen in sheep and goat rams [24].)

The teeth of the savannah buffalo show signs of sexual dimorphism (unpublished data). However, in the absence of true canine-shaped teeth, most of these differences between the teeth of bulls and cows are so subtle that they cannot be described and measured with ease. These criteria cannot therefore be applied for general usage by untrained people. To distinguish gender by using other morphometric data on the teeth (like the enamel crests on occlusal surfaces and tooth size differences), would necessitate elaborate statistical data from three-dimensional computerized models. Even if it might be of importance to Archeologists, Palaeontologists, Osteo-archaeologists or Zoologists, it falls beyond the scope of this study to develop such measuring techniques.

Til now, the easiest and most reliable method - in the absence of detailed studies - which remains useful to distinguish between the genders and often also between species (but not subspecies) - is the size, length and bulkiness of the horn and cornual process. In savannah buffalo bulls, the horn and cornual process is a lot more bulkier than in the cow where it is generally more slender. The general shape and typical curvature - but not necessarily the absolute longitudinal dimensions - are apparently absolutely typical for the species. However, regarding the horn and the Craniometric data taking as suggested for *Bos* species [143], measurements of the “horn core base” is inapplicable for the savannah buffalo bull, as it is incorporated in the vertex and frons (1 [12 & 13]) of the frontal bone. Similarly, the dorso-ventral diameter of the base of the cornual process - measured in a sagittal plane at the level of the zygomatic arch - is also misleading to take, as it may incorporate the temporal line and therefore part of the parietal bone too. Only digitized computer measurements may overcome such complex intra- and interspecies problems.

Apart from gross sexual dimorphism, the skull of savannah buffalo bulls and cows can be discussed along the following 23 specific points when considered macroscopically and when weighed against the ontogenetic model. That is despite potential flaws in the zoological classification and without having done an ontogenetic study.

SPECIFIC ANATOMICAL ASPECTS OF THE CRANIAL AND FACIAL BONES OF THE SAVANNAH BUFFALO:

1. The infraorbital canal and the infraorbital pillar :

(See figures **3.36, 3.37, 3.40, 3.44, 3.65, 3.67, 3.69 & 3.83**.)

Biomechanical aspects of the head in general, and the mechanical properties of individual bones of the skull and mandible of mammals, are fairly well documented [12, 13 & 14]. The biomechanical dynamics of the skull of the savannah buffalo does not differ principally from what is known for the large herbivores. However, the infraorbital canal and its boney lamellar attachment in the savannah buffalo - also attaching to the lingual side of the maxillary dental alveoli - is well developed. The canal is a laterally flattened tube-like structure and not just a canal in trabecular bone. It therefore renders mechanical support to the ipsilateral dental alveoli. Additional to the infraorbital canal, the infraorbital pillar - as a specific osseus structure and apparently with a definite function - is seen as a separate entity in the skull of the savannah buffalo that needs to be discussed.

The basic components of the infraorbital pillar are also present in the skulls of domestic bovine and *Bubalus,* even though it is not described as a specific entity in these animals as having mechanical properties for those skulls. In those animals it also consists of components from the ethmoid, lacrimal, palatine as well as maxillary bones. In the savannah buffalo, this pillar is striking, and is seen as a bold and prominent, laterally flattened strut. It renders mechanical support not only to the caudal end of the infraorbital canal but specifically also to the lingual side of the caudal maxillary dental alveoli. Without having done mechanical stress studies (as it falls beyond the scope of this study), it appears as if the pillar is specifically well developed in the savannah buffalo for four reasons **:**

(a) The internal lamina of the maxillary bone forms the nasal surface of the maxilla, which - apart from being delicately thin - is also marked by two fissures. That weakens the structural rigidity of the internal lamina of the maxilla on the lingual side of the dental alveoli, as would be experience during one-sided mastication of chewing or ruminating.

(b) Unilateral chewing is typical for ruminants and in the savannah buffalo - as is the case also for other animals with anisognathic dental arches - the superior dental arch is wider than the inferior dental arch. The relative difference in width appears to be the same as for the domestic bovine. However, caudally, the structural support of the superior dental arch via the osseus palate per se - but also across the palatine suture, to the bones and structures on the contralateral side - is hopelessly inadequate in the savannah buffalo. That can easily be tested by removing one or both the infraorbital pillars from prepared skulls. Furthermore, in the savannah buffalo, the vomer is not fused to the palatine part of the palate, and that appears to contribute to the need of an additional support system either to the palate or to the caudal dental arch. In those species of *Bubalus* where the vomer is fused to the caudal end of the osseus palate (in the median plane), one would expect the vomer to give that extra support to the caudal ends of the superior dental arch. In the one specimen that was available for study, it indeed appeared to be so, as the equivalent of the infraorbital pillar is less developed in that species.

(c) The external lamina of the maxillary bone lies far apart from the infraorbital canal (and its boney septum) and from the internal lamina of the maxilla. This is due to the large degree to which pneumatization separates these laminae of the maxilla. And as said above, the internal lamina is thin and weakened by fissures. (See under (a) above.) The obliquely position of the infraorbital canal (vide supra), renders solid support rostrally to the rostral dental alveoli, but not caudally. Furthermore - and in all likelihood of the greatest implication in this regard - is the absolute width of the skull at the level of the last upper molar. The demand for additional mechanical support on the lingual sides of the caudal dental alveoli (where the antimeres are separated far from each other by the arched palate that is very wide at that level), is perfectly met by the anatomical position of the infraorbital pillars.

(d) The absence of spongy bone around the proximal ends of the cheek teeth (especially in older animals) may be a contributing factor. If structural rigidity of the region is lost due to the absence of spongy bone, it will demand greater support from both the infraorbital canal and the infraorbital pillar. It can especially be so on the lingual sides of the cheek teeth more caudally. In all age groups, the external lamina of the maxilla (consisting of compact bone throughout) is strong enough from cranial to caudal to support the vestibular side on the cheek teeth.

The infraorbital pillar connects the caudal alveoli rostro-ventrally, joining them directly to the external lamina of the frontal bone dorso-caudally, in the region of the frontal fossa (1[14]). The components of the cranial bones in that region are well developed and overtly strong. Especially the facial part of the frontal bone is conveniently situated above the caudal end of the superior dental arch, to render that required support. The infraorbital pillar can therefore distribute forces directly from the facial part of the skull (the caudal dental alveoli) to the cranial part of the skull (the frontal bone). Apart from counteracting mechanical pressures directly and ipsilaterally, it appears as if the pillar has another function and that is to prevent the transfer of forces diagonally across the facial part of the skull to the contralateral side. It thereby prevents any tendency of torsion of the facial part of the skull during chewing on the one side, as ruminants do. (The inferior dental arch is discussed under the mandible in section A, and is no different to that of the domestic bovine. The rigidity of the mandible matches the supported strength of the superior arch. See footnotes 153 - 155 for remarks on the biomechanical aspects of the mandible.)

2. The caudal aspect of the skull regarding the formation of the occiput and the formation of a paired fontanelle in the temporal fossa (rather than a typical unpaired frontoparietal fontanelle caudo-dorsally in the median plane) :

(See figures **4.1 & 4.4**. Also see 3.8, 3.12, 3.13, 3.21, 3.27 & 3.31.)

The ontogenetic development of the caudo-dorsal aspect of the mammalian skull is complex. The caudal part of the skull forms the nuchal surface, and the dorsal part the summit and roof. Mainly three bones are involved viz. the occipital, parietal and frontal bones. But each of these three bones have sub-components, some of which are paired and some not. Some sub-components only exist in prenatal life. Part of the occipital bone form most of the nuchal surface whereas the parietal and the frontal bones together form the summit and roof. In mammalian skulls, fontanelles often occur in regions where these three bones (or their sub-components) meet each other, or where they fuse incompletely to other bones of the skull. The sites where fontanelles usually form in other mammalian skulls, is different in the savannah buffalo. Also, fontanelles in this animal form at sites where one would not expect to see fontanelles. What is even more extraordinary, is that these fontanelles - as per definition - are not seen in the skulls of recently born calves, but at a later stage in life when one would not expect to find fontanelles at all. The key to understand the state of affairs, lies in knowing the exact way that the occipital, parietal and frontal bones originally came together to fuse to each other. And that can only be found in a detailed study of the embryological development of these bone that includes a study of all the sutures involved. In the absence of having done such an ontogenetic study, only a retrospective analysis of the state of affairs before birth can be done with regards to those fontanelles as seen at birth, and a prospective projection can be made to fill the gap from that age to the time that the unusual fontanelles are found.

Regarding the above in general, it is above all unusual to find that the savannah buffalo shares more osteological detail regarding the fusion of the parietal bones (per se) as ascribed for the skull of the Water buffalo, but less so with skulls of archaeological sites in Europe and in USA, (i.e. of *Bison* and other *Bubalus* types). And even more unexpectedly, is that the formation of that part of the skull of the savannah buffalo apparently shares least osteological detail with the domestic bovine (*Bos* types) [34, 70, 106, 113 & 146]. In the domestic bovine, the Water

Buffalo and the savannah buffalo, the different permutations that are possible for the fusion of the occipital, parietal and frontal bones for each animal, should be particular for that species, as the formation of the occiput can be expected to form according to a set plan. In the savannah buffalo, the paired parietal bones, possible also an interparietal (whether paired or unpaired) or even an [prae-]interparietal bone or bones, fuse, to eventually form a single parietal bone as circumstantial evidence has it. (See Discussion point number 11 below **:** The interparietal process.) The unpaired parietal bone that remains after these early fusions can easily be identified as such in the skulls of animals younger than 16 months. After that age, the parietal bone subsequently fuses intimately with the squamous part of the occipital bone (that is the [supraoccipital bone]) and with the frontal bones. Ossification of the occipitoparietal suture occurs first and then the frontoparietal suture (9[5`]) on the external surface of the skull. Approximately at the age of 2 years the fusion (by total ossification) of these sutures (both the occipitoparietal and the frontoparietal sutures 2[23] & 9[5`]) are complete and no suture lines can be observed further on the external surface. When one evaluates that same region in very young calves to find a retrospective interpretation of the state of affairs, no large cartilaginous component remains (at least as seen in skulls of three to four-month-old calves) on the frontoparietal suture to justify the identification of a frontoparietal fontanelle (see 1[17`]) caudo-dorsally in the occipital region. (See figure 4.4.) This aspect though, regarding this "fontanelle", is similar to the situation in the domestic bovine[146]. However, internally, both sutures may just remain visible but the occipitoparietal suture is more marked by being represented throughout life as a deep groove or a recess. In some savannah buffalo, the groove may contain a single tentorial process that might be the evidence - and therefore indicates as to the presence of - an interparietal bone. The parietal component of the sagittal suture is absent due to its early fusion over the median plane, but the frontal component of the sagittal suture (the interfrontal suture) remains partly visible on the internal side. It disappears with advancing age in a rostral direction. However, even in old animals, faint evidence of it can be seen especially towards the rostral end of the interfrontal suture. A study on a larger number of very young savannah buffalo calves, as well as on fetuses, can elucidate the detail of both regions (nuchal and frontal) and how the sub-components of these bones that contribute to it, exactly ossify (from various centres) to form the nuchal region as well as the summit and the roof of the skull. Even though that information might be of value for zoological classification, the ontogenetic detail of what actually happens falls beyond the scope of this study. No special effort was made to try and determine whether the cornual process has an ossification centre of its own as no indication to such a possibility was ever noticed.

The occipital region of immature and mature animals is further remodelled with age, and more so in savannah buffalo bulls than in cows. Comparing the nuchal region among comparable species, the role and contribution of the frontal bone to the occiput becomes apparent and two aspects should be noted. The first is the degree to which the frontal bone contributes to the nuchal surface and secondly, the formation of an intercornual groove which appears to be typical only for the savannah buffalo.

In the savannah buffalo, the caudal ends of the frontal bone antimeres participate in the formation of the occiput, but not as much as is seen for instance in *Bos indicus* types of domesticated Afrikander or Brahman breeds of cattle [38, 39 & 40] . In these two breeds, the frontal bone may even project for a few centimetres caudally beyond the nuchal surface and beyond the level of the squamous parts of the occipital bone. In the savannah buffalo, the frontal bone only projects caudally to the level of the nuchal plane at the most and not further than that. (Not contributing to the region under discussion, are the bases of the cornual processes, even though they are part of the frontal bones. In old bulls, the bases of the corneal processes do however project caudally beyond the level of the nuchal plane. See section on the **Craniometric data**.)

In cattle, whether polled or not, an intercornual protuberance is always distinguished. However, in the savannah buffalo, there is no protuberance but rather an intercornual groove, separating the cornual bases. The groove extends caudally to participate in the formation of the nuchal plane (the occipital surface) especially in old bulls. In cows, the intercornual groove is more shallow and much wider.

Neither in the domestic bovine nor in the savannah buffalo, is a large frontoparietal fontanelle - like that of man - found immediately postnatally in the nuchal or occipital regions. (Vide supra.) But what is quite interesting (but apparently not unique to immature savannah buffalo), is that the rostral part of the frontoparietal suture is incomplete in a paramedian position (in the temporal fossa). It forms what can only be described as an **atypical and temporary fontanelle**. This fontanelle can be situated on or just next to the frontoparietal suture of that area and forms part of a larger "defect", which also involves the internal surface of the wing of the presphenoid bone and the internal surface of the frontal bone, i.e. at the presphenoidal part of the sphenofrontal suture (4[16]). The internal surfaces of these two bones make up part of the lateral wall of the cranial cavity. Of many skulls of domestic cattle studied to search for the presence also of this fontanelle, only two young ones of similar age showed some signs of the same phenomenon. A similar fontanelle was also observed in the skull of a young calf that could be a specimen of a Water Buffalo (*Bubalus*). (See **Materials and Methods**.) This fontanelle of the savannah buffalo (and apparently also of *Bubalus*) is however not exactly homologous to the sphenoidal fontanelle of man that also lies on this rostral part of the frontoparietal suture in the same temporal fossa [144]. The reasons for not being homologous to any fontanelle described till now, are the following **:**

The typical frontoparietal fontanelle (of man, domestic bovine as well as the savannah buffalo) lies as a single structure in the median plane (caudo-dorsally) and it is present as from birth, becoming smaller with age. Even though the term also exists in the *N.A.V.*, the term is not appropriate here.

The paired frontoparietal fontanelle of the savannah buffalo - in the temporal fossa - also involves the sphenoid bone and therefore the term "frontoparietal fontanelle" would be misleading. Also, it is not present as from birth and it only appears secondarily, apparently due to an osteolytic effect of secondarily activated cartilage of the wing of the presphenoid, to form the fontanelle itself. Therefore, it is **atypical**.

The involvement of the sphenoid bone on the internal surface of the wing of the presphenoid bone, makes this paired fontanelle in the savannah buffalo more likely to be homologous to the sphenoid fontanelle of man. However, the fact that it only develops to a maximum size and to the full thickness of the cranial wall between the ages of 16 months and two years of age (i.e. a fontanelle that forms long after birth and which is present only temporary in external view), makes it an entity of its own, and therefore a **temporary** fontanelle. Similar to other fontanelles, eventual ossification takes place from the periphery towards the centre. Dissimilar to other typical fontanelles, is that it is never membranous in nature.

The fontanelle in the temporal fossa of the savannah buffalo can therefore be described by the lack of a better term as a **temporary atypical** *Fonticulus sphenoidalis*, using existing nomenclature. It starts off as an un-ossified part of the lateral part of the wing of the presphenoid bone that is still cartilaginous at that age. It then enlarges (having osteolytic properties peripherally) and by that means involve the frontoparietal suture or just the frontal bone (9[5`]). (Also see the sphenofrontal suture / fissure 5[16].) Laterally, in the temporal fossa, it always ossifies, sometimes leaving a scar (5[16`]), but internally, some remnants of the fontanelle might remain. It then appears - erroneously - as a sphenofrontal **fissure** on the internal surfaces of the neuro-cranial wall. The external scar and the internal fissure can even be seen in the skulls of some old animals. It must be noted that the fissure occurs as an artefact in the preparation of skulls for anatomical studies because boiling dissolves the remaining cartilage of the fontanelle away.

The intricacy of this fontanelle of the savannah buffalo goes even further. It is known that secondary cartilage can develop from membranous bones and once ossified, can form dense bone or a scar as the case is here [42]. This fontanelle in the savannah buffalo is however different from what is known in that it develops not secondarily from the desmocranium (from a membrane bone) but from the original cartilage of the primordial [neuro-]cranium as it develops from the cartilaginous wing of the presphenoid bone. (See POSSIBLE ONTOGENETIC DEVELOPMENT OF THE SAVANNAH BUFFALO'S SKULL AS A WHOLE above. Also see Discussion point 23 below for Other examples of extended embryonic reshaping potential in the skull and mandible of young savannah buffalo.)

3. The paranasal sinuses :

(See figures **3.55 & 3.56**. Also see 3.8, 3.16, 3.17, 3.21, 3.26, 3.35, 3.37, 3.40, 3.41, 3.65, 3.67 & 3.69.)

Pneumatization of the frontal sinus is extensive and it extends into other cranial bones as well as into facial bones. It involves bones of membranous origin as well as of the chondrocranium. Bones that become pneumatized are the frontal, the ethmoid (i.e. the dorsal conchal sinus and the ethmoidal cells), the parietal, occipital, nasal and lacrimal bones (frontal sinus part of each), thereby forming a frontal sinus complex. Pneumatization of the maxillary bone, the lacrimal bone and the palatine bone, forms a maxillary sinus complex. Pneumatization occurs even between the vestibular side of the maxillary cheek teeth alveoli and the internal surface of the lamina externa of the maxillary bone. Having both a maxillary sinus complex and a frontal sinus complex as part of the paranasal sinuses, is typical for domestic bovine (*Bos*) and other related domestic species too [87 & 147] . These complexes drain separately into the nasal cavity. The frontal sinus complex drains via ethmoidal meatuses into the caudal part of the nasal cavity (into the nasal fundus). The maxillary sinus complex drains via the middle nasal meatus into the nasal cavity via a canal that is partially osseus and partly membranous. The development of both these sinus complexes in the savannah buffalo is more extensive than in the domestic bovine. All the components of both complexes are also more continuous with each other. Even though the paranasal sinuses of especially the frontal sinus complex in the savannah buffalo, have many intrasinal lamellae (similar to the situation in *Bos* and *Bubalus*), compartmentalization of the frontal sinus does not occur. This differs from the situation as seen in the Asian Water Buffalo (*Bubalis bubalis*) [115] . The lacrimal sinus consists out of at least two compartments. One compartment belongs to the maxillary sinus complex, the other to the frontal sinus complex. This also differs from what is seen in both the Asian Water Buffalo (*Bubalis bubalis*) [115] as well as in the domestic bovine (*Bos*) [100] . Furthermore, an additional sub-compartment of the lacrimal sinus is present in some savannah buffalos, and when present it communicates via ethmoidal cells to the nasal fundus. In two older skulls that were available of *Bubalus* types, the caudal lacrimal process (15 [11]) was pneumatized in these skulls as well. This process of the lacrimal bone never becomes pneumatized in the savannah buffalo or in *Bos indicus* species. The presphenoidal sinus of the savannah buffalo is separated from both the frontal and the maxillary sinus complexes. It is usually paired and each half communicates ipsilaterally with an ethmoid meatus.

On each side of the nasal cavity therefore, the paranasal sinuses originate from at least three different epithelial evaginations, viz. the first one from the middle nasal meatus (to the maxillary sinus complex), the second from the roof of the nasal fundus and ethmoid meatuses (to the frontal sinus complex) and a third one from the floor of the nasal fundus (to the presphenoidal sinus). Additional to the abovementioned three evaginations, ethmoidal cells and proper ethmoidal cells (respectively from the tectorial and the orbital plates of the ethmoid bone) as well as ethmoid turbinates from both these parts, also communicate with the fundic part of the nasal cavity via approximately 20 more foramina. Osteologically speaking, the ethmoid cells of the tectorial plate also communicate with the rostral compartment of the frontal sinus. Membranous linings of the ethmoid cells and turbinates may conceal some of the boney openings in live animals. That may reduce the functional number of communicating openings to less than 20. Detail of the membranous parts of the paranasal sinuses, ethmoid cells and turbinates, falls under a study on the splanchnological detail of the head. The cornual diverticulum of the frontal sinus keeps pace with the development of the cornual process. The connections of the paranasal sinuses with the nasal cavity, are via such small ducts and openings, that they can only serve two functions. Firstly, these connections would allow the drainage of mucous that is formed by the mucosal lining of the sinuses. (The mucosal type is expected to be respiratory epithelium, but that was not confirmed histologically as it falls beyond the scope of this study. Heads of savannah buffalo in which the arterial and venous systems were specially injected with latex to show the circulatory system more clearly, showed that the mucosal lining of the paranasal sinuses is very poorly supplied with blood.) Secondly, pressure variations inside the nasal cavity - caused by normal respiration - can be brought into equilibration with the pressures inside the voluminous sinuses by these connections. The volume of air that could be exchanged during the equilibrium process, physically cannot ever be of such a magnitude as to ascribe a cooling function to the paranasal sinuses of the savannah buffalo at all. The connecting ducts of both the maxillary and the frontal sinus complexes are just too small to make that possible. Furthermore, the poor blood supply to the mucosal lining of the sinuses does not indicate towards any heat exchange mechanism.

The ventral nasal concha has bullae and cellulae. Based on osteological evidence, these cavities appear to be isolated compartments that are neither connected to the paranasal sinus complex nor to the nasal cavity. Because the walls of the bullae and cellulae are both osseus and membranous, the absence of any connections can only be confirmed once the splanchnological detail of the head of the savannah buffalo has been done. Other aspects of the ventral nasal concha and the presphenoid sinus, are discussed under separate headings below.

4. The nasoincisive suture at the nasoincisive incisure :

(See figures **3.8, 3.32 - 3.34, 3.41 & 3.42**. Also see figures 1.3, 3.6, 3.7, 3.9, 3.11 & 3.37.)

No conclusion could be drawn from the variable presence of the nasoincisive suture or fissure, except that it is not gender related. (See also 18 [7] , 18 [7`] and footnote 123.) The presence of a nasoincisive suture is seen as a normal occurrence in domesticated goats. It is however never a normal occurrence in the skulls of domestic sheep or bovine [24 & 43] .

5. The cornual process and its relative position on the skull :

(See figures **3.7, 3.31 - 3.34, 3.52 & 4.1**. Also see 1.2, 1.3, 3.3 - 3.5, 3.11, 3.14, 3.16, 3.17, 3.26 & 4.4.)

The position of the cornual process relative to the frontal bone and the rest of the skull is different to what is seen in the domestic bovine. In the bovine the original position of the cornual process - when it starts to develop in young animals - is typically situated caudally on the roof of the skull and it remains in that position. In the domestic goat, the position of the cornual process is typically biassed to the rostral end of the frontal bone, immediately caudal to the boney orbit (13 [21]). It also occurs in that position in other non-Caprine wild ruminants of the Southern African subregion. In the savannah buffalo, the position of the process starts off from caudally on the roof of the skull. The base of the cornual process spreads out rapidly during the first year of live in rostral, caudal and medial directions. At the age of approximately 2 years or more - especially in males - the base of the cornual process extends from the nuchal region to the lateral orbital rim, and in old bulls, even to the supraorbital region. It then also extends medially to the intercornual groove. In some bulls it may become not only extensive but apparently also excessive. Regardless of gender, the final position of the centre of the basal attachment of the cornual process is somewhat biassed like that of the goat, i.e. immediately caudal to the boney orbit. In transverse section, the outline of the cornual process is oval, which is also similar to that of the goat. No histology was done to determine whether the cornual process starts off from a separate ossification centre as in the goat. The intercornual groove and the frontal fossa help to demarcate a glabella. The intercornual groove - as a structure that develops secondarily to the development of the cornual processes - appears to be typical only for the savannah buffalo. It is especially prominent in some old bulls where the cornual bases are excessively large.

6. <u>The ventral conchal bone</u> :

(See figures **1.4, 3.9 & 3.40 - 3.42**.)

The ventral conchal bone is a bone on its own and is regarded as such according to the *N.A.V.* However, clear distinction can be made in the savannah buffalo between the conchal scrolls and a body for this bone. The body also has a rostrally directed process. The body and its process have hitherto not been described, yet it is present and it has the same morphology in very old domestic bovine bulls. In the savannah buffalo however, the body is not as porous as in the domestic bovine and the "defects" in the nasal wall due to the large and compound permanent fissures (17^{2} and 17^{3}) are much smaller. The body of the ventral conchal bone forms the medial part of the boney canal (17^{5}) that drains the maxillary sinus complex. (See footnote 145.) The scrolls of the ventral conchal bone have isolated bullae and cellulae, which do not communicate with the frontal or the maxillary sinus complexes. Communication of the enclosed spaces within the cellulae and bullae to the common nasal cavity, is doubted.

7. The pterygoid bone and the vomer :

(See figures **3.1, 3.3, 3.8, 3.16, 3.17, 3.23 - 3.26, 3.38 & 3.39**. Also see 3.60 & 3.63.)

The pterygoid bone consists of a body (that participates in the formation of the pterygopalatine fossa) and processes (that contributes to the formation of the lateral osseus wall of the choana). One process of the pterygoid bone - as seen in the savannah buffalo - has until now been recognized as the only part of this bone. However, in many higher vertebrates, the pterygoid is known to actually develop from separate dorsal and ventral ossification centres. These centres would correspond to the body and processes respectively. It is also known that phylogenetically, the antimeric pterygoid bones and the unpaired vomer could originally have been a single bone in mammals [42] . The contributions of the vomer and the pterygoids to the [viscero-]cranium only - and not the [neuro-]cranium - questions their traditional classification as cranial bones.

8. The ethmoid bone and its fusion to the surrounding bones of the cranium and face :

(See figures **3.1, 3.6, 3.8, 3.9, 3.26, 3.35 - 3.38 & 3.40 - 3.42**.)

Fusion of the cribiform and basal plates of the ethmoid bone to the surrounding bones of the cranium and the face, is described in this study for the post-natal situation only. However, the intimate fusion of the basal plate of the ethmoid bone to the rostrum of the presphenoid bone apparently already occurs prenatally as separate entities for these two bones cannot even be seen in animals as young as three to four months of age. The sutures along the perimeter of the cribiform plate - where it is fused to the bones of the cranium - are also difficult to see in the skulls of young animals of that same age. It is therefore unclear which sutures involving the ethmoid bone - if any at all - could be considered for zoological classification, at what ages, and in what sequence of fusion. During embryological development, the ethmoid bone starts off from a paired anlage or primordium, but fuses later to form an unpaired bone with all its different laminae (tectorial, orbital, basal and perpendicular plates) [101] . Its paired origin does explain why some of its components - like the conchae and the cribiform plates - are paired, but it does not explain early fusion of the basal plates (as paired structures) to the sides of the rostrum of the presphenoid bone (an unpaired structure) nor the incomplete articulation of the perpendicular plate with the vomer to leave a vomeral canal. By logical reasoning, the ethmoid should therefore have both paired and unpaired origins, similar to the occipital, basisphenoid and presphenoid bones. In savannah buffalo of approximately three to four months of age, the rostrum [prae-]sphenoidale is cartilaginous and it is continuous with the perpendicular lamina of the ethmoid bone which is also still mainly cartilaginous at that age. It appears therefore that most of the nasal septum (excluding the vomer) is part of the presphenoid bone (and not part of any of the laminae of the ethmoid bone, or of the ethmoid at all). An alternative and more logical interpretation, can be that the rostrum of the presphenoid bone is in actual fact the unpaired part of the ethmoid bone, which would explain the "early fusion" of the basal plates with the "presphenoid". The single ossification centre in the presphenoid body (including the gallic crest and cribiform plates), spreads rostrally to the presphenoidal rostrum, and eventually also to the perpendicular plate. That interpretation of the scene of events explains the absence of any synchondrosis between the presphenoid and ethmoid components the best. Unfortunately, it falls outside the scope of this study to do a complete ontogenetic and early postnatal study to proof that both components of the presphenoid and all the components of the ethmoid, are in actual fact one and the same bone. Studies on the ontogenetic development of the ethmoid bone of the domestic pig have been done by using special staining methods on prenatal fetuses [28 & 29] . The same methods can be used for such a study on the savannah buffalo.

The number of the endo- and the ectoturbinates of the ethmoid bone in the savannah buffalo is similar to that of the domestic bovine.

9. <u>Secondary resonant function of the semi-tubular part of the tympanic part of the temporal bone</u> :

(See figure **3.29**.)

In the savannah buffalo, the ventral part of the semi-tubular part of the tympanic part of the temporal bone, ventral to the tympanic sulcus (7 [26]), may be aerated in some individuals to form a cavity (7 [41``b] ). (See footnotes 68 &72.) When present, this cavity communicates via an opening (7[41``a]) in the wall of the mesotympanic part (7[41``]) of the tympanic cavity (7[41]). This opening lies in the rostro-lateral wall of the tympanic bulla, between the annulus and the etched outlines of the base of the styloid process (as seen from inside the bulla). Aeration of this part of the skull must be seen differently from the pneumatized cavities of those bones in which the paranasal sinuses are connected to the nasal cavity - even though the principle method by which it occurs may be the same - as this aerated part connects to the tympanic cavity (of the middle ear) and not the nasal cavity. It can therefore be said that apart from the primary conducting function of this lateral part of the semi-tubular part of the tympanic part of the temporal bone, it could also have a secondary resonant function that could aid the animal in hearing. The cavity (7[41``b]) appears to be different from mastoid canals (or cells) as found in man [31]. (See 7[46``] and footnotes 68 & 81.)

The tympanic bulla of savannah buffalo appears to be more voluminous than that of the bovine.

10. <u>The lacerated foramen</u> :

(See figures **3.9, 3.13, 3.14, 3.24, 3.25, 3.29 & 3.30**.)

It is not typical for the domestic bovine or for ruminants for that matter, to have a lacerated foramen (1[20]) but rather to describe it as a petro-occipital fissure. However, in the savannah buffalo, a complex fissure is formed (7[1]) and it is convenient to describe this voluminous fissure as a lacerated foramen. (See also 2[8], 4[13] and 7[31 - 33].) Finding a lacerated foramen in the savannah buffalo is not seen as an abnormal situation, but just a different state of affairs when compared with the domestic bovine. Describing this fissure as a lacerated foramen conforms to the footnote in the *N.A.V.* regarding that opening in the skull. The foramen ovale is not included in this spacious fissure - as it is in the horse - but remains as a separate opening typical of ruminants.

11. The interparietal process :

(See figure **3.13**.)

Variations of fusion of the occipital bone and the other bones that contribute to the formation of the occiput and the nuchal plane can cause interesting phenomena **:** In humans, additional single or paired bones formed in the region of the foramen magnum, is regarded as "non-metric epigenetic anthropological markers" [141] . If additional bones are formed in the interparietal region, they are referred to in literature as either an interparietal ossicle when on the internal surface of the skull, or the remains of a [prae-]interparietal bone, or - if more extensive and visible on the external surface too - as "sutural bones", as "Inca bones", as "Ossicula Kerkringii" (human literature) and in Veterinary literature - especially in the facial region - as "Wormian Bones" [30] . In this study, the remains of an osseus structure on the internal surface of the occipitoparietal suture that is present in some individuals, is regarded as an interparietal process (3^{1}), or when well developed, as a processus tentoricus (3^{2}). No ontogenetic study was done on the development of the skull of the savannah buffalo to confirm the detail of the development of this process as it falls outside the scope of this study. It is described for *Bubalus bubalis*, that the interparietal bones fuse pre- or early postnatally with the parietal bone (or bones) to form an unpaired parietal bone but without an interparietal process. It is not typical for the domestic bovine to have such a process nor to have an osseus cerebellar tentorium (3^{3}) (which is rather more typical of the horse and the dog). It can be a useful structure to identify and describe, and possible even to use it in the zoological classification of animals, once its origin has been properly established. However, what appears to be an interparietal process, an interparietal ossicle or the remains of an [prae-interparietal] bone, may however just be an ossification of the membranous cerebellar tentorium of the dura mater and not the remains of a skull bone.

12. The presphenoidal sinus :

(See figures **3.21, 3.55 & 3.56**.)

The sinus in the presphenoid bone is small and single in the Egyptian Buffalo *Bos [Bubalus] bubalis* L [68] . For the (Asian) Buffalo, *Bubalus bubalis*, it is stated that the sphenoid sinus is "not noticeable"/ "absent" [115] . In the savannah buffalo it is present in some individuals. When present, it is situated in the rostrum [prae-]sphenoidale, as a paired structure. The two components of the sinus are not necessarily bilaterally symmetrical and may even be extensive in some old animals. Each communicates ipsilaterally with an ethmoid meatus. In the domestic bovine, the sphenoidal sinus is said to be present in more than 50 % of cases and situated in both the body and the wing of the presphenoid bone [101] .

13. Visceral bones :

Visceral bones do not actually form part of this study but they can be included. No visceral bone in the nasal region (*Os rostrale*) was specifically looked for in the preparation of the skulls or seen in median sections that were made of savannah buffalo heads. A visceral bone in the upper lip of old domestic bovines (*Bos*) is known to occur [101] . Detailed dissection on cadavers still has to be done for the Splanchnology, and then specific observations can be made to see whether this visceral bone is at all present in older animals. It is known that the *Ossa cordis* is present in the heart of old savannah buffalos at the origin of the aorta. It is very well developed in old bulls and much bigger than the equivalent bone of the domestic bovine. (Unpublished personal observations.) The rostral bone - if at all present in the savannah buffalo - can be the only bone that is not described in this study.

14. Particular articulation of the ventral margin of the keel of the vomer to the dorsal surface of the boney palate :

(See figures **3.1, 3.6, 3.8, 3.38, 3.39 & 3.63**. Also see figure 4.3.)

In the savannah buffalo, the ventral margin of the rostral two sections of the keel of the vomer is fused to the maxillary and the incisive parts of the osseus palate. The ventral margin of the caudal part of the vomer is not fused to the palatine part of the osseus palate. This pattern of fusion is similar to the situation in the domestic bovine. In *Bubalus* - at least in the Egyptian Buffalo - it is fused along its whole length to the nasal crest, including the caudal palatine part of the osseus palate [68, 116 & 119] . Among domesticated animals, such a pattern of fusion is only found in the pig and horse.

15. The palatine process of the incisive bone, its participation in the formation of the osseus palate and the cartilage filled palatine fissures : Readdressing what sutures, fissures and fontanelles could rather be defined as :

(See figures **3.25, 3.32, 3.33 & 3.41**. Also see 3.42, 3.59, 3.63 & 3.64.)

In the savannah buffalo as well as in the Egyptian Buffalo, the palatine processes of the incisive bones are fused to maxillary parts of the palate to participate in the formation of the rostral part of the boney palate. This is also similar to the situation in the domestic bovine. However, what is dissimilar, is that the caudal parts of the palatine processes of the incisive bones of the savannah buffalo, are also fused to the rostral part of the keel of the vomer. Thereby, in older animals, completely ossified vomeroincisive sutures are eventually formed. Usually, this fusion can be appreciated best in ventral view of the palate, but sometimes also in dorsal views of some old bulls. In ventral view, paired vomeroincisive sutures (in paramedian positions) can then be seen when the ventral margin of the keel is visible. In dorsal view, the ossified interincisive suture rostral to the rostral end of the keel, may present a sutural bone in some individuals. (See figure 3.32 or 3.59.) The interincisive fissure is therefore definitely a misnomer in the case of the savannah buffalo - clearly to be seen in old bulls - because the palatine processes of the incisive bone ossify completely to each other over the median plane, and - in that same process - also entraps the keel of the vomer.

In the living animal, the nasally situated and paired vomero-nasal organs, drain via the incisive ducts - through the cartilage filled paramedian palatine fissures - to the oral cavity. How much of this cartilage belongs to the tubular part of the vomero-nasal organ, and how much belong to the palatine fissure itself, needs to be established histologically for the savannah buffalo. That should proof whether it is also a misnomer to recognize the palatine fissure. However, the palatine fissure - as seen in the prepared skull - never becomes closed off by ossification of its cartilage, even in old animals. The pattern of fusion of the palatine processes to the maxillary part of the osseus palate of the savannah buffalo, corresponds well with what is seen in the skulls of sheep and goat [24] .

From the above, as well as what has been said under Discussion point number 2, fissures, sutures and fontanelles of the savannah buffalo were found to be utterly confusing in the descriptive osteology of the cranial and facial bone of the skull. An alternative approach to the terminology of these structures, can be as follows **:**

A fissure should be defined as a non-cartilaginous but loose connective tissue containing bond between two or more bones where they meet.

A suture should be defined as a cartilaginous containing bond between two or more bones where they meet.

A fontanelle should be defined as a membranous connection between two or more membranous bones where they meet.

As simple as it seems, it would solve quite a few problems in the descriptive anatomy as then, in the case of the fissure, no bone can be formed, and a fissure would be known as a structure that remains permanently un-ossified and filled by connective tissue only. In the case of the suture, bone can be formed from the cartilage and added to any of the adjacent bones that lie on either side of the suture. Such a suture can become less and less active as the animal ages, to eventually ossify partially or completely, but never leaving any sutural bones. Or, the cartilage of the suture can become more active at a certain stage in life if remodelling of the skull demands such activity, after which the activity of the cartilage formation returns to normal to eventually ossify partially or completely as any other suture would. In the case of the fontanelle, it can remain membranous or ossify intra-membranously, to eventually disappear totally. Or, by spontaneous ossification from a new centre or various centres in the membranous fontanelle - none of which fuses to any of the apposing or adjacent bones - it can form a sutural bone (or many of them) that remain clearly demarcated from the opposing bones by connective tissue filled lines. These lines remain visible but cannot be distinguished macroscopically from small fissures. Finally, ossification to form synostoses (whether from cartilage to bone or from connective tissue to bone), would be the natural destiny of all synchondroses and even of the intermandibular joint - even if it rarely becomes ossified in the savannah buffalo.

If these alternative definitions can be applied to the descriptive anatomy of the savannah buffalo, then the palatine fissure would just be the yet-to-be-ossified part of the cartilage model of the incisive bone, leaving a foramen for the duct of the vomero-nasal organ. The interincisive, nasomaxillary and nasolacrimal fissures would be the respective un-ossified - but still active - cartilaginous components of these sutures, and the atypical and temporary sphenoidal fontanelle (the *Fonticulus sphenoidalis* of the savannah buffalo) would be normal. The large and larger compound fissures around the body of the ventral conchal bone (17^2 and 17^3), as well as the lacerated foramen per se, would be the only true fissures in the skull of the savannah buffalo. And finally, synchondrosis would then be normal sutures.

16. <u>The vomeral canal</u> :

(See figures **3.8 & 4.3**. Also see 3.1, 3.6, 3.8, 3.38, 3.39 & 3.63.)

The perpendicular lamina of the ethmoid bone and the body and rostrum of the presphenoid bone forms the dorsal border of the vomeral canal (12^{11}). The vomeral or [septal] groove between the wings of the vomer, forms the ventral border of this canal. In young animals of approximately three to four months of age, the vomeral canal contains delicate loose connective tissue, some fat and at least two small arteries. This canal has hitherto not been recognized in literature for any of the domesticated species, but its existence is a standard feature in both *Bos* and *Bubalus* species. The continuity of the osseus components of the presphenoid and its rostrum with the perpendicular lamina of the ethmoid bone in the savannah buffalo, indicates towards a single cartilaginous origin for these bones (vide supra). The existence of the vomeral canal, separating the vomer from the nasal septum, supports this finding. Even though the vomeral canal contains connective tissue, it cannot be classified as a suture nor a fissure as it differs too much from these structures. Its contents demand its classification as a canal, just like other canals or foramina of the skull.

17. <u>Anatomical terminology</u> :

Great strides have been made in the standardization and even digitization of human anatomical nomenclature. Zoologists, Archaeologists, Palaeontologists, Osteo-archaeologists and Veterinary Anatomists should be dependant on a proper and correct list of standardized terms. Even though such an internationally recognized list of terms (the *N.A.V.*) is available for Veterinary Anatomists [53] , many terms that were used before standardization (especially between the different fields of expertise) might be outdated and confusing as measured against the latest guidelines. These problems make it nearly impossible for specialists of a particular field (and even worse so for any non-specialists) with an interest in any of the other fields, to disclose the scientific information buried under the confusing issues of the nomenclature of structures. It is however understandable because specialists in the different disciplines usually function independently, and their latest guidelines are not published yet, or are still evolving. For the same reason, it is possible that the archaeological terms - and the basic reference perused for this text [143] - became outdated in recent times, just because one is not familiar with the latest in other specialized fields. Some suggestions on the terminology are made in this study (by way of footnotes), to also accommodate the anatomical description of wild ruminants of Africa such as the savannah buffalo. These suggestions should in time be sent to the secretary of the *N.A.V.* for consideration to include it into an updated version of the *N.A.V.* The *N.A.V.*'s latest list cannot be regarded either as complete or as an ideal list for osteological descriptions of the head of wild animals in the present way it is, because it basically caters for the domestic animals from where extrapolations have to be made. Minor additions may make the value of the *N.A.V.* applicable over a much wider field. It is hoped that the official anatomical terminology will become more readily available and more user-friendly also for Zoologists, Archaeologists, Palaeontologists and Veterinary Anatomists.

18. <u>Applied biomechanical aspects of the skull</u> :

(See figure **3.83**. Also see 3.72 - 3.82.)

The biomechanical aspects of the skull should be considered as part of the understanding of the skull per se [12, 13 & 14] . The biomechanical aspects become even more applicable when the dentition is considered or when trajectories for hunting are worked out. It is even more so when the theoretical early fusion of one or more of the sutures need to be induced in experimental work. (See below under ASPECTS OF THE OSTEOLOGY OF THE SKULL HAVING POTENTIAL CLINICAL APPLICATION IN OTHER FIELDS.)

The infraorbital pillar (15 [17`]) as discussed (see Discussion point number 1), appears to play an important supporting role in sustaining the pressures and torsions to which the superior dental arc is exposed. This pillar is also visible in *Bos* as well as in *Bubalus* species, but has hitherto not been described as a specific anatomical entity for any of those species. This pillar is much better developed in the savannah buffalo and more obvious to see as an entity on its own than in those species. In order to understand some of the aspects of the attrition of the teeth - especially that of the upper and lower first molars - a few factors that are based on the biomechanical aspects of the skull have to be considered **:**

Firstly, the biomechanical aspects of the temporomandibular joint and the one-sided mastication process that is typical for ruminants.

Secondly, the relative position of the first molars in the cheek tooth rows, anisognathism and the sideways movement of the mandible during chewing. This might imply that the first upper and lower molars might have to “work” more (are exposed to more attrition) than any of the other cheek teeth.

Thirdly, the disadvantageous early eruption of the first molars. Possibly - and even of more significance in the whole scenario of teeth wear and the longevity of animals - are the consequences of delayed eruption of the other cheek teeth that immediately has to follow that of the first molars (unpublished personal observations).

With the aid of modern computers and suitable software programmes, the biomechanical aspects of significant points of stress at various places on the skull, could be digitalized and computed for Archeologists, Palaeontologists, Osteo-archaeologists, Veterinary Anatomists and Zoologists. Such data can be tied up with aspects like tooth wear, active bone formation at suture lines or the early ossification of it. Such data might become handy tools for use by those specialists involved in the management of the population dynamics of species such as the savannah buffalo (vide infra). Also, big game hunters should avoid trajectories of projectiles along pathways of high resistance as projectiles would tend to ricochet away from oblique surfaces of solid bone. Such detailed biomechanical aspects of the skull of the savannah buffalo falls beyond the scope of this study.

19. Synovial joints of the hyoid apparatus :

(See figures **3.50 & 3.51**.)

The different components of the hyoid apparatus and the differences between species are fairly well known [25, 93, 114 & 120]. In the savannah buffalo, synovial joints are found between the basihyoid and each of the ceratohyoids in animals of all ages. That is also well known in the domestic bovine. As savannah buffalo age, the joints between the ceratohyoid and epihyoid, as well as between the epihyoid and the stylohyoid bones changes from fibrous joints to synovial joints. This phenomenon has not been described hitherto in detail and only superficial reference to the existence of more synovial joints has been made [55 & 101].

20. The rationale behind describing the detail of sutures of the skulls of wild animals :

The fine detail of the sutures may be so different between skulls, that the descriptive data on all the sutures accompanied by photographic evidence seem specific enough to distinguish between different savannah buffalo skulls. Having a detailed description of these sutures, can therefore render some form of "fingerprinting" of skulls. For instance, fingerprinting of an individual hunting trophy may prevent the illegal re-entry of that trophy for other competitions if the rules would state so. The occlusion pattern of cheek teeth (between teeth of the superior and inferior arches), as well as the detail of the enamel ridges on the occlusal surfaces, can also be used for this purpose as well as in forensic cases where DNA methods cannot be applied. The application of having suture- and dentition-based fingerprinting detail, may be of use in Palaeontology in general.

21. Remnants of Meckels' cartilage in the mandibles of young and old savannah buffalo :

(See figure **4.2**.)

Remnants of Meckel's cartilage (21 [31]) appear as small defects of ossification on the lingual surface of the mandible of young animals of approximately three to four months of age. The defects are located on the medial side of the mandible, rostro-dorsal to the pterygoid fossa and measures approximately 9 x 5 x 3 mm in size at that age. Evidence of these defects can still be seen as a mark ($21^{31'}$) in the mandibles of old animals. It serves as an example of the extended embryonic reshaping potential of young skulls and mandibles of the savannah buffalo. (See Discussion point 23 below.) Remnants of Meckels' cartilage must be distinguished from false marks ($21^{31''}$) caused by protruding roots of mandibular cheek teeth.

22. <u>Gubernacular canals in the maxilla and mandible associated with the development of the permanent premolars</u> :

(See figure **3.49**.)

Temporary canals associated with the development of the permanent premolars are referred to in human literature as gubernacular canals where they are associated with the development of the upper permanent incisors in the premaxilla [92]. (In Veterinary Anatomy, the "premaxilla" is known as the Incisive bone.) These canals have not yet been described in any domestic or wild animal although similar gubernacular canals are found in the domestic horse. However, what is different about these canals in the horse are that these canals are associated with the permanent incisors and the molars and not the premolars. (Unpublished personal observations.) In the savannah buffalo, these canals develop lingual to each deciduous premolar (upper and lower) at a time when the enamel organs of that particular permanent premolar starts to develop. These gubernacular canals disappear again after the successor teeth have formed and have nothing to do with the pathway of eruption of the permanent tooth - as is claimed in some literature on human dental development.

23. <u>Other examples of extended embryonic reshaping potential in the skull and mandible of young savannah buffalo</u> :

(See figure **3.33**.)

Examples of retained embryonic potential discussed above, are the formations of the temporary atypical sphenoid fontanelle and the remnants of Meckels' cartilage (vide supra under Discussion points 2 and 21). Three other examples of extended embryonic reshaping potential in the skulls of young savannah buffalo are noted. In all three examples, increased osteolytic activity and / or secondary cartilage formation appears to be involved **:**

(a) A "defect" in the central part of the nasal bone.

This area of apparent increased reshaping does not involve any of the sutures around the nasal bone nor the nasomaxillary fissure. Increased sub-periosteal osteolytic activity on the ventral surface of the nasal bone appears to be the cause. It causes a longitudinal "defect" to develop in the central part of the nasal bone itself, to form a temporary longitudinal nasal "fissure" (14[7]). In the live animal, the "defect" (apart from the periosteum) would be covered by nasal mucous membrane ventrally, and skin dorsally. This "defect" appears at the age of approximately 2 years, before and after which the intactness of the bone becomes unquestionable again. It is similar to the sphenoidal fontanelle - as seen in the temporal fossa - in the sense that it appears to form due to excessive bone resorption due to remodelling demands. It differs however from the sphenoidal fontanelle in one major respect viz. no cartilage appears to be involved. No indications could be found that the "Roman noses" of some bulls are a direct result of natural correction of the defect. Nor were any signs found that a scar remains due to subsequent ossification of the defect.

(b) "Defects" that form in the medial wall of the boney orbit.

Signs of excessive osteolysis are seen on the deep side of the medial wall of the orbit, in the orbital part of the frontal bone that directly overlies the proper ethmoid cells. The orbital part of the frontal bone becomes so thin in these regions that it becomes transparent. Over some cells, the intactness of the frontal bone may even be interrupted to "break through" into the boney orbit in what appears to be a "pseudo-fontanelle" in prepared skulls. This is also seen in animals of approximately 2 years of age. No true fontanelle forms because the orbital plate of the ethmoid bone remains ossified to fill the "pseudo-fontanelle". Before and after that age, it is not noted and once again - as in the case of the nasal bone - the intactness of the bone is unquestionable again. Due to a lack of specimens of that age and without leaving any scars to trace the further course of the condition in older skulls, the true cause of the condition can only be speculated about. Two possible explanations can be put forward **:**

Most probable, it is a cartilaginous remnant of the orbital plate of the ethmoid bone that becomes reactivated at that age due to a drastic remodelling phase of the ethmoid bone. Having peripheral osteolytic potential, it dissolves away bone between the itself and the frontal bone at the frontoethmoidal suture. Subsequently, it erodes away the deep side of the overlying frontal bone. That is as seen in prepared skulls where the cartilage components have been boiled away. The resulting "defect" is therefore similar to the sphenoidal fontanelle as it is then a secondary cartilage component of one bone that dissolves away adjacent bone. It is also similar in the sens that the "defect" becomes larger at a certain age, just to disappear again. It differs from the sphenoidal fontanelle - if size can be a measure - in that no fontanelle is formed.

Alternatively, it could be formed due to a disproportionate enlargement of the ethmoidal cells at that age - also due to a drastic remodelling phase of the ethmoid bone - at the expense of the orbital plate of the frontal bone.

Histological and macroscopic studies on more specimens have to be done to confirm the nature and development of the sphenoidal fontanelle, the "defects" in the nasal bone and the medial wall of the orbit, plus those remnants of Meckels' cartilage.

It appears as if these osteolytic changes (referred to above), occurs at a time when there is either a drastic remodelling of the skull due to accelerated growth, or at a time that the rate of enamel deposition on many newly formed permanent teeth, is demandingly high on the metabolism of the animal. Or, obviously, it might also occur subsequent to both conditions being present simultaneously. At that age, accelerated skull growth would be needed to accommodate the permanent teeth, which appears to be the most logical explanation. Or, less probable, it might not have anything to do with tooth formation at all, but only with drastic skull growth. Least probable is that is has nothing to do with accelerated skull growth, but only with enamel deposition.

(c) The facial surface of the maxilla.

In some old bulls, the facial surface of the maxilla - the lamina externa of the maxilla in the region where the masseter muscle takes origin - gets eroded away to such an extent that the roots of the molar teeth become exposed. This appears to be not associated with any pathological condition of the animal or local pathological changes [41] . These changes in old animals are totally different from those defects discussed above (due to skull reshaping in young animals of about 2 years of age). Exposure of the roots of molar teeth has also been noticed in the domestic horse where it is also not associated with any pathology. (Unpublished personal observations.)

ASPECTS OF THE OSTEOLOGY OF THE SKULL HAVING POTENTIAL CLINICAL APPLICATION IN OTHER FIELDS :

At the first glance, the osteology of the skull appears to be of very basic value. But sutures - as embryological remnants - usually have high potentials for growth. These potentials decrease with age and only stops once ossified. In the savannah buffalo, some sutures ossify early in life and others later in life, or never. Thus, in an applied way, halting one or more of the sutures artificially, can cause early fusion that would precipitate in distorted skull growth. Such a cascade of events would affect not only the shape of the skull but also the wear of teeth, especially if occlusal surface matching is also distorted.

The dentition of the savannah buffalo shows that specific teeth, typically has critical lengths. The eruption of those teeth and the delay in eruption of other teeth, determines the longevity not only of individuals but also groups of animals and even whole herds. The effect that a viral infection may have on the development of the dentition, is less theoretical than halting growth of a suture as discussed above. Epitheliotrophic viruses are known to occur, and if these viruses also have an affinity for the enamel organ, it may even be of greater importance. That might be of special importance for any animal, because the enamel organs in general are products of the gingival epithelium. It was observed during this study that the enamel organs of some cheek teeth - especially the first molars of some young animals - indeed showed signs of defective enamel formation. (Unpublished personal observations.)

In addition to that, is the potential for the remodelling of bone at endosteal and periosteal levels. One only has to consider the dimensions that normal - and even more so abnormal cornual processes and horns - can obtain, to appreciate the potential magnitude that hyper-stimulated osteogenic activity may have on in certain parts of the skull [44 & 153] . In contrast to that would be hornless animals. Although hornlessness has not been described in the savannah buffalo, it has been described in buffalo elsewhere in the world [76] . The effect that either hornlessness, or excessively long horns (genetically or iatrogenically) could have on the monetary value of savannah buffalo bulls, should be seen from the perspectives of big game hunters.

The need for a balanced development between the bones of the face and the cranium, including the mandible, as well as the critical length of some teeth (even though it is part of the digestive system), is obvious from the above, as each aspect is interdependent on the other for the general health status of the animal. With the above in mind, it could be possible to manipulate the population dynamics of a species like the savannah buffalo by interfering with something as basic as a suture or a single tooth - that is, if it can be done selectively.

CONCLUSION:

The osteology of the savannah buffalo is so dissimilar to that of the domestic bovine and to that of the Egyptian / Asian and Water buffalos, that extrapolation of facts should not be done when finer detail is considered. This descriptive study on the cranial and the facial bones should render adequate data for most readers that needs accurate detail on the skull of the savannah buffalo, *Syncerus caffer caffer* (Sparrman, 1779). As Applied Anatomical aspects as well as the Craniometric data were all integrated into this study on the Osteology, it is trusted that this work will also fulfill the needs not only of Veterinarians and Zoologists but also Archaeologists, Osteo-archaeologists, Palaeontologists as well as big game hunters.

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GLOSSARY OF TERMS

IMPORTANT NOTES TO REMEMBER WHEN USING THE GLOSSARY OF TERMS :

Terms in italics	:	Terms in italics are Official Veterinary Anatomy terms that appear in the *Nomina Anatomica Veterinaria* (*N.A.V.*). These terms always start with a capital letter.
Terms with a # sign	:	Terms and abbreviated terms followed by hash signs, indicates terms that are typically used by Osteo-archaeologists. These terms do not appear in the *N.A.V.* and they are therefore not in italics.
Terms with an *	:	An asterisk directly after a term, indicates that the term is not officially taken up in the *N.A.V.* even though it might often be used by Veterinary Anatomists, Palaeontologists or Osteo-archaeologists.
Terms with an § sign	:	This typographic sign indicates the newly proposed measurements to be taken up in Craniometry of the skull of the savannah buffalo. In the Glossary, this sign also precedes the abbreviations of the newly introduced points.
Numbers in brackets	:	Numbers with superscript numbers, refers to a specific term or structure as discussed in the osteological description under section A.

A

aboral(ly)*# **:** Aboral refers to that end of the skull opposite to the mouth or rostral end. Even though it is a term foreign to Veterinary Anatomy, it is a handy term to use.

Aditus orbitae **:** The entrance or opening to the boney orbit (20[4`]) or space that contains the eye.

acoustic* **:** Pertaining to the ear canal or hearing.

acute intra-cranial haemorrhage **:** Severe instant bleeding on the inside of the cranial cavity, between the brain and the meninges, causing direct pressure on the brain.

Akrokranion (A)*# **:** The Akrokranion is the median aboral point on the vertex of the skull which is furthest away from the Prosthion (P). (See figures 3.58, 3.59 & 3.61.) The position of A is allocated to a point on the vertex when the skull of the savannah buffalo is viewed from dorsally at such an angle that the nuchal crest just disappears from sight. (See L`.) The Prosthion (P) is the most rostral point on the apex of the skull. A - P gives the profile length of the skull. (See measurement 1 under the **Craniometric data** section.) The point A is to be distinguished from the Opisthokranion (Op) because A and Op are two different points on the skull of the savannah buffalo. (See Op and figures 3.58, 3.59 & 3.61.) The profile length must also be distinguished from the maximum skull length P - P` which is referred to in this study as the condylar ridge - Prosthion length. (See P\` and measurement 63**§**, figure 3.58.) Technically, the point A is situated somewhere between L# and Br# (vide infra) as can be seen in a caudal view of a skull. (See L & Br in figure 3.57.)

§ A\` **:** The point A\` is allocated to the existing median point of the intersecting line that joins the most rostral points of the nasal parts of the frontal bones. (See measurement 9 under **Craniometric data**, as well as figures 3.59 & 3.61.)

alveolus* **:** The alveolus (or dental alveolus) is that osseus component of the maxilla or mandible that contains, surrounds and attaches the embedded parts of a tooth. It consists of a more dense "lamina dura" towards the periodontal ligament (best seen radiographically), and a variable amount of spongy bone around that. Together, all the alveoli form the dental alveoli of teeth. (See 16 [10] , 21 [25\`\`] & 21 [25\`\`\`]).

Angiologia / angiology* **:** Angiology is the study of the arteries, veins and lymph vessels of the body.

angle* / *Angulus* **:** An angle formed between two lines, axes or planes, as used under the section on the **Craniometric data**. What is not meant with the term angle therefore, are the caudal processes of the mandible and the stylohyoid bone which are also referred to as "angles" under section A. (See 21 [4] & 22 [8] .) The medial and lateral corners (or angles) of the eye, are two further concepts of Osteological "angles" which are also not meant here. Thus, only the following two angles are meant **:**

craniofacial angle* **:** The angle formed between the basal (I) and the facial (II) axes. (See measurement **§**60 and figures 1.4, 3.58 & 3.63.)

gnathic angle* **:** The angle formed between the basal axis (I) and the skull axis (III). (See measurement **§**59 and figures 1.4, 3.58 & 3.63.)

antimeres* **:** Antimeres are bones or structures (or even spaces) to the left- and to the right-hand side of the median plane that are mirror images of each other. This concept remains applicable whether considering unpaired structures that lie on the median plane or whether considering paired structures fused to each other over the median plane, and even when considering paired structures situated some distance away from the median plane. (See *Medianus* and *Planum medianum* for information on the median plane.)

antimeric* **:** See 'antimeres'.

apex **:** See under *Apicalis*.

Apicalis / apically* / apex* **:** Apically refers to the apex or apical part (the most pointed part) of a structure, due to its three-dimensional shape or the form of its surface. The general shape of the skull is for instance pyramidal in form. The paranasal sinuses therefore also tend to be pyramidally shaped and - like the skulls - tend to have apical ends. Often less conspicuous, are the opposing ends of such pyramidal or triangular structures, shapes or surfaces. Opposite to the apical ends therefore, are the bases or basal parts which are usually (but not always) directed caudally and towards the nuchal or occipital surface of the skull. (Vide infra under 'base / *Basalis*'.)

Arcus / arc* / arch* / arcade* **:** Used in the context of the teeth, the dental arc is an arched line that can be drawn when connecting all the teeth of either the upper or the lower rows of teeth. The dental arc in the case of the upper row of teeth - inclusive of the dental pad that covers the incisive bone and which bears no teeth in the live animal - describes the upper or superior dental arc (16 [25]). A line connecting all the mandibular cheek teeth as well as the lower incisors, describes the lower or inferior dental arc (21 [26]). The inferior dental arc also includes the alveolar arch (21 [24]) which is that part of the arcade that contains the incisor teeth. (See figures 3.46 & 3.47.)

Arthrologia / arthrology* **:** Arthrology is the study of the joints of the body.

articulatory facets* **:** Facets form the surfaces for articulation. For example, those of the skull that articulate with the first cervical vertebra (the atlas), are the condylar facets or condyles of the occipital bone (2 [14]).

Asterion*# **:** A term that is used in Human osteology but not in the savannah buffalo. The term is therefore not used in the section on the Craniometric data.

atlanto-occipital joint* **:** The joint between the skull and the first cervical vertebra (the atlas), *Articulatio atlanto-occipitalis*.

Atlas **:** The first cervical vertebra.

Auris / *Auricula* **:** Pertaining to the ear, as does *Oticus* / otic.

auriculo-infraorbital plane* **:** See 'Frankfort plane'.

Axis / axis* / axes* **:** In this context, it is not the second cervical vertebra (the *Axis*) that is meant, but an imaginary line of a spindle that connects two points on a structure in a straight line. It can either be in the median plane of the skull, along the central axis of the orbit or along the centre of a defined plane of a tooth. Axes are the plural of axis. Listed below are examples of axes viz. the basal axis, facial axis, general longitudinal axis of the skull, skull axis, orbital axis and the vestibulo-lingual axis of a tooth **:**

basal axis* **:** A line (I) connecting B and B`. (See 'basal axis' below, and figures 1.4, 3.58 & 3.63.)

facial axis* **:** A line (II) connecting B` and P. (See 'facial axis' below, and figures 1.4, 3.58 & 3.63.)

general longitudinal axis of the skull as a whole* **:** (See 'longitudinal axis' below and figures 1.4, 3.58 & 3.63.)

skull axis* **:** A line (III) connecting P and B. (See also the definition of the longitudinal axis below to differentiate it from the skull axis, and see figures 1.4, 3.58 & 3.63.)

orbital axis* **:** A line along the centre of the conically shaped boney orbit (13 [21]). (See figures 3.7, 3.74 & 3.80.) The axis goes through the centre of the entrance to the orbit (the base) and through the centre of the foramen orbitorotundum (the apex). (Also see 'orbital axis' below.)

vestibulo-lingual axis* / [bucco-]-lingual axis* of a tooth **:** This axis lies centrally on the vestibulo-lingual plane of any tooth. (See 'vestibulo-lingual axis' and figures 3.69 & 3.70.)

B

basal axis***:** The bodies of the bones which constitute the base of the skull (i.e. the occipital, the basisphenoid and presphenoid bones) lie more or less in straight line, forming the basal axis (I). (These bones are described under subheadings 2, 4 & 5.) The basal axis lies between the points B and B` at the caudal and rostral ends of these bones respectively and it forms the true [neuro-]cranial length as measured in measurement §64. (See also *Axis*, 'Basion', and figures 1.4, 3.58 & 3.63.) Note however that in other scientific references, this axis is referred to as the basicranial axis, which is a confusing term and therefore avoided in this study. (See section on **Craniometric data**.)

Basalis / basally* / base* **:** Base or basally is towards or pertaining to the base or basilar part of a structure or of a particular bone. The base also lies opposite to the apex of a pyramidally shaped structure, or opposite the apex of a triangular surface. (Vide supra under '*Apicalis* / apically / apex' for antonym.)

Basion (B)*# **:** B is the median point on the ventral edge of the foramen magnum (2[1]). (See figures 3.57, 3.58, 3.63 & 3.64.)

§ B` **:** The point B` is allocated to the rostral end of the rostrum [prae-]sphenoidale (5[8]) and B - B` forms the basal axis (axis I) and is used as the true [neuro-]cranial length. (See figures 1.4, 3.58, 3.63 and measurement §64 under the **Craniometric data** section.)

§ B`` **:** The point B`` is allocated to the greatest vertical height of the skull in the region of the squamous part of the frontal bone, measured from B. (See also measurement 40 under the **Craniometric data** section as well as figures 3.57 & 3.58.) B - B `` must be differentiated from O - O` which is the least height of the skull, as taken in measurement 41 under the **Craniometric data** section.

bilateral(ly)* **:** Occurring on both sides of the median plane or axis. (See also 'unilateral', 'ipsilateral' and 'contralateral'.)

boney orbit* **:** The boney walls of that part of the skull which contains the eye, the muscles of the eye and related glands and structures. Even though this boney wall is incomplete laterally and ventrally, the orbit (13[21]) is regarded as a cone-shaped osseus structure. (See also *Axis* / orbital axis, and figures 3.7, 3.74 & 3.80.)

brachydont tooth **:** A tooth type that has a short crown and two or more longish roots, similar in shape to the cheek teeth of man.

brainstem* **:** The cerebral hemispheres as well as the cerebellum are connected to the brainstem which is continuous caudally with the cervical spinal cord via the 'pons' and 'medulla oblongata'. (See 'pons' and 'medulla oblongata'.)

Bregma (Br)*# **:** A median point on the frontoparietal suture (9[5`]). (Also see 1[17`]). This suture becomes ossified in savannah buffalo of approximately 2 years of age after which only the internal component might still be discernable with difficulty. (See figures 3.4 - 3.6, 3.8, 3.31, 3.57 & 3.58.)

C

canal* / *Canalis* **:** Canals can either form through the substance of a bone, or between adjacent bones. In the latter case, a canal effectively forms by defects in one or more sutures over a specific distance, resulting in a canal. (Vide infra under 'foramen' for further information on canals like the 'infraorbital canal', 'pterygoid canal', 'vomeral canal' and 'boney canal'.)

Caudalis / caudally* **:** Caudally, in the direction of the tail, i.e. in the direction of - or pertaining to - that side of the skull opposite to the nose or mouth. (Also see 'rostrally' for antonym, and figures 1.1 & 1.2.)

Centralis / centrally* **:** Centrally, lying in the middle or the centre of a circular, oval, coiled or spiral structure.

centrifugalis* **:** Centrifugally, coming out of a coiled or spiral structure, leaving the centre and going peripherally.

centripetalis* **:** Centripetally, going into a coiled or spiral structure, from the periphery towards the centre.

cervical* **:** Pertaining to the neck, also meaning a constricted region. Cervical vertebrae refers to the bones of the neck region.

cerebral part* **:** The larger part of the brain that consists of two cerebral hemi-spheres. It is connected indirectly via the brain stem with the cerebellar part of the brain.

cerebellar part* **:** The smaller part of the brain that consists of the unpaired "small brain". It is connected via the brainstem with the cerebral part of the brain as well as via the 'pons' and 'medulla oblongata' with the spinal cord.

cheek bone* **:** See *Zygomaticus*.

cheek tooth row*# **:** It refers to a specific measurement that can be taken of the total length of the combined premolars and molars as they are situated next to each other. (See also 'molar tooth row' and 'premolar tooth row'.) Somewhere along the phylogenetic line of animals - other than the domestic horse - the first premolar failed to develop and henceforth remained absent from the cheek tooth row. Also in the savannah buffalo, it does not develop during any ontogenetic stage as no remnants of it could be seen macroscopically on sculptured skulls of all ages. (See figures 3.64 - 3.70.) The cheek tooth row of the savannah buffalo is therefore the distance between the mesial border of the second premolar and the distal border of the third molar of the maxillary or mandibular cheek teeth. (See measurements 20 - 22 and 7 - 9 pertaining to the skull and mandible respectively in the section on **Craniometric data**.)

Choana **:** The choana (13 [12]) are actually paired (boney) openings which together form the single caudal nasal opening, the choana. It is best seen in ventral views of skulls. (See figures 3.19, 3.25 & 3.39.) The choana - the caudal nasal opening - must be differentiated from the rostral osseus nasal opening as well as from the fleshy nostrils. In the savannah buffalo, the keel of the vomer divides the choana incompletely. In the living animal, nasal mucosa may enhance the appearance of the degree to which the caudal nasal opening appears to be divided.

concha(e)* **:** The dorsal (11 [21]), ventral (17 [10]), middle (11 [23]) and ethmoidal conchae (11 [16]) are shell-like structures in the nasal cavity referred to as nasal conchae or turbinalia. The delicate skeletal framework of the conchae is covered in the living animal by nasal mucous membrane. The ventral and some of the ethmoidal conchae enclose isolated cavities. The cavity of the dorsal concha communicates with the paranasal sinuses. The various conchae fill most of the left and right nasal cavities. (See also 'nasal cavity' below and figures 3.40 - 3.42.)

contact surface* / *Facies contactus* **:** Contact is made between the mesial and distal surfaces (*Facies mesialis / distalis*) of adjacent teeth (cheek teeth as well as incisors). Subsequently, these surfaces wear against each other towards their distal ends, because teeth of ruminants like the savannah buffalo are not solidly embedded in the dental alveoli. Even though cheek teeth are less 'mobile' than incisors, contact surface wear can be significant between them due to steep converging vestibulo-lingual axes.

contralateral* **:** Contralateral usually refers to an antimeric structure on the other side of the median or axial plane. (See 'ipsilateral' for the antonym, but also see 'bilateral' and 'unilateral'.)

Cornea **:** The transparent superficial layer of the eye. It is covered by the eyelids during blinking.

Coronion (Cr)*# **:** The most dorsal point of the coronoid process of the mandible. (See figures 3.66, 3.68 & 3.70.)

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corticalis* **:** Pertaining to the outermost layer or part, the *Cortex.* (Also see *Medulla.*)

cranial part of skull* **:** That part of the skull - the *Cranium* (1[2]) - that surrounds the brain, to form the [neuro-]cranium. (See ‘cranial cavity’ and figures 3.7 & 3.8.)

cranial cavity* **:** The “cavity” (1[1`]) in the skull which contains the brain. It is actually a misnomer to describe it as a ‘cavity’.

craniofacial angle* **:** The angle formed between the basal (I) and the facial (II) axes. (See figure 3.58 and measurement §60 in the **Craniometric data** section.)

Crura **:** Pleural for *Crus*. A ‘crus’ means a branch or a root of some sort. Also a leg-like part, or one (of two or more) branches.

crus* **:** See ‘Crura’.

D

datum plane* **:** The datum plane is that specific spacial orientation in which the skull must be kept, before consideration to some scientific evaluations can be made. (See figures 1.4 & 3.11.) The datum plane needs to be defined because the longitudinal orientation of the skull - as it is placed on a table - differs from the longitudinal orientation in the living animal at rest. The datum plane is determined by placing the skull (with or without the mandible) on a horizontal surface first. The longitudinal axis of the skull is then determined by drawing a line from the centre of the apex of the skull caudally in such a way that the line lies parallel to the dorsum of the nose. (See ‘longitudinal axis’ and *Planum* for more detail.) The specific spacial orientation that the skull will be in - when the longitudinal axis lies horizontally - is the **datum plane** of the skull. (See figures 3.58, 3.63 & 3.73.)

deciduous* **:** Temporary (teeth). (See figures 3.65 - 3.68.)

dental* / dentition* **:** Pertaining to a tooth or teeth.

dental alveolus* **:** See under ‘alveolus’.

dental pad* **:** Anatomically and functionally, a specialized part of the gingiva of the oral mucosa. The presence of this pad and the absence of “upper” incisors, is typical of ruminants. The dental pad overlies the ventral aspect of the incisive bone and it is the structure against which the lower incisors come into occlusion with when the mouth is closed.

Dentes incisiva / *molares* / *permanentes* / *premolares* or [*praemolares*] / *decidui* **:** The incisors*, molars*, premolars*, permanent teeth* and temporary teeth* respectively, are discussed under these headings in this Glossary. (See figures 3.65 - 3.70 and Table 3.4.)

Dexter **:** Pertaining to a structure on the right of the median plane. Note that the observer is facing the same way as the standing animal with the head and skull in the datum plane. (Also see *Sinister* for left.)

Diploë **:** See 'spongy bone'.

diploïc canals* **:** Blood-vessel-containing canals which run through 'spongy bone'.

Distalis / distally* **:** Distal, distally, or away, that which is further apart from the particular reference point. The opposite of 'Distalis' is 'Proximalis'. (Vide infra under *Proximalis*.) In the case of a tubular or "hollow" organ like the mouth or oral cavity (see 'facial part of skull'), proximally would mean closer to the circumference and away from the lumen (the cavity). In teeth, distally is towards the distal free end of the tooth. The distal end of a structure and the distal surfaces of teeth, are however different concepts in that one refers to the one end of a bipolar structure (further away from the main body or the attached end), the other to very specific surfaces at the free ends of teeth. (See 'distal surface' and 'mesial surface' of teeth, as well as 'contact surface' of teeth.)

distal surface* (of teeth) **:** The distal surface of a tooth is that surface of a tooth - as seen in its normal spacial relationship in the specific dental arch in which it lies - which is directed away from the rostro-medial point of the arc. (Also see 'contact' and 'mesial surfaces'.)

Dorsalis / dorsal* / dorsally* **:** Dorsally must be considered with the head and neck in an extended and forward position, in the datum plane. (See 'datum plane' and 'longitudinal axis'.) Dorsally would then be in a direction away from the ground, parallel to the horizontal level but towards the dorsal aspect or the mid-dorsal "top-line" - *Linea mediana dorsalis* - of the head or skull. The dorsal plane *Planum dorsalis* lies in the horizontal or X plane, perpendicular to the median and transverse planes (in the Y and Z planes) respectively. The opposite to dorsal is ventral. (See 'longitudinal axis' for further detail. Also see figures 1.1 - 1.4, 3.11 & 3.76.)

Dorsum nasi / dorsum of the nose* **:** The dorsal aspect of the face is formed by the guesstimated average level of the dorsal aspect of the nasal bone, the 'Dorsum nasi'. Any other dorsal plane lies parallel to the (average) dorsal aspect of the nasal bone and to the 'dorsum of the nose' and would also be in the horizontal if the skull is held in the datum plane. In most cows and in some bulls, the dorsal aspect of the nasal bone is flat. However, in some particular bulls with so-called "Roman noses", the nasal bones are curved, and therefore the plane cannot be determined as defined, and therefore has to be the guesstimated average. (See figures 1.2, 1.4, 3.11, 3.58 & 3.63.)

dura mater* **:** A tough membrane which it tightly adherent to the inside of the bones that make up the cranial cavity. The *Dura mater encephali* surrounds cerebral and cerebellar parts of the brain. However, caudal to the skull, the dura mater of the spinal cord, the *Dura mater spinalis*, is tightly adherent to the spinal cord and not to the surrounding bone. In the savannah buffalo, the cerebral and cerebellar dura mater tends to ossify partially in the dorso-rostral and caudal parts of the cranial cavities of old animals to form ossified parts of the usually membranous *Falx cerebri*. Ossified parts of the falx cerebri may therefore conceal the shallow median groove (9[9]) on the internal surface of the interfrontal and sagittal sutures. Caudally, in the occipital region, partially ossified meninges (*Dura mater encephali*) that surround the cerebellar area, can also be found (2[30]).

E

Ectorbitale (Ect)*# **:** The most lateral point of the orbital margin, at the lateral angle or corner of the eye. (See figures 3.59, 3.61, 3.62, 3.64, 3.65, 3.67 & 3.69.)

enamel organ* **:** The enamel organ (*Organum enameleum*) is responsible for inter alia, the shape, size and formation of the enamel of a tooth - in a process of "casting" - prior to eruption. Another part of the enamel organ continues to deposit dentine on the inside of the enamel covered crown throughout life. Enamel organs for permanent teeth are abbreviated "**EO**" , and "**oe**" for deciduous teeth respectively in Table 3.4. In illustrations, only the specific anatomical number of that tooth - as per Table 3.4 - are given. (See figures 3.65 - 3.68 and Table 3.4.)

EO & eo **:** See 'enamel organ'.

entoconide*# **:** See 'occlusal surface'.

Entorbitale (Ent)*# **:** The most medial point of the orbital margin at the medial angle or corner of the eye. (See figures 3.59, 3.61 & 3.62.)

ethmoidal conchae* **:** All the endoturbinates and ectoturbinates (11 [18 & 19]) of ethmoid bone origin that form ethmoid turbinalia (11 [16]) in the nasal cavity and in the nasal fundus. (See 'fundus nasi'.)

Epitheliotrophic viruses* **:** Viruses that have an affinity for epithelial tissues.

Euryon (Eu)*# **:** The Euryon (Eu) is defined as the most lateral point of the non-pneumatized [neuro-]cranium and is easy to determine in other domestic species like the horse and even in the camel. However, in the savannah buffalo it is not easy to take this measurement at that point as it is positioned under the cornual process and deep in the temporal fossa. Specially curved calipers are needed to fit into the temporal fossa when taking this measurement from a caudal approach in some individuals. The lateral walls of the [neuro-]cranium - and therefore the original Euryon points (Eu) in the temporal fossa - can either be slightly wider or narrower than the "least parietal width at the aboral borders of the temporal line / fossa" on the nuchal surface. As both measurements are an indication of the maximum [neuro-]cranial width, this measurement is preferably taken on the nuchal surface at a newly allocated point Eu`.

§ Eu` **:** The point Eu` is allocated to the least parietal width aborally in the temporal fossa to indicate the maximum (non-pneumatized) [neuro-]cranial width. It is the same as the "least occipital breadth **;** the distance between the most medial points of the aboral borders of the temporal fossa". (See measurement 30 in the **Craniometric data** section and also see figure 3.57.)

Externus / Internus **:** The terms external* (outer) and internal* (inner) are only used with reference to layered structures (1 [3 / 4]) and to body cavities and are not synonymous with lateralis and medialis. (Also see 'lateralis' and 'medialis'.)

F

Facies **:** See 'facial part of skull', *Facies occlusalis* ('occlusal surface'), *Facies vestibularis* ('vestibular surface'), *Facies lingualis* ('lingual surface') and *Facies contactus* ('contact surface').

facial axis* **:** The facial axis (Axis II) lies in the median plane, connecting a point on the rostral end of the rostrum [prae-]sphenoidale (B`) to a central point on the apex of the skull, the Prosthion or P. (Also see *Axis* and figures 1.4, 3.58 & 3.63.)

facial part of skull* **:** The facial part of the skull is that part - the *Facies* - (13[1`]) which surrounds the nasal as well as the oral cavities. It is convenient to refer to these osseus components of the facial part of the skull as the [viscero-]cranium, as it clearly distinguishes it from the [neuro-]cranium. The facial part of the skull is associated with the intake of food and respiration. The mouth or oral part of this region form part of the system of "hollow" organs of the intestinal tract (visceral organs). The term is derived from *Viscus*, which refers to a single visceral organ. (Also see '[viscero-]cranium'.)

falx cerebri* **:** See under 'dura mater' for the formation of the *Falx cerebri*.

Frankfort plane*# **:** Originally from human anatomy, this plane is determined by two pairs of bilateral points on the skull viz. Ot` (- the tuberous enlargements of the retrotympanic processes), the ventral-most aspects of the infraorbital margins and the respective antimeric counterparts. The plane drawn through these four points, forms an 'auriculo-infraorbital plane', the Frankfort plane. (See figures 3.62, 3.65, 3.67 & 3.69 and also compare it to 'Reid's base' line.)

Frontal midpoint (F)*# **:** The median of the line joining the Ectorbitalia (only in Carnivores).

foramen* **:** A term used to indicate an opening - usually right through the substance of a bone. In the case of the skull, a foramen usually refers to an opening through either the [neuro-] or the [viscero]-cranial walls. Two openings (foramina) can also merge to form a single larger foramen, indicated by a combined term for the newly formed foramen. The combined orbital and round foramen, or *Foramen orbitorotundum* (4[12]) is specifically referred to in the section on the Applied Anatomy. (See figures 3.72 - 3.74, 3.76 & 3.80.) When the distance from the one opening (on the inner or one side of a bone) to the other opening (on the other side) is substantial in length - as is typical in large skulls like that of the savannah buffalo - a canal is formed. The 'infraorbital canal' (16[28]) is a good example. Canals can however also be formed by spaces that remain between adjacent bones. The 'pterygoid canal' and the 'vomeral canal' are two typical examples of that. The 'boney canal' (17[5]) - that drains the maxillary sinus - is another example although it is a slightly more complex example of a canal.

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fundus nasi* **:** The most caudal part of the nasal cavity is the nasal fundus. (See ‘nasal cavity’, ‘ethmoidal conchae’ and footnote 121.)

G

general longitudinal axis* **:** See under ‘longitudinal axis’.

Gingiva / gingival line* **:** The gingiva is the specialized membranous lining of the oral mucosa which surrounds teeth and attaches to the enamel that covers the crowns. The line of attachment of the gingiva, divides the erupted part of the enamel-covered crowns of teeth, into a stained clinical crown, and an unstained part (equal to the thickness of the gingiva itself) just distal to the alveolar margin of the maxilla and mandible. In prepared skulls, the difference between the stained and the unstained parts of the crown remains clearly visible, and it thereby forms a clear line, the **gingival line**. The gingiva is continuous with the specialized mucosal coverings of the tongue and dental pad.

glabella* **:** The glabella (10 [12``]) forms due to a pronounced summit or vertex (1 [12]) of the skull of the savannah buffalo. The glabella is a specific but poorly circumscribed unpaired area on the facial part of the frontal bone, rostral to the forehead or frons (1 [13]). More specifically, it lies between the supraorbital foramina, the most rostral parts of the bases of the cornual processes and the nasal bones. The surface texture of this area is often smoother than the cornual bases. The region that is ascribed to the glabella, lies in a larger concavity, the frontal fossa (1 [14]). The frontal fossa and the glabella can be either more pronounced in some individuals or less pronounced in others, but is always poorly defined in cows. (See figures 3.6, 3.7, 3.32 & 3.59 as well as figures 3.72 & 3.73 under the Applied Anatomy section.)

gnathic angle* **:** The angle formed between the basal axis (I) and the skull axis (III). (See also ‘angle’, ‘skull axis’ and figures 1.4, 3.58 & 3.63.)

Gonion caudale (Goc)*# **:** The most caudal point of the angle on the ramus of the mandible. (See figures 3.66, 3.68 & 3.70.)

Gonion laterale (Gol)*# **:** The most lateral point of the angle on the ramus of the mandible. It is not an applicable point in the case of the savannah buffalo.

Gonion ventrale (Gov)*# **:** The most ventral point of the angle on the ramus of the mandible. (See figures 3.66, 3.68 & 3.70.)

gubernacular canal* **:** Gubernacular canals are small temporary openings that form in the maxilla and the mandible on the lingual side of deciduous upper and lower premolars. They only occur during those times that the permanent premolars are formed by the enamel organs. (See figure 3.49.)

H

Hormion (H)*# **:** The most caudal point of the vomer in the median plane. It is superimposed over the intersphenoidal synchondrosis when seen in ventral view. (See figures 3.38, 3.39, 3.60, 3.63, 3.64 and also see 'Synsphenion' S*# below.)

§ H` **:** The point H` is allocated to the rostral end of the keel of the vomer as seen in ventral view. (See figures 3.38, 3.39, 3.60, 3.63 & 3.64.)

§ H`` **:** The point H`` is allocated to the rostral end of the wings of the vomer as seen in dorsal view. (See figures 3.38, 3.59, 3.60, 3.61 & 3.63.)

hyoid bone* **:** The hyoid bone - or rather the hyoid apparatus - is a system of bones which renders attachment to the muscles of the tongue, effectively suspending the tongue. It is therefore also referred to as the "tongue-bone" even though it is also partially attached to the larynx. When considered on its own, the hyoid bone resembles a swing or a compound pendulum. (See figures 3.50, 3.51 & 3.71.)

Hyoideus **:** Pertaining to the "hyoid apparatus" or the "tongue bone" as described in section A. (Also see 'hyoid bone'.)

hypocone*#, hypoconide*# **:** See 'occlusal surface'.

I

iatrogenic* **:** A condition caused due to faulty interference by man / qualified professionals.

incisive ducts* **:** The incisive duct (*Ductus incisivus*) is a small duct that is surrounded by a cartilage of its own. The incisive duct drains the secretions of the vomero-nasal organ that is situated in the rostral nasal cavity as a structure with a blind end caudally. (See 'vomero-nasal organ'.) The vomero-nasal organs are paired, and therefore the paired incisive ducts connect the organs (in the nasal cavity) with the rostral part of the oral cavity via the palatine fissures. (See 13 [7] and Discussion point 15.) The incisive ducts of the left and right hand sides open in common just behind the dental pad on the palate.

incisors* **:** The "cutting type" of teeth in the rostral part of the mandible ["lower jaw"] in the inferior dental arc. There are four incisors on either side of the median plane. However, no *Dentes incisivi* forms in the incisive bone in the superior dental arc. The lower fourth incisor ($I_{\overline{4}}$) is usually said to have phylogenetically developed from a canine teeth, *Dentes canini*, but it has the same morphology as all the other incisors. The occlusal surface of the (mandibular) incisors wear against the dental pad in the life animal. (See figures 3.66, 3.68 & 3.70.)

index* / indexes* **:** An index is calculated by dividing the width (or dimension) of the particular criterium by the length of the other criterium, and by multiplying the result with a hundred. The following indexes can be calculated for the skull. (See LIST OF INDEXES under section D on **Craniometric data** for detailed descriptions of index calculations.)

Facial index* **:** $^{Æ}/_{E}$ x 100. Æ in this formula is the maximum facial width and E in this formula is the true [viscero-]cranial length.

Cranial index* **:** $^{G}/_{D}$ x 100. Two alternative configurations for the cranial index can be calculated. When excluding the effect of the frontal sinus complex, G in the formula is the true [neuro-]cranium width, whereas D in that formula is the true [neuro-]cranium length. When the effects of the frontal sinus are included in the calculation of the index, then the value of G in the formula is the maximum width of the [neuro-]cranium taken at the tuberous enlargements of the retrotympanic processes, and D in the formula then includes the effect of the frontal sinuses.

Skull index* **:** $^{K}/_{Y}$ x 100. K in this formula is the maximum width of the [neuro-]cranium, measured at the tuberous enlargements of the retrotympanic processes. Y in this formula is the maximum skull length.

Palatal index* **:** $^{J}/_{I}$ x 100. J in this formula is the true inter-alveolar palatal width. I is the total palatal length.

Frontal sinus index* **:** $^{Œ}/_{M}$ x 100. In this formula Œ is the maximum frontal sinus width. M in this formula is the total frontal sinus complex length.

Index of orbital aditus* **:** $^{V}/_{W}$ x 100. V and W in the formula are the greatest near vertical and near horizontal diameters of the orbital margin respectively.

Nasal index* **:** $^{Q}/_{R}$ x 100. Q in this formula is the greatest width of the nasal bones. R in this formula is the greatest length of the nasal bones.

index of orbital aditus* **:** See 'index' / 'indexes'.

Inferior / *Superior* **:** Lower / Upper. In Veterinary Anatomy, these terms are only used in three exceptional cases where paired structures lie above and below one another viz. the eyelids, the parts of the orbital rim and the dental arches. The other directional terms - such as dorsal(ly), ventral(ly), rostral(ly), caudal(ly), apically and basally, and those terms that are related to planes - are used in all other cases.

Infradentale (Id)*# **:** The Infradentale is the most rostral point of the alveolar arch of the mandible. This term is preferred above the synonymous term 'Pogonion'. (See figures 3.66, 3.68 & 3.70 and footnote 162.)

infraorbital canal **:** See under 'foramen'.

Infraorbitale (If)*# **:** The caudo-dorsal edge of the infraorbital foramen. (See 'infraorbital canal' and 'foramen', as well as figures 3.61, 3.62, 3.65, 3.67 & 3.69.)

Inion*# **:** The Inion is a central surface point on the external occipital protuberance (2[25]) of other domestic animals. It is not a standard point of reference in the skulls of ruminants. In the savannah buffalo, the Inion is dwarfed by the nuchal crest and the allocated point L` is used as the preferred point. (See under **§** L` below.)

interlobar colonette* **:** These structures are tube-like evaginations of the external enamel layer of cheek teeth. Interlobar colonettes are found on the lingual surfaces of maxillary molars but on the vestibular surfaces of mandibular molars. It is also seen vestibularly on the lower fourth deciduous premolar. (See figures 3.66, 3.68 & 3.70 where they can be seen, but they are not annotated because the detail of the Dentition of the savannah buffalo falls beyond the scope of this study.)

Intermedius **:** When distinction must be made between three similar structures situated next to each other, then the term 'intermedius' refers to the structure that lies between the other two.

Internus / Externus **:** Vide supra under *Externus*.

ipsilateral* **:** Ipsilateral refers to a (non-antimeric) structure on the same side of the median or axial plane. (Also see 'contralateral', 'bilateral' and 'unilateral'.)

L

Lambda (L)*# **:** A median point on the occipitoparietal suture (2 [23]). The external part of the suture becomes ossified between the ages of 16 to 24 months in the savannah buffalo.

§ L\` **:** The point L\` is allocated to a median point on the nuchal crest because the occipitoparietal suture (2 [23]) ossifies after which the point Lambda (L) cannot be seen anymore. (Also see 'Akrokranion'.) L\` is then used to indicate the most caudal extent of the frontal sinus complex. At that point the thickness of the external lamina of the occipital bone is approximately 3-5 mm. (See figures 3.57, 3.58 & 3.59.) L\` replaces the point Inion which is dwarfed by the nuchal crest of the savannah buffalo. (Also see 'Inion'.)

§ L\`\` **:** The point L\`\` is allocated to the most rostral extent of the nasal sinus which is also the most rostral extent of the frontal sinus complex. The extend of the nasal sinus can only be accurately determined when the skull is cut in the median plane and sculptured on both sides. (See figure 3.58.)

Lamella / e **:** Plate-like structures. (Also see *Lamina / e*).

Lamina / e **:** Plate-like structures are either laminae or lamellae, and in the context of this osteological study are synonymous to each other.

Lamina cribrosa **:** The boney plate (11 [9]) which separates the nasal and cranial cavities from each other. It is perforated by a multitude of foramina and hence the name.

laryngopharynx* [188] **:** That part of the pharynx at the entrance to the larynx and trachea, the *Pars laryngea pharyngis*, of the live animal. It communicates with the oro- and nasopharynx.

Larynx / larynx* **:** The so-called "voice-box".

Lateralis / lateral / laterally* **:** Laterally is towards or pertaining to the (out)side, or away from the median plane.

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188 A much wider description is called for when describing the splanchnological detail of the different parts of the pharynx. However, for the purpose of this osteological discussion, these terms have to suffice.

lingual surface* / *Facies lingualis* **:** That surface of a tooth (or of the mandible) facing towards the tongue. The opposite surface of a tooth or of the mandible - *Facies vestibularis,* or 'vestibular surface' - faces towards the inner side of the cheek.

longitudinal axis* / longitudinal plane* **:** Equivalent to the (general) longitudinal axis and plane of the skull. When the skull (with or without the mandible and hyoid apparatus) is put on a flat and horizontal surface like a table, then the **general longitudinal axis** of the skull must coincide with that **horizontal line** that is drawn from the centre of the apex of the skull to somewhere in the basal region of the skull. This line does not necessarily lie perpendicular to the occipital or nuchal planes. For descriptive purposes of the skull and mandible of the savannah buffalo, it is proposed that this horizontal line - when coinciding with the general longitudinal axis after slight repositioning of the skull - must also be such that it lies parallel to the guesstimated average of the dorsal aspect of the nasal bone (*Dorsum nasi*). When a plane is then drawn through this line, it will form the **general longitudinal plane** and when in that spacial orientation, the skull would be in the **datum plane**. (See *Planum* for more detail on planes.) All other imaginary dorsal planes that can then be drawn through the skull will ipso facto always be parallel to the longitudinal plane. Coincidentally in the buffalo, dorsal planes are also fairly parallel to the ventral surface of the boney palate and the occlusal surface of the maxillary cheek teeth. (In the savannah buffalo, the cornual processes in prepared skulls needs to be cut off short before this can be done.) To have the datum plane in the savannah buffalo established for used in scientific work, also has important implications in the understanding of the Applied Anatomical aspects of the skull. Note that a line drawn from the Basion to the Prosthion - from B to P - would not lie on the longitudinal axis / plane as it describes the skull axis, axis III. The skull axis does not coincide with the longitudinal axis. (See 'gnathic angle' and figures 1.4, 3.58 & 3.63.)

Longitudinalis / longitudinally* **:** Longitudinally refers or pertains to the general length or longitudinal axis of any bipolar or pyramidal structure, and therefore even to the skull as a whole. (See 'general longitudinal axis'.)

M

mandible* **:** The *Mandibula* is that bone which holds the mandibular cheek teeth or the "lower cheek teeth", as well as the "lower incisors". Scientifically, it is incorrect to refer to this bone as the "lower jaw" bone. (See 'inferior dental arch' and 'cheek tooth row', and also see figures 3.43 - 3.47, 3.66, 3.68 & 3.70.)

mandibularis* **:** At, towards, or pertaining to the mandible.

mark **:** See under 'Wormian bone'.

Maxilla **:** The maxilla is that bone of the facial part of the skull which holds the maxillary cheek teeth or "upper cheek teeth". It is incorrect to refer to this bone as the "upper jaw". (See 'arc' for 'superior dental arch', 'cheek tooth row', and also see figures 3.44 - 3.46, 3.64, 3.65, 3.67 & 3.69.)

maxillaris* **:** At, towards, or pertaining to the *Maxilla*.

maximum skull length* **:** In the savannah buffalo, the (maximum) skull length is preferred over the condylobasal length, and is the distance between the Prosthion (P) and the condylar ridge (P`). (See FINAL COMMENT 11 and measurement §63 under the **Craniometric data** section. Also see figure 3.58.)

Medialis / medial / medially* **:** Medially is towards, or pertaining to, the inside or nearer to the 'median plane'. (See figures 1.1 - 1.3.)

Median plane* **:** Vide infra under *Planum medianum* under *Medianus*. (See figures 1.1 - 1.3.)

median* **:** Exactly in the mid-line. In the case of the skull, this line can be best seen if the skull is considered in dorsal or ventral views. (See *Planum medianum* under *Medianus*. Also see figures 1.1 - 1.3.)

Medianus **:** Pertaining to the median plane, *Planum medianum* i.e. the only longitudinal vertical plane that divides the head (or skull) into equal left and right halves or antimeres. (Also see 'antimeres' and figures 1.1 - 1.3.) The median plane lies in the Y plane of spacial orientation.

Medulla oblongata **:** The medulla oblongata is part of the central nervous system inside the cranial cavity. (Also see 'brainstem' and 'pons'.)

medullaris* **:** Pertaining to the innermost layers or core part, the *Medulla*. (Also see *Cortex*.)

meninges* **:** The *Meninges* are made up of three separate membranes that surround the

 GLOSSARY OF TERMS

brain and spinal cord. The outer layer of the meninges around the brain - the dura mater - is intimately attached to the bones of the cranial cavity. That layer of the meninges is separated from the brain by a small fluid-filled space between itself and another layer of the meninges. Caudal to the brain, the membranes of the meninges are intimately attached to the spinal cord itself and not to the surrounding bone of the vertebrae that contains the cord. (See 'dura mater'.)

mesial surface* (of teeth) **:** The mesial surface of a tooth is that surface of a tooth - in its spacial relationship in the specific dental arch in which it lies - that is directed towards the rostro-medial end of the arch. (Also see 'contact' and 'distal surfaces'.)

mesostyle*# **:** See under 'vestibular surface'.

metacone*#, metaconide*# **:** See under 'occlusal surface'.

metastyle*# **:** See under 'vestibular surface'.

molars* **:** The three larger cheek teeth, on either side (left and right) in both the maxilla and the mandible. Molars are denoted by numbers from rostral to caudal.

molar tooth row*# **:** The molar tooth row refers to a measurement. (Also see 'premolar tooth row' and 'cheek tooth row'.) It is the distance between the mesial border of the first molar and the distal border of the third molar (maxillary or mandibular). The molar teeth *Dentes molares*, are numbered from one to three. Maxillary molars are designated $M^{\underline{1}}$, $M^{\underline{2}}$, $M^{\underline{3}}$ and mandibular molars as $M_{\overline{1}}$, $M_{\overline{2}}$ and $M_{\overline{3}}$.

Myologia / Myology* **:** Myology is the study of the musculature of the body.

N

nasal cavity* **:** In the living animal, the outer dimensions of the nasal cavity appears to be large but the inner dimensions reveals that it is not, as it is filled with various conchae. (See 'conchae'.) Effectively, only narrow passages remains for air to pass, connecting the openings at the fleshy nostrils or nose (rostrally) via the subdivided *Choana* (caudally), to the nasopharynx. The nasal cavity is divided by the nasal septum into left and right hand sides.

nasal index* **:** See under 'index / indexes'.

nasal concha(e)* **:** See under 'concha(e)'.

nasalis* **:** Pertaining to the nasal region. As a term of direction, it refers more particularly to the dorsum or bridge of the nose, the *Dorsum nasi*.

Nasion (N)*# **:** A median point on the frontonasal suture (10 [26]). (See figures 3.58, 3.59 & 3.61.)

Nasointermaxillare (Ni)*# **:** The most caudal point of the nasal process of the incisive bone on the nasoincisive suture. This suture does not form in some savannah buffalo and for the purpose of this study, the point is changed to Nasoincisivum with the same abbreviation. (See figures 3.59 & 3.61 as well as footnotes 123 & 163.)

nasopharynx* [189] **:** The most caudal part of the nasal cavity where it joins the caudal part of the cavity of the mouth (oropharynx) and where both of them meet the opening to the larynx (laryngopharynx).

[neuro-]cranium* **:** See under 'cranial part of skull'.

nuchalis* **:** Pertaining to the nuchal region, the back of the skull, or the *Nucha.* (Also see 'occipitalis'.)

O

Occipitalis / Occipital* **:** The occipital region pertains to the caudal part of the skull, the *Occiput.* (See 'nuchalis', or 'nuchal plane' under *Planum*.)

occlusal surface* / *Facies occlusalis* **:** The occlusal surface is that surface of a tooth that wears against the tooth or teeth - or dental pad in the case of the incisors - of the opposing dental arch. (See figures 3.44 - 3.47 and also see 'contact surface'.) The distal end of a recently formed tooth ends in various cusps. As soon as teeth starts to come into wear, attrition wears the cusps of the original distal tooth down, to form the occlusal surface. Each branch of the divided pulp cavity - underlying each original cusp - is gradually filled up with (secondary) dentine which can be identified as such on the (partially worn) occlusal surface. Even though secondary and tertiary dentine can be identified, it has no further significance apart from being dentine that was deposited at ensuant times in life. The different cusps of cheek teeth - and for that matter also the different regions on the occlusal surface - are best described by using a combination of the terms mesial / distal and

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189 See **footnote 188.**

lingual / vestibular. However, in archaeology / palaeontology and rarely in Veterinary Anatomy of French origin, these areas on the occlusal surface can be annotated as follows **:** In the maxillary cheek teeth, the lingual cusps are named as follows **:** the mesial cusp is the protocone# and the distal cusp is the hypocone# **;** the vestibular cusps are the paracone# and the metacone# respectively. In the mandibular cheek teeth, the lingual cusp mesially is the metaconide# and distally it is the entoconide#. On the vestibular side, the cusps are the protoconide# and the hypoconide# respectively. Apart from making reference to these terms here, they are avoided elsewhere in this study where any reference is made to the dentition of the savannah buffalo. (Also see metastyle#, mesostyle# and parastyle# under 'vestibular surface'.)

ontogenetic development* **:** The embryological development prior to birth. (Also see under 'primordia', and see 'phylogenetic development'.)

Opisthion (O)*# **:** A median point on the dorsal edge of the foramen magnum. (See figures 3.57, 3.58 & 3.64.)

§ O` **:** The point O` is allocated to the least height of the skull as measured from O. (See measurement 41 and compare it with B - B`` as taken in measurement 40. Also see figures 3.57 & 3.58.)

Opisthokranion (Op)*# **:** A median point on the line that joins the most caudo-dorsal level of the skull on the cornual bases. In the savannah buffalo, the Opisthokranion is therefore a point in space, and separated for some distance from the point A. (See Akrokranion, FINAL COMMENT 4 under **Craniometric data**, and also see figures 3.58, 3.59 & 3.61.)

Opthalmicus / opthalmic* / ocular* **:** The terms opthalmic and ocular pertains to the eye.

oralis* **:** Oral or oralis pertains to the mouth. The scientific term which is often used in a clinical sense for the mouth (Os, derived from the term *Ostium*), should not be confused with the scientific term for bones (*Os* and *Ossa*). The term oralis is not synonymous with rostralis.

orbital axis* **:** The boney orbit (13 [21]) is cone shaped and the orbital margin is taken as the base of this cone shaped structure. (See figures 3.74 & 3.80.) An axis for the boney orbit can be drawn from the centre of the orbital entrance (or *Aditus orbitae*), to the centre of the foramen orbitorotundum at the apex (*Foramen orbitorotundum* 4 [12]). This orbital axis makes an angle of approximately 45 degrees with the general longitudinal axis of the skull (towards the "front" of the skull or rostro-laterally). It also makes an angle of approximately 30 degrees with the dorsal plane (varying between 25 degrees and 35 degrees). (See figures 1.1, 1.2 & 3.76.) The orbital axis is not exactly the same as the optical axis *(Axis opticus*) or the visual axis, but would be fairly parallel to it. (Also see *Axis*.)

oropharynx* [190] **:** The most caudal part of the mouth where it joins the most caudal part of the nasal cavity (nasopharynx) and the opening to the larynx (laryngopharynx).

Os : Latyn for bone. The pleural is *Ossa*.

Osteologia **:** Osteology* is the study of the bones of the body, including those of the cranium, face, mandible, hyoid apparatus and the middle ear.

Oticus / otic* **:** Otic pertains to the ear as does *Auris / Auricula*.

Otion (Ot)*# **:** As seen in caudal view, the Otion is the most lateral point of the mastoid process in cattle but not in savannah buffalo. (See figure 3.57, FINAL COMMENT 9 under **Craniometric data**, as well as **§** Ot\` and **§** Ot\`\` below.)

§ Ot\` **:** The point Ot\` is allocated to the most lateral point of the retrotympanic process that bears a tuberous enlargement. (See figures 3.57, 3.62, 3.64, 3.65, 3.67 & 3.69.) It forms the most lateral point of the skull in older animals. The distance Ot\` - Ot\` is used to measure the maximum width of the [neuro-]cranium in the calculation of the skull index. It is also used in the calculation of the cranial index where the effect of the frontal sinus needs to be included.

§ Ot\`\` **:** The point Ot\`\` is allocated to the centre of the external acoustic meatus. (See figures 3.57, 3.62, 3.64, 3.65, 3.67 & 3.69.). The point Ot \`\` is used as one of the two reference points in 'Reid's base line' **;** the other reference point for that line is the point Rh. (See Rhinion and also FINAL COMMENT 9 under **Craniometric data**.)

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190 See **footnote 188.**

P

palatal index* **:** See 'index / indexes'.

Palatino-orale (Po)*# **:** A median point on the most rostral level of the palatomaxillary suture (19 5). (See figures 3.58 & 3.64.)

paracone*# **:** See under 'occlusal surface'.

paramedially* **:** See *Plana [paramediana] sagittalia* under *Planum*.

paranasal sinuses* **:** Literally meaning the sinuses "next to" the nasal cavity - *Sinus paranasales*. In the savannah buffalo, bones of the cranium as well as of the face are aerated or pneumatized to form these sinuses.

parastyle*# **:** See under 'vestibular surface'.

permanent teeth* / *Dentes permanentes* **:** The permanent set of teeth develop from individual enamel organs. The enamel organs can be seen in sculptured skulls or on radiographs of animals from after birth till approximately five or six years of age. In the case of the upper and lower premolars and the incisors (only lower incisors), they displace the respective temporary precursors (*Dentes decidui*). The temporary set of teeth - which also developed from enamel organs - consists of deciduous incisors and deciduous premolars (*Dentes incisivi* & *Dentes premolares*). In the case of the molars however, no temporary precursors occur. Even so, the molars themselves are regarded as part of the permanent set of teeth. (See figures 3.65 - 3.70.)

perpendicular lamina* **:** The perpendicular lamina (19 10`) is that part of the palatine bone which lies in a paramedian or sagittal plane, perpendicular to the horizontal part (19 2) of the palatine bone. However, the perpendicular lamina can also refer to that part of the ethmoid bone (11 13), which lies in the median plane, forming part of the boney nasal septum (13 11).

phylogenetic development* **:** Essentially, 'phylogenetic development' refers to the developmental stages that occurred throughout the evolutionary history of animals.

Planum **:** A plane or a flat surface. The plane that connects the dorsal and the ventral median lines of the head - *Linea mediana dorsalis / ventralis* - forms the median plane - *Planum medianum*. (See *Medianus* for more detail.) The median plane lies in the Y-plane of spacial orientation. (See figures 1.1 - 1.3.) Other planes drawn perpendicular to the median plane are either in the X (dorsal) or in Z (transverse) planes. Multiple planes (*Plana*) parallel to the abovementioned primary planes in the X, Y and Z orientations can also be drawn to form *Plana dorsalia, Plana* [*paramediana*] *sagittalia* & *Plana transversalia* respectively. (See figures 1.1 - 1.4 & 3.76). Planes can also be formed against certain bones which have more extended surface areas (*Planum nuchalis* / *parietale* / *temporale*). Other planes that can also be drawn are the longitudinal plane (in the vertical or the horizontal) or a plane through the vestibulo-lingual axes of teeth, to form the longitudinal and vestibulo-lingual planes of the skull and teeth respectively. Note the following **:**

(i) Convenient axes can also be drawn through some of these planes if two central points are defined e.g. the vestibulo-lingual axes of teeth and the longitudinal axis of the skull. (See *Axis*.)

(ii) The dorsum on the nose (vide supra under *Dorsum nasi*) lies parallel to a dorsal plane, and a dorsal plane in the extreme dorsal position would touch the summit of the skull.

Pogonion*# **:** Vide supra under 'Infradentale' - it is synonymous to this term. (See figures 3.66, 3.68 & 3.70 and footnote 162.)

Pons **:** The pons is part of the central nervous system. (Also see 'brainstem' and 'medulla oblongata'.)

Postdentale (Pd)*# **:** A median point on the line which joins the disto-vestibular borders of the third upper maxillary molars (M $\frac{3}{}$). (See figure 3.64.)

prepared skulls* **:** Skulls are studied for various reasons, one of which is to study the osteological detail. Skulls that are intended for scientific study should be cleaned from all material that can decompose. Degradation due to exposure to sunlight and oxygen after cleaning, must also be prevented. Hygienic reasons determine that the preparation of the skulls should be thorough, and scientific reasons determine that it should be done without damage to the skull itself. Both these aspects are best achieved by physical removal of all the flesh as a first step. Thereafter, the skulls are boiled in water for an adequate period of time to aid the final cleaning process. In some cases, and for various reasons, the decapitated heads of animals are first boiled and then cleansed from all flesh. Finally, any remaining fat impregnated into the bone, has to be removed. It is usually done by boiling the bones of the skull in the vapours of fat solvents such as trichloroethylene in specially designed boilers. The latter process can be extremely dangerous to the health of workers and researchers if proper care is not taken. Skulls of especially younger animals may have more cartilaginous parts, and these parts will have disappeared after having had the skull boiled in water for too long. That will leave artefacts that can be difficult to interpret. Therefore, the skulls of young animals should rather be dissected by hand and kept in preservative liquids. The effect of boiling skulls in water, and leaving them to dry, may cause some distortion of bones and even major fractures. Teeth - in all their stages of development or wear - are also affected by the preparation processes. Irreparable damage to the bones of the skull and to the teeth, can therefore still occur despite the best intentions of the preparation techniques.

premolars* **:** The premolars are the three smaller cheek teeth - *Dentes* [*prae-*] *premolares* - on either side of both the maxilla and mandible. (See 'premolar tooth row'.)

Premolare (Pm)*# **:** A median point on the line which joins the mesio-vestibular borders of the first maxillary premolars (P^{2}) at the caudal end of the diastema. (See figure 3.64.)

premolar tooth row*# **:** The premolar tooth row, is a measurement like the 'molar tooth row' and a subdivision of the 'cheek tooth row' of either the maxilla or the mandible. The premolar tooth row is the distance between the mesial border of the second premolar and the distal border of the fourth premolar tooth. Phylogenetically, the first premolars in both arches ceased to develop. In the ontogenetic development of the skull of the savannah buffalo, no stage or remnant (see 'primordia') of it is seen macroscopically. That is unlike for instance in the domestic horse, where deciduous remnants of that tooth sometimes do develop, and is referred to as "Wolf" teeth. Therefore, the numbers of the teeth in this premolar row starts at number two, ending at number four. Maxillary premolars of the permanent set are designated P^{2}, P^{3}, P^{4} and mandibular premolars as P_{2}, P_{3} and P_{4} , the *Dentes* [*prae-*] / *premolares.*

primordia* **:** Usually referring to an embryological state e.g. the state of the enamel organ long before it has attained its maximum outer dimensions, and even before much enamel has been deposited. (See figures 3.65 - 3.68.) Primordia of the skull refers to bones of the skull during early embryonic (ontogenetic) development. (Also see 'remnant'.)

Processus pterygoideus **:** Part of the wing of the basisphenoid bone which forms part of the lateral boney wall of the *Choana*.

profile length* **:** The profile length is taken from the Akrokranion (A) to the Prosthion (P) in measurement 1. (See **Craniometric data** section). The profile length differs from the (maximum) skull length P` - P, as taken in measurement §63. (See 'maximum skull length'.)

Prosthion (P)*# **:** A median point at the apex of the skull that joins the most rostral points of the bodies of the incisive bones. (See figures 3.58, 3.59, 3.61 - 3.65.)

§ P` **:** The point P` is allocated to the medial edge on the ridge on the most caudal border of the occipital condyle. (See 'articulatory facets'.) P` - P forms the condylar ridge - Prosthion length that is the maximum skull length. (See figures 3.57, 3.58 & 3.64.)

protocone*#, protoconide*# **:** See under 'occlusal surface'.

Proximalis / proximally* **:** Proximally means closer to the particular reference point. In the case of a tubular or "hollow" organ like the mouth or oral cavity (see 'facial part of skull'), proximally would mean closer to the circumference and away from the lumen (the cavity). In teeth, proximal is towards the attached part. (See *Distalis* as antonym, but also see 'distal surface' and 'contact surface' for information regarding those specific surfaces of teeth.)

Pterion*# **:** A Craniometric term used in Human osteology, but not in the savannah buffalo.

pterygoid* **:** Literally meaning "wing-like", inter alia referring to the masticatory muscles that take origin from the pterygoid fossa and the pterygoid crest * [191] . Pterygoid also refers to the "wing-like" bone, a small bone of the skull, or to wing-like processes of other bones.

pterygoid canal **:** See under 'foramen'.

pterygopalatine fossa* **:** The *Fossa pterygopalatina* is a concave area of much importance below the orbit, at the junction between the cranial and the facial bones of the skull.

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191 The masticatory muscles of the savannah buffalo differs in at least two aspects from that of the domestic bovine **:** Firstly, it has besides a lateral and a medial pterygoid muscle, also an additional pterygoid muscle. This muscle originates from the region of the pterygoid crest, and inserts both in the pterygoid pit (21^{11}) and on the articular disc ($7^{23`}$). (See **footnote 152**.) Secondly, the implantation of the sternocephalic muscle is mainly on the facial tuber of the maxilla (16^{6}) with only a minor insertion on the angle of the mandibular ramus (21^{4}) and not only on the mandible as would be typical of a sternomandibular muscle (which it apparently represents). (See **footnote 140**.) The tendon of implantation of the sternocephalic muscle is partially embedded into the masseter muscle, proximal to its implantation. The osseus components of the temporomandibular joint of the savannah buffalo also presents some other variations to the norm. (See **footnote 59**.)

R

Reid's base line*# **:** Originally from human anatomy, this line connects the centre of the external acoustic meatus (Ot``) to the Rhinion (Rh). (See figures 3.62, 3.65, 3.67 & 3.69. Also see 'Frankfort plane'.)

remnant **:** Remaining evidence of rudimentary scale, usually of embryological development. (See under 'primordia'.)

retractor bulbi* **:** The retractor bulbi muscle (*Musculus retractor bulbi*) is a muscle of the eyeball that retracts the eye caudally, into the boney orbit (13[21]). The muscle surrounds the optic nerve.

Rhinion (Rh)*# **:** A median point on the most rostral ends of the nasal bones. (See figures 3.58, 3.59, 3.61, 3.62, 3.65, 3.67 & 3.69.)

Roman nose* **:** See 'Dorsum nasi'.

Rostralis / rostrally* **:** Rostrally means towards the apex or apical part of the skull, in the direction of the nose. (See 'apex'.)

rostrum of the presphenoid bone* **:** The rostrum [prae-]sphenoidale (5[8]) (both spelling forms are used in this study) is a rostral extension of the presphenoid bone which projects into the nasal cavity. It forms the floor of the nasal fundus. (See 'fundus nasi'.)

S

Sagittalis / sagittal / sagittally* **:** Sagittal or sagittally pertains to any [paramedian] plane or *Plana sagittalia* that lies parallel to the median plane.

scar **:** See under 'Wormian bone'.

Sclera **:** The sclera is that spherical outer wall of the eye ball, to which the extrinsic muscles of the eye are attached on the outside. The retina attaches to the inside of the sclera.

Septum **:** Osteologically speaking, a 'septum' is a boney division. The septum between the left and right-hand sides of the nasal cavity is unpaired. (See 'perpendicular lamina'.) However, each frontal bone of the skull also has such a septum as a remnant of pneumatization. Therefore, the left and the right halves of the frontal sinus are separated by a paired septum. (See *Septa*.)

Septa **:** Pleural for septum.

Sinister **:** To the left of the median plane. Note that the observer is facing the same way as the standing animal. (Also see *Dexter.*) By convention, illustrations are left views of anatomical structures, looking at the left side of the skull or a particular bone. Or, if it is a median section of the skull, then the right half is viewed from the left and it becomes a medial view of that half.

skull axis* **:** The skull axis (axis III) is formed by connecting the two points P (Prosthion) and B (Basion). The skull axis length is the distance between P and B as taken in measurement 3. (See figures 1.4, 3.58 & 3.63 and **Craniometric data** section.)

skull base* **:** The base of the skull consists out of three rod-shaped bones, the occipital, basisphenoid and presphenoid bones. The bodies of these bones lie along a natural axis that forms the basal axis (axis I) directly ventral to the brain. The rostral extension of the presphenoid bone (the rostrum [prae-]sphenoidale) affects the direction of the basal axis. (See 'rostrum of the presphenoid bone' and figures 1.4, 3.58 & 3.63.)

skull index* **:** See 'index / indexes'.

skull length* **:** See 'maximum skull length'.

Splanchnologia / splanchnology* **:** Splanchnology is the study of the visceral organs of the body. Regarding the skull, the splanchnology includes the paranasal sinuses and the teeth.

spongy bone* **:** In prepared skulls, this type of bone (also referred to as diploë) resembles the micro-architecture of a sponge and hence the term. In the skull, it is always found between two layers of compact bone. Due to the micro-architectural arrangement of the boney plates that form this type of bone, spongy bone encloses many small compartments that can contain either red bone marrow in younger animals or fat in older ones. Or, the spongy bone can become displaced in those bones of the skull which are pneumatized by different parts of the paranasal sinuses. In the case of the tooth bearing parts of the mandible - and to a lesser extent in the maxilla - spongy bone also serves to form the dental alveolus. (See 'alveolus'.)

Staphylion (St)*# **:** The most caudal point on the horizontal lamina of the palatine bone in the median plane. (See figure 3.64.)

Superior / *Inferior* **:** Upper / Lower. (Vide supra under '*Inferior*'.)

Supraorbitale (Sp)*# **:** A median point on the line that connects the centres of the supraorbital foramina. (See figures 3.59 & 3.61.)

Symphysis **:** The fibro-cartilaginous joint (22 [10]) between the stylohyoid part of the 'hyoid bone' and the styloid process of the temporal bone. It does not ossify even in old animals.

Synchondrosis **:** A type of joint between two bones where cartilage form the junction. It is best seen between the unpaired bones at the base of the skull. (See 'skull base'. In later life, total fusion between the adjoining bones usually takes place by complete ossification of the cartilage to form a 'synostosis'. (See figures 3.2, 3.18, 3.21, 3.52 - 3.54.)

Syndesmosis **:** A type of joint between two bones, formed by connective tissue of a firm fibrous type. In the savannah buffalo, the destiny of syndesmotic joints in the hyoid bone and the intermandibular joint (after having reverted from a synchondrosis to a syndesmosis) is interesting, as it can be one of two extremes. In the case of the stylohyoid-epihyoid articulation (see 22[6] in figure 3.51.), the syndesmosis can revert to a synovial joint in old animals. In the case of the intermandibular synchondrosis - that have changed to a syndesmosis - it may rarely undergo partial or complete ossification to form a 'synostosis'.

Synostosis **:** An ossified 'synchondrosis' or an ossified 'syndesmosis'. (See figure 3.54.)

Synsphenion (S)*# **:** The midpoint of the intersphenoidal synchondrosis (or synostosis once it is ossified). In the savannah buffalo, the Synsphenion lies at the same level as the most caudal extend of the vomer - or hormion (H) - which in intact skulls may conceal the Synsphenion in ventral views. (See figures 3.58 & 3.64.)

T

tympanic membrane* / *Membrana tympani* **:** The membranous eardrum separates the external ear canal from the middle-ear.

temporary teeth* / *Dentes decidui* **:** The temporary teeth develop from those enamel organs that are destined to form the deciduous teeth. The temporary teeth are the deciduous upper and lower premolars and the deciduous incisors (lower incisors only). They are replaced by teeth of the permanent set (See 'permanent teeth' and figures 3.65 - 3.68.)

temporal fossa* **:** Osteologically, a deep 'cavity' ventral to the base of the cornual process of the horn which accommodates one of the muscles of mastication (the temporal muscle). The medial wall of this fossa forms part of the lateral wall of the cranial cavity.

total skull length* **:** The term “total length” or “total skull length” is not used in this thesis on the savannah buffalo. (See‘maximum skull length’.)

trabeculum* **:** A trabeculum is a septum of bone that is usually of gross dimension. Or, it is one of the many smaller trabecula of spongy bone. (See ‘trabecula’.)

trabecula* **:** Plural for trabeculum. Trabecula - being many - are usually much smaller septa of bone, the smallest of which will form a spongy type of bone. (See ‘spongy bone’.)

Trachea **:** The so-called “wind pipe”.

Transversalis **:** Pertaining to any transverse plane, *Planum transversalis* i.e. at right angles to the longitudinal axis of the skull, in the Z plane. (See figure 1.3.)

Transversus **:** Lying transversely, across the long axis of a structure, but not necessarily in the transverse plane.

U

unilateral(ly)* **:** Occurring on one side of the median plane or axis. (Also see ‘bilateral’, ‘ipsilateral’ and ‘contralateral’.)

V

vagosympathetic trunk* / *Truncus vagosympathicus* **:** The vagosympathetic trunk is a large paired nerve that is found in the neck. On each side, this nerve trunk actually consists of the vagus nerve, the sympathetic trunk and the recurrent laryngeal nerve. The close association of the combined structure with the common carotid artery of the same side, necessitates that the two structures are separated from each other before catheters can easily be installed into the artery for embalming purposes.

Ventralis / ventrally* **:** Ventrally means at or pertaining to (towards) the mid-ventral “under-line” of the head or skull or body. The *Linea mediana ventralis* lies between the mandibular halves, facing towards the ground. (Also see ‘dorsal’ or *Dorsalis* for antonym.)

vertebrae* **:** The bones which surround the spinal cord **;** those in the region of the neck are the cervical vertebrae.

vestibular surface* / *Facies vestibularis* **:** The surface of a tooth / mandible that faces towards the cheek, faces towards the oral vestibulum on the inside of the cheek, and hence the name. (The opposite surface of a tooth / mandible - *Facies lingualis* - faces the tongue.) The vestibular surface of maxillary cheek teeth is marked by three ridges **;** the mesial ridge is the metastyle#, the distal ridge is the parastyle# and the central ridge is the mesostyle#. Apart from making reference to these terms here, they are avoided elsewhere in this study where any reference is made to the dentition of the savannah buffalo. (Also see 'interlobar colonette'.)

vestibulo-lingual axis* **:** The vestibulo-lingual axis lies centrally on the vestibulo-lingual plane of a tooth, whether it is a cheek tooth or an incisor. (See figures 3.69 & 3.70 and also see *Axis* and *Planum*.) The [bucco-lingual axis] has the same meaning but that term is outdated.

[viscero-]cranium* **:** See 'facial part of skull'. (Also see 'facial index' under 'index'.) The length of the true [viscero-]cranium is measured between the points N and P.

vomeral canal **:** See under 'foramen'.

Vomer **:** A delicate bone in the skull that - even though it belongs to the bones of the cranium - only lies in the facial part of the skull. Together with the perpendicular lamina of the ethmoid bone, it contributes to the formation of the boney nasal septum that separates the nasal cavity into left and right compartments. (See figures 3.1, 3.6, 3.8, 3.60 & 3.63. Also see 'Hormion', 'H`' and 'H``'.)

vomero-nasal organs* **:** The blind-ending vomero-nasal organs are paired tube-like structures that are found on the floor of the nasal cavity on either side of the median plane. They drain via the incisive ducts from the nasal cavity to the oral cavity. (See 'incisive ducts'.)

W

Wormian bone(s)* **:** A Wormian bone is an additional small bone of the skull that forms on a suture. It is synonymous to a sutural bone and it cannot be distinguished from an osseus "scar", but it is doubtful whether is should also be considered the same as an osseus "mark". (See 21[31`] and footnote 28.)

Z

Zygion (Zy)#* **:** The most lateral point on the zygomatic arch. In young animals Zy - Zy forms the most lateral points of the face. In older animals the Ectorbitale (Ect - Ect) are the widest point of the [viscero-]cranium. (See Ot` for widest points on the [neuro-]cranium.)

Zygomaticus **:** Pertaining to the skull's zygomatic arch or cheek bone.